THE CONTRIBUTION OF POSTURAL ADJUSTMENTS TO BODY BALANCE AND MOTOR PERFORMANCE

EDITED BY: Eric Yiou, Alain Hamaoui and Gilles Allali
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THE CONTRIBUTION OF POSTURAL ADJUSTMENTS TO BODY BALANCE AND MOTOR PERFORMANCE

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The control of balance by the central nervous system is crucial to maintain our posture and perform efficiently our daily motor tasks. This control requires the development of dynamical phenomena sub-served by highly-coordinated patterns of muscle activation/deactivation disseminated throughout the whole-body and called "postural adjustments". Establishing the interaction between balance control, locomotion and cognition has important clinical implication, especially in term of falls prevention, and will improve our knowledge on the underlying neural correlates.

This Research Topic provides an up-to-date picture of the relationship between postural adjustments, body balance and motor performance in healthy (young and older adults) and pathological participants. It includes 36 contributions (1 editorial, 28 original articles, 4 reviews and 3 methods articles) which are separated into four sections: 1. Postural maintenance and multisensory integration,

2. Anticipatory postural adjustments associated with voluntary movement, 3. Postural adjustments associated with predictable and unpredictable external perturbation, 4. Gait assessment and rehabilitation in aging.

Beside their basic interest of unveiling the mechanisms behind motor control, results from the investigations of this topic are relevant to develop new methods or tools to improve postural stability and motor performance, with applications in the fields of neurodegenerative conditions, rehabilitation, ergonomics and sports sciences.

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EDITORIAL
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Editorial: The Contribution of Postural Adjustments to Body Balance and Motor Performance

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Editorial on the Research Topic

The Contribution of Postural Adjustments to Body Balance and Motor Performance

INTRODUCTION

The control of balance is crucial to maintain our posture and perform efficiently our daily motor tasks. Humans, as all terrestrial species, indeed evolve in a gravity field that permanently tends to induce postural destabilization by its attracting effect toward the center of the earth. Other external forces, arising from the environment such as those elicited by the acceleration of a train in which one stands, may also challenge body balance. In addition, many studies from the last decades and to date pointed out the disturbing effect of internal forces induced by voluntary segmental movements, even the tiniest ones such as single index movements. To keep the body (or part of it) steady, these disturbing forces must be compensated, at least partly. It is known that this compensation involves dynamical phenomena sub-served by highly-coordinated patterns of muscle activation/deactivation disseminated throughout the whole-body and called "postural adjustments."

This research topic provides an up-to-date picture of the relationship between postural adjustments, body balance and motor performance in healthy (young and older adults) and pathological participants. It includes 35 contributions (28 original articles, 4 reviews, and 3 methods articles) which are separated into four sections: (1). Postural maintenance and multisensory integration, (2). Anticipatory postural adjustments associated with voluntary movement, (3). Postural adjustments associated with predictable and unpredictable external perturbation, (4). Gait assessment and rehabilitation in aging.

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CONTRIBUTIONS

Postural Maintenance and Multisensory Integration

This first section includes original articles investigating (i) the multisensory control of postural maintenance and movement, and (ii) how postural constraints influence sensory transmission, brain function and behavior. This section also reports articles focusing on new methods for measuring postural control.

The role of somato-sensorial information on postural maintenance and movement was investigated in the three following articles. In Teasdale et al. participants were exposed to vibrations of the Achilles tendons (sensing a backward body displacement) or *tibialis anterior* muscle tendons (sensing a backward body displacement), and pointed to a target (without vision). Main result

showed that the target was undershot in both conditions. To explain these findings, authors proposed that ankles proprioceptive inputs are integrated into the upper limb planning, and that motor planning would then be adjusted on the basis of the expected consequences of movement on postural stability. Dupuy et al. investigated the perception of verticality and postural stability in patients with Ehlers-Danlos Syndrome, hypemobility type (EDS-HT). EDS-HT is a condition characterized by generalized joint hypermobility, variable skin hyperextensibility, and impaired proprioception. Authors showed that EDS-HT was associated with changes in the relative contributions of somatosensory and vestibular inputs to verticality perception. Moreover, postural impairment observed in these patients was offset, at least partially, by wearing somatosensory orthoses (i.e., compressive garments and insoles). Maitre and Paillard investigated the effects of age and physical activity status on balance control adaptation to different supporting surfaces, thus modifying sensory inputs from the feet. Elderly were more disturbed than young adults when standing on a foam surface, probably because of the structural and functional involutions of plantar cutaneous sole and foot with aging. In contrast, no difference between active and sedentary groups was found, probably because the postural task was not difficult enough to discriminate these two groups. Now, it is possible that alternative data analysis methods may be necessary to reveal between-group differences during standing. This point is stressed in the three following articles.

Hansen et al. compared various entropy measures to assess the dynamics and complexity of center-of-pressure (COP) displacements during standing. These entropy measures describing COP regularity at different scales were compared to traditional measures of COP variability. Results showed that entropy measures analysis techniques are more sensitive in the incremented time-series compared to classical parameters and entropy measures of original time-series. Such surplus value of the non-linear dynamical analysis of COP trajectories to gain insight into the mechanisms involved in the control of bipedal posture was further stressed by Isableu et al. Earlier findings based on COP classical variables showed that gymnasts exhibited a better control of balance but only in demanding stances. These authors showed that the effect of expertise in Gymnastic could be uncovered in non-demanding postural stance, from the analysis of non-linear dynamic patterns of COP trajectories. In addition, dos Anjos et al. tested whether the distribution of ankle muscle activity differs between aged and young subjects during standing. Surface EMGs were sampled at multiple skin locations from *tibialis anterior*, *soleus* and medial, and lateral *gastrocnemius* muscles in young adults and elderly. Their results showed that the duration and size of active muscle volume, as quantified from spatial distribution of surface EMGs, discriminate well aged from young individuals. Their results further suggest that different conclusions on active control of standing posture may be drawn depending on skin location from where EMGs are collected.

The influence of vision on postural stability was investigated in the two following studies. Chatard et al. investigated the impact of unilateral vs. bilateral age-related macular degeneration (AMD) on postural sway, and the influence of different visual conditions. Main result showed that bilateral and unilateral AMD subjects had lower stability than healthy elderly, a finding that led authors to suggest that ADM subjects may have poor postural adaptive mechanisms. Olivier et al. evaluated the relative contribution of visual information to horseback riders' postural stability and the coordination modes to regulate balance according to expertise. Results showed that professional riders exhibited greater overall postural stability than Club riders. In particular, head variability was lower in Professional in visually altered conditions, suggesting a greater ability to use vestibular and somesthetic information according to task constraints with expertise. Professional exhibited specific coordination modes that, unlike the Club riders, departed from pure in-phase and anti-phase patterns and depended on visual conditions. These findings provide evidence of major differences in the sensorimotor processes contributing to postural control with expertise in horseback riding.

Thus, as shown in the above-reported articles, sensory signals from visual, vestibular, and mechano-receptors are crucial to control posture and balance. In turn, postural constraints are crucial for gating sensory information to the brain, as shown in the two following articles. Mouchnino et al. investigated the effect of plantar sole unweighting on the sensory transmission to the cortical areas during standing. Cortical somatosensory evoked potentials were recorded following cutaneous plantar sole stimulation in different conditions of unweighting (100% bodyweight BW to 40% BW). Contrary to what was expected, authors found an attenuation of sensory information when the BW was unweighted to 41%. Authors argued that this attenuation was not solely due to the absence of forces acting on the sole of the feet but rather to the current relevance of the afferent signals related to balance constraints. The effect of posture on brain activity was also addressed in the review of Thibault and Raz. These authors challenged the tacit assumption that brain processes and cognitive performance are comparable across a spectrum of posture. An integrative synthesis regarding the increasingly prominent influence of imaging postures on autonomic function, mental capacity, sensory thresholds, and neural activity, is provided in the review. Arguing that neuroimagers and cognitive scientists could benefit from considering the influence posture wields on both general functioning and brain activity, authors examined existing imaging technologies and the potential of portable and versatile imaging devices. Finally, authors discussed ways that accounting for posture may help unveil the complex brain processes of everyday cognition.

APAs Associated With Voluntary Movement

This second section reports original articles and reviews focusing on the postural phenomena occurring before movement onset (the so-called "anticipatory postural adjustments," APAs). These phenomena are known to be crucial for stability maintenance and motor performance. A better knowledge of their characteristics is therefore of uttermost importance to the researchers and the clinicians. The articles of this section include various

experimental models for the investigation of APAs (from whole-body movements to distal movements, discrete, or cyclical), as well as a large panel of populations (healthy or pathological). This section thus offers the reader a broadened view on the different facets of APAs.

Gait initiation (GI) is an experimental model that is classically used to investigate postural control during a whole-body movement. It has received a large consideration in this topic. GI is a functional task, which corresponds to the transient phase between static posture and steady-state locomotion. It includes COP shift toward the swing foot (frontal plane shift) and the heels (sagittal plane shift), which allows establishing stable body progression and desired step length/velocity. Honeine et al. investigated the neuro-mechanical process that underlies APAs in the frontal plane. These authors demonstrated that the coordinated activation of hip abductors and ankle dorsiflexors was responsible for the anticipatory COP shift toward the swing leg, and for setting the contact position for the swing foot. These findings corroborate with Bancroft and Day, which proposed a "throw-and-catch" hypothesis of human gait where APAs are organized to generate momentum for the body to fall ballistically along a specific trajectory during the step. The hypothesis predicted a strong coupling between APAs and step location. It was validated by the results of their experiments where participants had to step as accurately as possible onto targets that required either different step directions or different step lengths, and that could jump to a new location during APAs.

In addition to step location, APAs are also sensitive to the potential instability elicited by an environmental constraint in the form of an obstacle to clear. This is a main result of Yiou et al.'s study which proposed a mechanical model of the body to highlight the role of mediolateral APAs in stability control during GI over obstacles of different height and distance. Results showed that postural stability at the time of foot-contact was the same in all conditions of obstacle height and distance, which was made possible thanks to adapted modulation of mediolateral APAs. This finding led authors to suggest that the CNS is able to predict the potential instability elicited by obstacle features and that it scales APAs parameters accordingly. This idea that the CNS is able to modulate APAs so as to maintain an equivalent stability was further reinforced in Caderby et al. which focused on the effects of changing initial body weight distribution between legs (with external loads) on mediolateral stability during GI.

Besides such external constraints, APAs and related-postural stability and motor performance also depend on postural chain mobility. This is the main result of the four following studies, which experimentally manipulated the mobility of various articulations of the postural chain.

Delafontaine et al. reported that APAs associated with GI decreased when the stance ankle mobility was reduced with an ankle foot orthosis (AFO). As a consequence, the vertical braking of the COM during swing phase (an indicator of postural control) and motor performance were both affected. In contrast, the mediolateral stability was increased thanks to a larger step. Authors proposed that rehabilitation perspective could be to prescribe passively- or actively-powered assistive AFO. The results obtained by Hamaoui and Alamini-Rodrigues corroborate with these findings. These authors investigated the influence of cervical spine mobility (CSM), which was modulated by means of splints, on the focal and postural components of the sit-to-stand transition. These authors showed that restricted CSM leaded to a lower motor performance and a reorganization of the APAs. Authors proposed that preserving the articular free play of the cervical spine might be useful to favor sit-to-stand performance and autonomy. In a complementary study, the same authors (Hamaoui and Alamni-Rodrigues) focused on the influence of a restricted mobility of the trunk on the sit-to-stand organization. This time, restricted mobility was induced by means of varying the muscular tension along the trunk. Results showed that beyond a given level, higher trunk muscular tension resulted in longer APAs. In contrast, motor performance remained unchanged. Restricted trunk mobility thus requires an adaptation of APAs programming to keep the same level of performance. These findings may have implications in treatment strategies aimed at preserving functional autonomy in pathologies including a rise of muscular tension.

Ditcharles et al. also investigated the relationship between postural chain mobility and postural control in a dynamical task but, this time, mobility was experimentally sought to be increased by a manual thoracic spine manipulation (High Velocity Low Amplitude, HVLA). These authors showed that, despite the HVLA-manipulation was efficient to improve spine mobility, APAs and speed performance associated with GI were reduced. A neural effect induced by the manipulation, possibly mediated by a transient alteration in the early sensory-motor integration, might have masked the potential mechanical benefits associated with increased spine mobility.

Balance control is known to be impaired in elderly (and particularly in fallers) and patients with Parkinson's disease (PD). The results of the following studies contribute to a better understanding of GI impairments in these populations. New approaches were also proposed to improve dynamic balance in elderly.

As stressed by Cohen et al. freezing of gait in PD has been linked with deficits in inhibitory control, but causal mechanisms are not established. Freezing at GI (start hesitation) is often accompanied by multiple APAs. Cohen et al. investigated how inhibition deficits could contribute to freezing in PD patients. Their findings revealed that start hesitation is not caused by multiple APAs *per se*, but may be associated with difficulty recovering from multiple APAs, due to difficulty releasing a previously inhibited step. Tisserand et al. highlighted changes in the capacity of elderly fallers vs. non-faller to step quickly under a choice stepping reaction-time test (CSRT). Authors found that fallers used a more cautious APAs strategy than non-fallers, which resulted in longer step duration and larger margin of stability at foot-off. Such a choice in balance strategy probably comes from muscular limitations and/or a higher fear of falling and paradoxically indicates an increased risk of fall.

Kaminski et al. also stressed the need to evaluate older adults' ability to maintain balance and examining new approaches to counteract age-related decline in balance control for fall prevention and healthy aging. These authors investigated the

influence of transcranial direct current stimulation applied over the leg area of the primary motor cortex (M1) on dynamic balance task (DBT) learning of healthy elderly. Results indicated that this method did not elicit DBT learning enhancement. However, a regression analysis revealed that DBT performance can be predicted by the kinematic profile of the movement, a finding that may provide new insights for individualized approaches of treating balance and gait disorders. Finally, Lelard et al. showed that leg electromyographic and COP path pattern during GI could discriminate yoga practitioners among physically active older subjects.

The above papers investigated the characteristics of APAs associated with complex movements that induced substantial perturbation of whole-body balance. Such APAs involve the coordination of muscles that may be disseminated through the whole-body, and were thus called *inter-limb* APAs. In their review, Cavallari et al. questioned the role of APAs associated with movements involving tiny mass limbs that do not endanger whole-body balance (e.g., index finger extension etc.). Such APAs involve muscles acting on the proximal joints and correspond to *intra-limb* APAs. These authors proposed that these APAs would be involved in refining movement precision by granting a proper fixation of body segments proximal to the moving one. In line with this idea, Bruttini et al. proposed that the higher precision in pointing with the preferred vs. non-preferred hand would be due to an earlier intra-limb APA in the preferred arm. Cavallari et al. further argued that inter- and intra-limb APAs are manifestations of the same phenomenon, and that APAs and prime mover activation are driven by a shared motor command.

Finally, it is noteworthy that, in all the above-reported articles, APAs features associated with *discrete* movements were performed. However, in daily life, *rhythmical* voluntary movements involving distant limbs may also be performed. Voluntary movement may also be combined with postural tasks requiring more or less attentional resources. The two following articles focused on how the brain organizes movement production under the neural/attentional constraints inherent to such combined tasks. For example, rhythmical isodirectional flexion-extensions of ipsilateral hand and foot are known to be easily performed, while antidirectional movements require attentive effort and irresistibly tend to reverse into isodirectional when frequency increases. In their review, Baldissera and Tesio reported results of experiments indicating that this direction-dependent easy-difficult dichotomy is caused by interference of APAs commands associated to movements of one limb with voluntary commands to the other limb. Huang et al. investigated how brain networks are organized to optimize a suprapostural motor task when the postural load increases and shifts postural control into a less automatic process. A force-matching task was made from a level surface (a relative automatic postural task) and from a stabilometer board while maintaining balance at a target angle (a relatively controlled postural task). Increasing stance difficulty altered the neurocognitive processes in executing postural-suprapostural task. Suprapostural performance was not degraded by increase in postural load, due to (1) increased effectiveness of information transfer, (2) an anterior shift of processing resources toward frontal executive function, and (3) cortical dissociation of control hubs in the parietal-occipital cortex for neural economy.

Postural Adjustments Associated With Predictable and Unpredictable External Perturbation

This third section reports original articles and a review that focus on the adaptability of the postural response associated with an external perturbation applied under various sensorimotor contexts.

Abboud et al. proposed a systematic review to assess the quality of evidence of studies investigating trunk neuromuscular responses to unexpected trunk perturbation applied under condition of muscle fatigue, spinal tissue creep or in the presence of low back pain. Authors stressed that if the literature provides some evidence with regard to trunk adaptions in a context of spinal instability, most of the evidence was inconclusive due to high methodological between-studies heterogeneity. The same research team (Abboud et al.) further investigated, in an original article, the influence of lumbar muscle fatigue on trunk adaptations to repeated sudden external perturbations. By using high-density electromyography technique, these authors showed that muscle fatigue leads to reduced spatial distribution of back muscle activity and suggest a limited ability to use across-trial redundancy to adapt EMG reflex peak and optimize spinal stabilization using retroactive control.

In Camernik et al. immediate and transitionary effects of supportive hand contacts during continuous perturbations of stance were elicited by automated waist-pulls. Kinematical analysis showed that the utilization of the supportive hand contacts facilitates balance control, and that postural readjustments after the release of the handle occurred at different time scales in the hip, knee, and ankle joints. These findings corroborate with the study of Sozzi et al. where continuous perturbations were elicited by sinusoidal platform displacement cycles administrated to eyes-closed and eyes-opened participants. Authors showed that ankle muscles activity decreased over time, and that the level of attenuation depended on the muscle (*soleus* or *tibialis anterior*) and on the nature of the response (reflex or anticipatory). Vision more than doubled speed and amount of EMG adaptation, rapidly enhanced body segment coordination, and crucially reduced head displacement.

Globally, these findings bring new and important insights on the mode of amplitude- and time-modulation of motor output during adaptation in a balancing task, advocate for new protocols for assessing flexibility of balance strategies, and provide references for addressing balance problems in patients with movement disorders.

Gait Assessment and Rehabilitation in Aging

Gait disorders are a major source of disability in aging affecting more than 30% of non-demented older adults. Neurological (i.e., Parkinson's disease) and non-neurological causes contribute to

gait disorders in aging (Verghese et al., 2006). Osteoarthritis is a major cause of non-neurological gait disorders (Snijders et al., 2007). Barden et al. compared gait parameters between older adults with and without bilateral knees osteoarthritis. They demonstrated a loss of gait regularity in older adults with bilateral knees osteoarthritis in comparison to healthy older adults. This study represents a good example on how gait measurement has improved our understanding of the mechanisms of gait disorders in aging. However, there is a need for guidelines on gait measurement in aging and for studies assessing the reliability of gait parameters. In this research topic, an international panel of experts proposes a consensus guideline for gait evaluation and spatiotemporal gait analysis, as well as reference values for healthy older adults (Beauchet et al.). In a methodological study, Szturm et al. assessed the reliability of spatiotemporal gait parameters recorded on a treadmill, while using an original dual task paradigm (i.e., walking while performing a cognitive task) relying on visuomotor and visuospatial tasks.

Various rehabilitative pharmacological and non-pharmacological interventions have been developed in older adults with and without cognitive impairment to tackle gait disorders and falls (Allali and Verghese, 2017). This research topic includes a promising non-pharmacological rehabilitative method based on the use of visual kinematic perturbations (Luu et al.). The study findings suggest an interesting adaptation learning that needs further investigations in disease population.

CONCLUSION

Beside their basic interest of unveiling the mechanisms behind motor control, results from the investigations of this topic are relevant to develop new methods or tools to improve postural stability and motor performance, with applications in the fields of neurodegenerative conditions, rehabilitation, ergonomics, and sports sciences. Establishing the interaction between postural control, locomotion, and cognition has important clinical implication, especially in term of falls prevention, and will improve our knowledge on the underlying neural correlates.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Sensory Integration during Vibration of Postural Muscle Tendons When Pointing to a Memorized Target

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Vibrating ankle muscles in freely standing persons elicits a spatially oriented postural response. For instance, vibrating the Achilles tendons induces a backward displacement of the body while vibrating the tibialis anterior muscle tendons induces a forward displacement. These displacements have been called vibration induced falling (VIF) responses and they presumably are automatic. Because of the long delay between the onset of the vibration and the onset of the VIF (about 700 ms), and the widespread cortical activation following vibration, there is a possibility that the sensory signals available before the VIF can be used by the central nervous system to plan a hand pointing action. This study examined this suggestion. Ten healthy young participants stood on a force platform and initially were trained to point with and without vision to a target located in front of them. Then, they were exposed to conditions with vibration of the Achilles tendons or tibialis anterior muscle tendons and pointed at the target without vision. The vibration stopped between each trial. Trials with vision (without vibration) were given every five trials to maintain an accurate perception of the target's spatial location. Ankle vibrations did not have an effect on the position of the center of foot pressure (COP) before the onset of the pointing actions. Furthermore, reaction and movement times of the pointing actions were unaffected by the vibration. The hypotheses were that if proprioceptive information evoked by ankle vibrations alters the planning of a pointing action, the amplitude of the movement should scale according to the muscle tendons that are vibrated. For Achilles tendon vibration, participants undershot the target indicating the planning of the pointing action was influenced by the vibration-evoked proprioceptive information (forward displacement of the body). When the tibialis anterior were vibrated (backward displacement of the body), however, shorter movements were also observed. Longer movements would have increased the backward response of the sensed body movement. Thus, it is possible that pointing actions were adjusted on the basis of the expected consequences of the planned pointing action to avoid a response that could have compromised postural stability.

Keywords: sensory integration, posture, vibration, vibration induced falling response, hand pointing

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INTRODUCTION

Since the pioneering work of Goodwin et al. (1972), we know that vibrations to the tendon of a muscle produce sensations of limb movements. The vibration activates mainly the muscle spindle primary endings and gives rise to an instantaneous afferent pattern (Goodwin et al., 1972; Burke et al., 1976; Roll and Vedel, 1982). The primary endings respond to low amplitude vibrations in a one-to-one manner for vibration frequencies as low as 3 Hz up to 80 Hz. Cutaneous receptors also can contribute to the sensation (Collins and Prochazka, 1996; Aimonetti et al., 2007, 2012).

When a person stands freely with the eyes closed, vibrating the Achilles tendons generate sensory signals similar to those that would be observed if the body would be moving forward (Eklund, 1972; Gurfinkel et al., 1988; Roll et al., 1989a,b). The postural response following the onset of the vibration is in the opposite direction, towards the back as if it was generated to compensate the stretching signals of the calf muscles generated by the vibration of the Achilles tendons. A similar, but reversed response occurs when vibrating the tibialis anterior muscle tendons; the sensory signal indicates the body is moving backward and a forward postural response is observed. These postural responses have been described as "vibration induced falling" responses (VIF; Eklund, 1972, 1973). It is believed that VIF responses are involuntary and represent an automatic reaction originating from supraspinal centers (e.g., Eklund, 1972; Gurfinkel et al., 1988; Roll et al., 1989b). Several recent cerebral imaging studies have shown that a widespread cortical activity is observed when a muscle tendon is vibrated (for a review, Naito et al., 2016). The areas activated include the primary motor cortex, dorsal premotor cortex, supplementary motor area. Activation also occurs in somatosensory areas. The time course of VIF responses is quite slow. For instance, Quoniam et al. (1995) reported that the VIF response starts about 700 ms after the onset of the vibration on the tendon of the tibialis anterior. There are also reports of an initial faster (within 200 ms after vibration onset) but small center of foot pressure (COP) response in the direction opposite to that of the following (and related) main evoked postural displacement (Caudron et al., 2008). It has been suggested this initial response is automatic because it was observed when subjects self-triggered the vibration stimuli or when they could expect the onset of the stimuli through specific timing cues.

Because of the observed delay and the widespread cortical activation, there is a possibility that before the VIF response (which presumably is also automatic), an internal representation of the body (body scheme) is updated to indicate a change in the postural orientation. To examine this possibility, we asked subjects to point at a memorized target (hence without vision) from a standing posture. Specifically, if signals arising from vibrating the tendons reach higher level structures during the planning phase of the pointing movement, the motor commands for the upper arm should scale according to the muscles being vibrated when the movement is produced before the onset of the VIF. Hence, vibrating the Achilles tendons, because it gives rise to afferent signals indicating a forward displacement of the body, should lead to shorter movements than those without vibration. Alternately, vibrating the tibialis anterior tendons, because it gives rise to afferent signals indicating a backward displacement of the body, should lead to longer movements than those without vibration. Such results would provide strong support to the hypothesis that the sensory signals arising from the vibration induce an update of the internal representation of the body. This representation of the spatial position of the body could be available for the planning of motor commands of upper arm goal-directed movements.

MATERIALS AND METHODS

Participants

Prior to commencing, participants were briefed about the experiment and provided a written informed consent. All forms and procedures were approved by the Human Research Ethics Committee of Université Laval. A total of 10 right-handed volunteers (6 males, 4 females; mean age: 24.3 $\pm$ 4.1 years old; mean body mass: 70.3 $\pm$ 11.9 kg; mean height 1.70 $\pm$ 0.10 m) with no known history of neurological or motor disorders participated in this investigation. After an initial analysis, data for one male participant were discarded because of systematic large overshooting of the target, even with vision of the target location.

Task and Procedures

Participants stood barefoot on a force platform with their feet externally rotated by 10° and their heels 10 cm apart. Landmarks on the platform allowed maintaining a relatively constant position for all trials. In the start position, the participant's right index finger touched the xiphoid process of the sternum with the elbow flexed and the arm at, approximately, 60° abduction. The contralateral arm was along the body. A target was located in front of the participant at about 80% of each participant's arm length just below the height of the xiphoid process. For all trials, the task was to move rapidly the arm across the transverse plane and to stop with the right index finger just over the target with as much accuracy as possible. Participants were told to hold their index over the target for approximately 1 s before returning to the start position.

For each trial, a ready signal indicated the subjects to adopt the starting posture. The approximate initial anterior-posterior position and stability of the COP was verified visually on an oscilloscope (Hewlett-Packard 54601A) through monitoring the platform force moment around the mediolateral axis. For trials with vibration of the ankle muscle tendons, vibrators on both gastrocnemii or tibialis anterior muscles tendons were activated once the participant adopted a stable starting posture and the vibration lasted until the end of the trial. An auditory stimulus (4 kHz, 250 ms) presented 400 ms after the onset of the vibration was the imperative signal to point at the target. Assuming a mean reaction time of 300 ms, we postulated that most pointing actions would be planned before or around the onset of the VIF response. This is so because Quoniam et al. (1995) reported that the VIF response starts approximately 700 ms after the onset of vibration.

Each participant performed a total of 45 pointing movements with an interval of approximately 30 s between trials. All participants first pointed to the target without any vibration with full vision (Vision, five trials), and without vision (No Vision, five trials). Then, before each subsequent block of five trials, two trials with vision and without vibration were given to recalibrate the participants (i.e., to maintain an accurate perception of the target location). After another block without vision and without vibration, two blocks of five trials with vibration of the Achilles tendons and two blocks of five trials with vibration of the tibialis anterior muscle tendons followed. Trials with ankle vibration were performed without vision. Hereafter, the four experimental conditions are named Vision, No-vision, Vibration Achilles and Vibration TA.

Instrumentation

Two custom-made vibrators served to stimulate the muscle proprioceptors. Each vibrator is made of a small DC motor inserted into a plastic cylinder (10 cm long, 3 cm in diameter). They generate a mechanical oscillation of 1-mm amplitude at a frequency of 80 Hz. The vibrators were securely fixed with rubber bands over the Achilles or tibialis anterior tendon.

A force platform (AMTI, OR-6 with MSA-6 MiniAmp, Watertown, MA, USA) fixed on the floor allowed recording the ground reaction force (Fz) and the moments around the sagittal (Mx) and frontal (My) axis. The platform was surrounded by a large wooden base (1.5 m wide $\times$ 2 m long) leveled with the platform. All signals were filtered (fourth-order zero-lag Butterworth filter, 7 Hz cut-off frequency) prior to calculating the COP.

An 8-camera video system (MaxPRO ver. 1.4.2.2, Innovision Systems Inc., Columbiaville, MI, USA) allowed recording the three-dimensional position of reflective markers placed bilaterally on the acromion, greater trochanter, lateral epicondyle of femur, lateral malleolus, and unilaterally (right side) on the lateral epicondyle of the elbow, styloid process of ulna and tip of the index finger. A target also was placed on a tripod in front of each participant just below the height of the xiphoid process at about 80% of each participant's arm length. For the first two subjects, the markers were sampled at 100 Hz. Because the data processing increased the delay between trials, we then collected all subsequent data at 30 Hz.

Disposable self-adhesive surface electromyography (EMG) electrodes (Thought Technology Ltd., Uni-Gel^{TM} Single electrodes T3425, Montreal West, QC, Canada) were placed on the right side of the body on the anterior portion of the deltoid (AD), biceps brachi (BB), triceps brachii (TB), gluteus maximus (GM), semitendinosus (SEM) and on the left side for the tensor fasciae latae (TFL), biceps femoris (BF) and rectus femoris (RF). The ground electrode was placed at the olecranon process. The placements were defined in accordance the Surface EMG for Noninvasive Assessment of Muscles (SENIAM) guidelines (Hermens et al., 2000). All EMG signals were amplified at subject dependent gains (Octopus Bortec Biomedical Ltd., Calgary, AB, Canada) and analog band-pass filtered from 10 Hz to 1000 Hz.

A microcontroller (Basic Stamp® BS2sx, Parallax Inc., Rocklin, CA, USA) served to control the timeline of each trial, the activation of the vibrators and the piezoelectric buzzer, and to synchronize recording of all data. All signals, but the kinematics, were recorded at 1 kHz with a 16-bit A/D converter (PCI-DAS6031, Measurement Computing, Norton, MA, USA).

Data Analysis

Data were analyzed using custom Matlab software (Matlab, the Mathworks Inc., Natick, MA, USA). **Figure 1** presents the timeline for a trial with vibration. Reaction time was defined as the delay between the onset of the auditory stimulus and that of the index finger. The onset of the index was defined using a custom made algorithm detecting the first change in the signal above a baseline level (Teasdale et al., 1993). For each trial, the COP position of the participants along the antero-posterior axis was rebased using the mean position of the COP for a 500 ms period at the onset of a trial. To document the occurrence of the VIF response, the mean COP position then was computed for three different periods of 500 ms (a, b, c on **Figure 1**): (a) before the onset of the vibration (about 1.5 s before the onset of the movement for conditions without vibration); (b) just before the onset of the movement; and (c) when the participant's index finger was stabilized at the endpoint. We hypothesized that the VIF response would be observed only during the third period (a backward position of the COP when the Achilles tendons were vibrated and a forward position when the tibialis tendons were vibrated).

The 3D positions of all markers were obtained using MaxPro (Innovision Systems Inc. Columbiaville, MI, USA). All kinematic signals were then imported in Matlab and synchronized with all other signals prior to further processing (fourth order low-pass zero-phase lag Butterworth filter with a cutoff frequency of 7 Hz). Constant error (CE) and absolute error (AE) were computed by comparing the end position of the index finger with that of the target. All statistical tests were performed with Statistica (version 12.0, StatSoft, Tulsa, OK, USA). Mean and standard error of the mean (SE) are presented throughout the manuscript.

RESULTS

Reaction Time and Movement Time for the Pointing Movements

As stated above, for trials with vibration of the ankle tendons, an auditory stimulus to indicate participants to point at the target was given 400 ms after the onset of the vibration. With this procedure, we wanted participants to plan and initiate their pointing action before the VIF response. On average, reaction time was 419 $\pm$ 30 ms and it was unaffected by any of the vision or vibration conditions ($F_{(3,24)}$ = 1.84, p = 0.165, η^2 = 0.19). This indicates that on average, the delay between the onset of the vibration and that of the pointing action was 819 ms. Movement time for the pointing action also was not different across all conditions (on average, 353 $\pm$ 30 ms, $F_{(3,24)}$ = 7.73, p = 0.067, η^2 = 0.25).

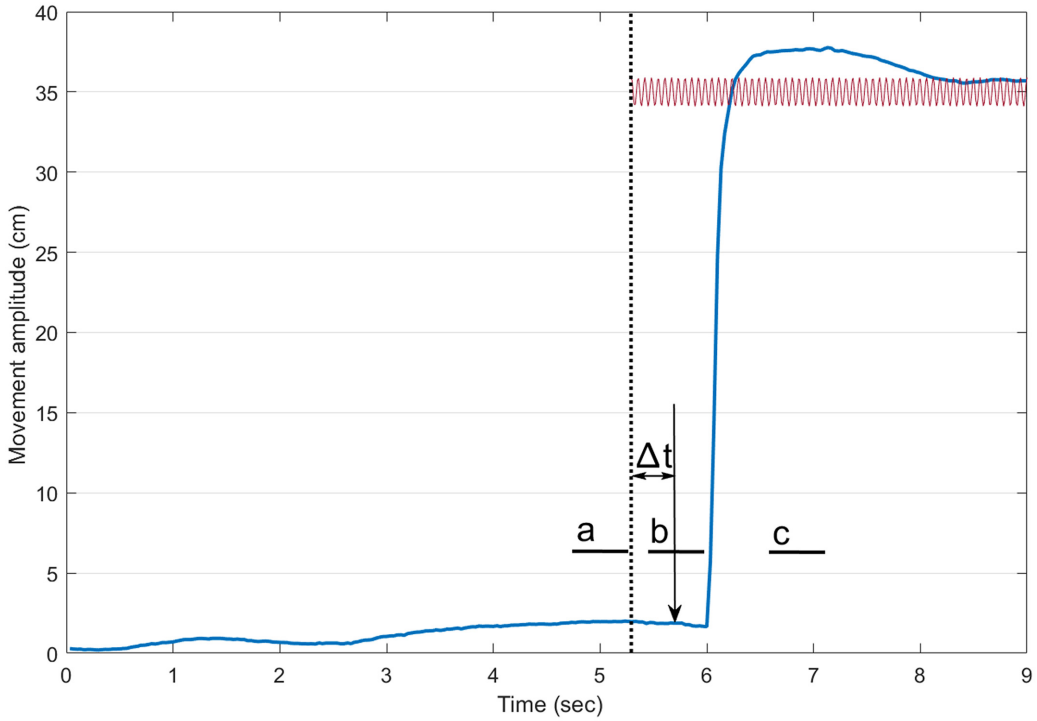

FIGURE 1 | Timeline of a trial with vibration. The thick blue line illustrates the index finger displacement. The dotted vertical line shows the onset of the vibration. The sound (vertical arrow pointing down) arrived 400 ms after the onset of the vibration. The small thick horizontal lines indicate the three 500-ms periods where the mean center of foot pressure (COP) position along the antero-posterior axis was computed (a: before the onset of the vibration, b: before the onset of the pointing movement and c: at the end of the pointing). For trials without vibration, a similar timeline was adopted.

COP Along the Antero-Posterior Axis

Figure 2 presents the mean COP position along the antero-posterior axis for the No-vibration (Vision and No-vision) and Vibration (Vibration Achilles, Vibration TA) conditions for the three periods analyzed (i.e., a, b and c on **Figure 1**). The ANOVA revealed a significant interaction of Condition × Period ($F_{(6,42)} = 6.61$, $p = 0.000$, $\eta^2 = 0.48$). A difference between the conditions was observed for the last period only, that is, once the subjects had reached the target (i.e., after the end of the pointing action). As expected, the COP moved forward when the tibialis anterior tendons were vibrated while it moved backward when the Achilles tendons were vibrated (see **Figure 2**). It is important to note that, as expected, no difference in the COP position was observed before the onset of the pointing action. This suggests participants planned their movement before the VIF response had occurred.

Amplitude and Accuracy of the Pointing Movements

To test our main hypothesis, for the pointing actions, we calculated both the CE and the AE. The ANOVA for CE (**Figures 3**—upper panel) showed a significant effect of Condition ($F_{(3,27)} = 3.79$, $p = 0.023$, $\eta^2 = 0.32$). As hypothesized, when the Achilles tendons were vibrated, the CE was negative (undershoot of the target). On the other hand, we did not observe a positive CE when the tibialis anterior tendons were vibrated as the CE was negative as well. For the AE (**Figure 3**—lower panel), the error was smaller with vision than for all other conditions but this difference was not significant ($F_{(3,27)} = 2.27$, $p = 0.10$, $\eta^2 = 0.22$).

It could be argued that the negative CE observed when the Achilles tendons were vibrated resulted from a backward displacement of the body arising from the VIF response and not from a planned shorter hand movement. To verify this possibility, we computed the distance between the right acromion and the index finger. A shorter amplitude when the Achilles tendons were vibrated would indicate that the pointing response was shorter since the amplitude is now referenced to the body and not to an external referential. On average, the amplitude for the Vision, No-vision and re-calibration trials were 56.4, 55.6 and 55.8 cm, respectively. Mean values for these control conditions were compared using *T*-tests and all differences were non-significant ($t_{(8)} = 1.03$, $p = 0.33$ for the comparison between the Vision and No-vision conditions; $t_{(8)} = -0.99$, $p = 0.35$ for the comparison between the Vision and the re-calibration trials). The mean amplitude when the Achilles tendons were vibrated was significantly shorter than the mean amplitude of the preceding trials (on average, 53.97 cm when the Achilles were vibrated; $t_{(8)} = 4.60$, $p = 0.001$). This suggests that the negative CE (shorter amplitude) did not result from a backward movement of the

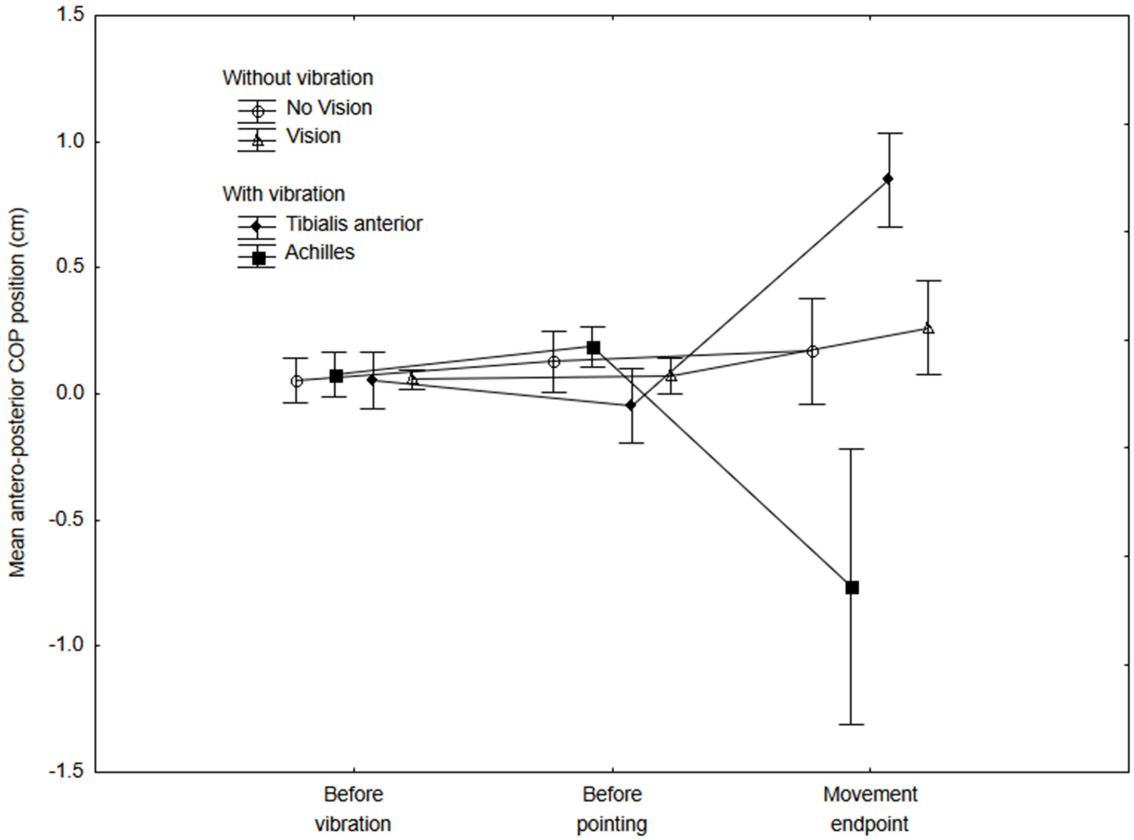

FIGURE 2 | Mean COP position along the antero-posterior axis at three different periods for the no-vibration (vision and no-vision) and vibration (Achilles and tibialis anterior) conditions. The mean COP was calculated for the three 500-ms periods (i.e., before the vibration, before the onset of the pointing movement and at the end of the movement). Positive values indicate a forward COP position with reference to baseline values (that is, once a participant adopted the initial posture and showed a stable COP position within the first 4 s). Negative values indicate a backward COP position with reference to baseline values.

body associated with the VIF but from a shorter pointing action with respect to the shoulder joint. The analyses for trials when the tibialis tendons were vibrated also showed a shorter pointing amplitude with respect to the shoulder joint (on average, 53.8 cm when the tibialis tendons were vibrated; $t_{(8)} = 4.25$, $p = 0.002$).

We also compared CE for the first pointing movement with vibration to subsequent trials. None of the participants had experimented the vibration before the first trial and a shorter amplitude for this trial could not be associated with a feedforward motor plan to avoid a potential destabilization. Specifically, we compared CE for the first trial with a vibration of the Achilles tendons (-3.4 ± 0.9 cm) to the mean of trials with (-0.4 ± 0.4 cm) and without vision (-0.6 ± 1.0 cm) preceding the first trial with vibration. Compared to trials with vision, the CE was negative (i.e., systematic undershoot of the target) and significantly smaller for the first trial with vibration of the Achilles tendons ($F_{(1,8)} = 11.896$, $p = 0.008$, $\eta^2 = 0.85$). A similar result was observed when comparing the CE for the first trial with vibration of the Achilles tendons to those without vision ($F_{(1,8)} = 7.29$, $p = 0.027$, $\eta^2 = 0.65$). These results suggest the vibration-evoked sensory information was integrated into the motor plan for the pointing action of the very first trial with vibration.

We conducted similar analyses for trials with vibration of the TA tendons, although participants had already experienced 10 trials with vibration of the Achilles tendons when they first were submitted to the first trial with the vibration of the TA tendons. The first trial with vibration of the TA tendons also showed a negative CE (-3.1 ± 1.1 cm), but the comparisons with trials without vision and with vision showed that these differences were not significant ($F_{(1,8)} = 4.69$, $p = 0.064$, $\eta^2 = 0.37$, and $F_{(1,8)} = 1.8$, $p = 0.216$, $\eta^2 = 0.18$, respectively for the comparisons with the Vision and No Vision conditions).

EMG Activity

Finally, we examined the EMG activity for three muscles involved in the pointing action, the anterior deltoid, the biceps and TB. We specifically wanted to determine if the activity of the main agonist (TB) and antagonist (BB) muscles would show any modulation associated with the vibration of ankle tendons (for instance, smaller activity for the triceps and greater activity for the biceps when the Achilles tendons were vibrated). After

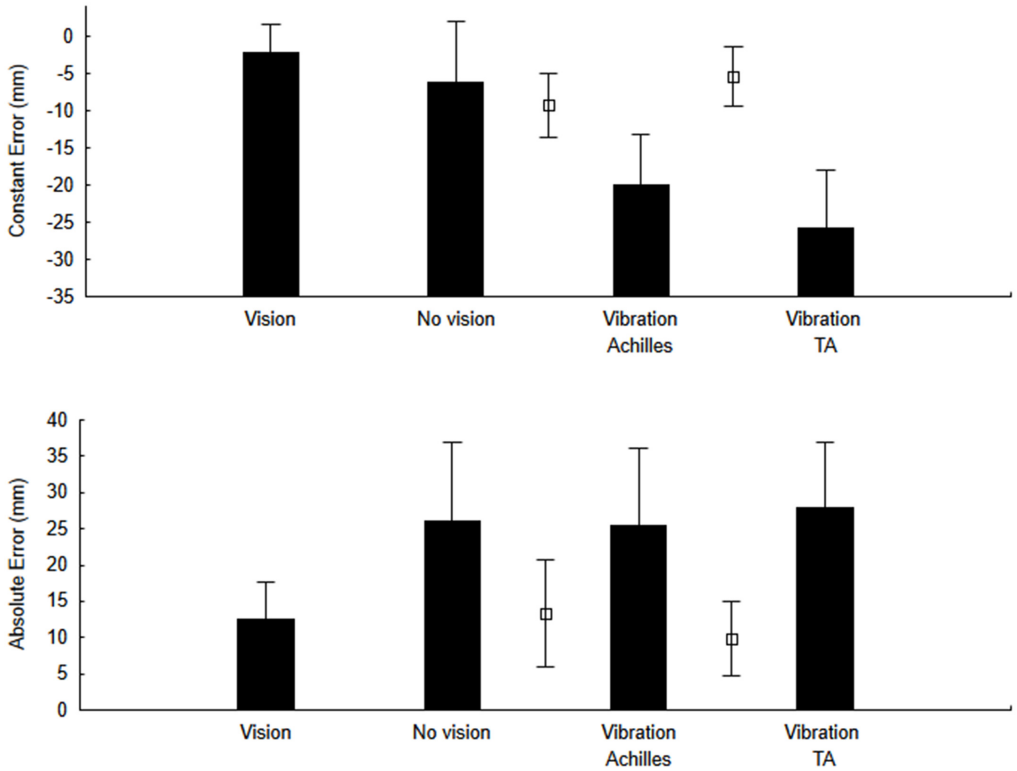

FIGURE 3 | Constant error (CE) and variable error (VE) for the no-vibration (vision and no-vision) and vibration (Achilles and tibialis anterior) conditions. For comparison purposes, open square symbols depict mean values for the re-calibration trials (i.e., trials when pointing was performed with vision before each block of trials with vibration and without vision).

a visual inspection of all data to insure EMG signals were normal within this period, data for one participant were removed because of irregular triceps signals. For the remaining eight participants, we calculated the $\int_{-50}^{100} EMG$ from 50 ms before the onset of the hand movement to 100 ms after the onset for each conditions. To allow between-subjects comparisons, the $\int_{-50}^{100} EMG$ obtained for the conditions No Vision, Vibration Achilles and Vibration TA were normalized using the same period from the condition Vision. Then, for each muscle, data for these three conditions were submitted to a one-way ANOVA. All ANOVAs were non-significant ($F_{(2,14)} = 0.29$, $p = 0.75$, $\eta^2 = 0.04$, $F_{(2,14)} = 2.46$, $p = 0.12$, $\eta^2 = 0.26$ and $F_{(2,14)} = 1.75$, $p = 0.21$, $\eta^2 = 0.20$ for the anterior deltoid, BB and TB, respectively).

DISCUSSION

Vibration applied to ankle tendons is known to induce a body displacement in freely standing subjects and an illusory body tilt in restrained subjects. For instance, vibrating the Achilles tendon induces a backward body displacement in freely standing subjects and an illusory forward tilt when the body is restrained (Eklund, 1972; Kavounoudias et al., 2001; Adamcova and Hlavacka, 2007; Ceyte et al., 2007). The body displacement observed in freely standing subjects is presumed to represent an automatic reaction (e.g., Eklund, 1972; Gurfinkel et al., 1988; Roll et al., 1989b). In the present study, and as observed previously in freely standing subjects, vibrating the Achilles tendons led to a backward body displacement and conversely vibrating the TA tendons led to a forward body displacement. Importantly, in our study, whole body large displacements were observed after the pointing action and not before. No large VIF response was noted between the onset of the vibration and the onset of the pointing action. On average, the delay between these two events was 819 ms which is slightly longer than the latency of the body displacement after a tendon vibration (VIF response) reported by Quoniam et al. (1995). This first observation is important as it clearly suggests that the planning of the pointing action was made while vibration-evoked proprioceptive information could be interpreted by the central nervous system as a change in the postural orientation while this was not the case yet. The key question of this study was whether this information was included in the motor plan of the pointing action. Our hypothesis was that if this sensory information reaches higher level structures and is interpreted as a change in postural orientation during the planning phase of the pointing action, the amplitude of the movement should scale according to the muscles being vibrated. As expected, the amplitude of the pointing actions was shorter when Achilles tendons were vibrated. Vibrating the TA tendons, however, also yielded shorter movements while we expected longer movements.

There is a possibility that the shorter movements were not the result of integrating the postural orientation *per se* but rather a general response to conditions of postural instability. This has been proposed by Slijper and Latash (2004). In their study, they observed an increased co-contraction of distal muscles and reciprocal adjustments in trunk muscles when subjects were submitted to vibration of the Achilles tendons. They suggested these adjustments served to ensure equilibrium when subjects were submitted to conditions of postural instability (vibrating Achilles tendons being one of their conditions). In our study, movements of shorter amplitude and lower speed could have served to limit the instability induced by the pointing action. There are some arguments against this possibility, however. First, if the shorter amplitudes were a strategic response to control postural instability, slower movements could have been observed for the vibration conditions. This was not the case as movement times were similar for all conditions. Another argument is based on the lack of difference between the amplitude of the first trial with vibration of the Achilles tendons and the amplitude of pointing actions with and without vision. None of the participants had experimented the vibration before this first trial and a shorter amplitude for this first trial could not be associated with a feedforward motor plan to avoid potential destabilization.

The suggestion that sensory information from ankle proprioception and plantar sole mechanoreceptors serve to estimate body orientation when planning a motor response is in agreement with recent observations by Mouchnino et al. (2015). In this study, the authors measured the cortical response to somatosensory stimulation of cutaneous inputs during the planning phase of a step initiation and during its execution. They observed a facilitation of the P50-N80 SEP component in the early planning phase of the step initiation. The authors suggested that this mechanism could enhance the perception of cutaneous input leading to a more accurate planning and execution of the forces needed to unload the moving limb. In their study, the cutaneous inputs were directly involved in the motor action. Here, our results suggest that similar mechanisms may exist to update the motor plan of an upper-limb goal directed movement. For instance, the control of posture does not only serve the motor planning of an upper limb action by receiving feedforward commands and contributing through feedback processes once the movement is initiated. Rather, sensory information about body orientation during the actual planning of the upper arm movement can be integrated rapidly to modify and update the motor plan of the upper limb movement.

There is also a possibility that foot pressure distributions affected this result as it has been shown that vibration induced postural responses are dependent on the pressure distributions (Kavounoudias et al., 2001; Thompson et al., 2011). These authors proposed that ankle proprioception and plantar sole mechanoreceptors might be processed simultaneously following a vector addition mode to determine body orientation. For example, in Thompson et al. (2011) study, participants were submitted to a support platform perturbation (toes up or toes down) and the concurrent application of a vibration to the Achilles tendon and to the rear foot had differential effect on posture. Vibration of the Achilles tendon increased the influence of the rear foot vibration for toes up perturbations. On the other hand, it decreased the influence of the rear foot vibration when toes down perturbations were given. The authors suggested that this indicates the central nervous system uses both sources of sensory information to build a reference of verticality influencing the control of equilibrium during quiet and perturbed stance. A similar mechanism may have occurred in the present study and this could explain why we did not observe any overshoot when the TA muscle tendons were vibrated. In this particular case, the sensory signals from the TA (before the onset of the pointing action) suggested a backward movement of the body. A rapid pointing response of a greater amplitude would have produced a greater backward body movement that could have compromised postural stability. This was not the case when the Achilles tendons were vibrated as the sensory signals (before the onset of the movement) indicated a forward movement of the body allowing to produce a pointing movement of a shorter amplitude that did not compromise postural stability. Additional studies will be needed to examine if this could explain the shorter amplitudes observed when the TA tendons were vibrated (for example, by using movements of shorter amplitudes that would be less likely to destabilize subjects).

As for all studies, there are some limitations to this study. Presentation of the vibration conditions was not randomized. The main dependent variable in this study was the amplitude of the pointing action. The pointing action was made to a memorized target and included the usual motor variability associated with producing fast goal-directed motor actions (Schmidt et al., 1979; Harris and Wolpert, 1998; Scott, 2004). We felt that randomizing conditions could add some additional undesirable variability. This has been observed in several postural studies. For instance, Horak et al. (1989) showed that the scaling of a postural response (muscle and torque responses) to postural perturbation amplitudes disappeared when perturbation amplitudes were randomized. Martin et al. (2000) also reported that the uncertainty about a visual perturbation (double-step paradigm) modified the planning of pointing actions to a target.

In conclusion, our results suggest that the sensory signals evoked by vibrating Achilles tendons prior to the VIF responses are integrated into the motor plan of a pointing action. We did not observe longer movements when the tibialis anterior tendons were vibrated. This indicates subjects integrated both the sensory signals evoked by vibrating muscle tendons and the expected consequences of the planned pointing action.

AUTHOR CONTRIBUTIONS

NT and MS contributed to conception, design, preparation, analysis and interpretation of the data and writing. MPF contributed to conception, data collection and analysis and writing. FCLO contributed to data collection and analysis. MGR contributed to preparation and data analysis. All authors approved the final version.

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Ehlers-Danlos Syndrome, Hypermobility Type: Impact of Somatosensory Orthoses on Postural Control (A Pilot Study)

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Elhers-Danlos syndrome (EDS) is the clinical manifestation of connective tissue disorders, and comprises several clinical forms with no specific symptoms and selective medical examinations which result in a delay in diagnosis of about 10 years. The EDS hypermobility type (hEDS) is characterized by generalized joint hypermobility, variable skin hyperextensibility and impaired proprioception. Since somatosensory processing and multisensory integration are crucial for both perception and action, we put forth the hypothesis that somatosensory deficits in hEDS patients may lead, among other clinical symptoms, to misperception of verticality and postural instability. Therefore, the purpose of this study was twofold: (i) to assess the impact of somatosensory deficit on subjective visual vertical (SVV) and postural stability; and (ii) to quantify the effect of wearing somatosensory orthoses (i.e., compressive garments and insoles) on postural stability. Six hEDS patients and six age- and gender-matched controls underwent a SVV (sitting, standing, lying on the right side) evaluation and a postural control evaluation on a force platform (Synapsys), with or without visual information (eyes open (EO)/eyes closed (EC)). These two latter conditions performed either without orthoses, or with compression garments (CG), or insoles, or both. Results showed that patients did not exhibit a substantial perceived tilt of the visual vertical in the direction of the body tilt (Aubert effect) as did the control subjects. Interestingly, such differential effects were only apparent when the rod was initially positioned to the left of the vertical axis (opposite the longitudinal body axis). In addition, patients showed greater postural instability (sway area) than the controls. The removal of vision exacerbated this instability, especially in the mediolateral (ML) direction. The wearing of orthoses improved postural stability, especially in the eyes-closed condition, with a particularly marked effect in the anteroposterior (AP) direction. Hence, this study suggests that hEDS is associated with changes in the relative contributions of somatosensory and vestibular inputs to verticality perception. Moreover, postural control impairment was offset, at least partially, by wearing somatosensory orthoses.

Keywords: subjective vertical, proprioception, compressive garments, proprioceptive insoles, postural sway

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INTRODUCTION

The Ehlers-Danlos syndrome (EDS) is a heterogeneous group of hereditary connective tissue diseases, which are present in at least 1/5000 individuals with a majority of women (Sobey, 2014). Degradation of the composition and elasticity of connective tissue results in a broad, pronounced and unspecific symptomatology. Consequently, the revised Brighton criteria classified EDS in six subtypes, according to the predominance of their clinical manifestations (Beighton et al., 1998). The EDS hypermobility subtype (hEDS) is the most frequently encountered. Besides common symptoms with other subtypes such as fatigue and pain, hEDS is characterized by generalized joint hypermobility combined with variable cutaneous hyperelasticity and proprioceptive impairment (Beighton et al., 1998; Castori, 2012). Indeed, few studies that have investigated proprioceptive sensitivity (i.e., joint position sense) in hEDS, have demonstrated the existence of proprioceptive impairment in this population (Rombaut et al., 2010a; Clayton et al., 2015). A strong hypothesis to explain the neurophysiological basis of this impairment suggests that the generalized joint hypermobility specific to hEDS induces excessive and repeated extension of the ligaments, which damages the surrounding proprioceptive receptors (Ruffini's and Pacini's corpuscles; Golgi tendon organs). Additionally, changes in cutaneous elasticity probably affects pressure information transmitted by cutaneous tactile mechanoreceptors to cortical areas. Hence, it is likely that hEDS induces not only a proprioceptive deficit but, more broadly, a somatosensory deficit. Consequently, the major functional disabilities expressed by these patients, including clumsiness and falls, which sometimes lead to kinesiophobia, could be the result of this somatosensory impairment (Rombaut et al., 2012).

Indeed, somatosensory information, arising from muscles, skin, and joints, plays a key role in perception, balance and, more broadly in movement. Currently, there is growing evidence that balance and movement are both based on heteromodal integration of three types of sensory modality, visual, vestibular, and somatosensory, which carry redundant, specific and complementary information (Massion, 1992; Lacour et al., 1997). The integration of these sensory modalities by the central nervous system provides three spatial frames of reference—egocentric (i.e., body), geocentric (i.e., gravity) and allocentric (i.e., external cues)—which contribute to the development of internal models crucially involved in balance and movement (Gurfinkel et al., 1981; Massion, 1994; Mergner and Rosemeier, 1998). In the sensorimotor processes, internal models refer to a neural process responsible for synthesizing information from sensory modalities and combine efferent and afferent information to resolve sensory ambiguity (Merfeld et al., 1999). Furthermore, sensory processing is a flexible mechanism (Peterka, 2002). The central nervous system continually modulates weight assigned to each sensory modality to provide a dynamic internal representation, making it possible to always generate an appropriate muscle response to maintain and adapt balance to the continuously changing environment (Van der Kooij et al., 2001; Zupan et al., 2002; Peterka and Loughlin, 2004; Logan et al., 2014). Within this process, the somatosensory system specifically provides information about the position of different parts of the body with respect to one another. Moreover, it allows characterization and localization of touch and pain (Dijkerman and De Haan, 2007). Thus, the somatosensory system mainly contributes to the sensorimotor map of body space in internal models, an unconscious process also called the "body schema" (De Vignemont, 2010).

Mittelstaedt (1983) reported that information provided by proprioception contributes considerably to the maintenance of body verticality. The perception of vertical is considered be the outcome of synthesizing visual, somatosensory and vestibular information (Brandt et al., 1994; Bisdorff et al., 1996; Merfeld et al., 1999; Van Beuzekom and Van Gisbergen, 2000; Bronstein et al., 2003; Barbieri et al., 2008; Pérennou et al., 2008; Tarnutzer et al., 2009). However, it is known that the contribution of each sensory modality in verticality perception varies between subjects and, to a greater extent, in populations presenting either vestibular impairments (e.g., patients with unilateral vestibular loss; Lopez et al., 2008) or somatosensory impairments (e.g., stroke patients with a hypoesthesia pressure and paraplegic patients; Barra et al., 2010). Interestingly, the Aubert effect, consisting in tilting of the visual vertical towards the body during lateral body tilt due to the resultant of the gravitational vector (i.e., perception of the otolith organ) and the idiotropic vector (i.e., perception of the main longitudinal axis of the body), is modified in favor of gravitational vector proportionally to the degree of somatosensory impairment (Barra et al., 2010). Hence, it seems reasonable to inquire whether somatosensory impairment in hEDS patients might modify the Aubert effect. At the same time, it has been previously shown that hEDS patients develop body schema disorders resulting in partial loss of movement control (Rombaut et al., 2010b) and postural instability (Galli et al., 2011). This deterioration in postural stability is manifested in both static (standing) and dynamic (walking) conditions (Rombaut et al., 2011; Rigoldi et al., 2013). Previous studies have already shown a strong connection between somatosensory impairments and balance disorders, especially in Parkinson's disease (Jacobs and Horak, 2006; Vaugoyeau et al., 2011). Typically, these patients, as in normal aging, compensate for their sensory deficit by an overreliance on visual information (Lord and Webster, 1990; Isableu et al., 1997; Azulay et al., 2002). Therefore, one can speculate that somatosensory impairment could be responsible to a large extent for this postural instability, and that it could be compensated for by using a high level of visual information.

Compression garments (CG) have been tested empirically in clinical practice in hEDS, resulting in beneficial effects on pain, fatigue and mobility. Speculatively, the CG, due to their mechanical effect, are thought to enhance joint coaptation and increase the pressure of the subcutaneous connective tissue to a normal range. Hence, CG may enhance somatosensory feedback to the brain and, thus, its contribution to postural control. Similarly, proprioceptive insoles (PI) may enhance plantar cutaneous afferents and postural stability. Therefore, somatosensory orthoses (i.e., CG and PI) offer a

therapeutic solution to reduce somatosensory impairments, however weakly evaluated. Along with these observations, previous studies have demonstrated that CG induced an improvement in knee proprioception, and PI decreased the attentional demand for gait (Clark et al., 2014; Ghai et al., 2016). Conversely, these two ortheses showed no impact in healthy young subjects, and CG appeared to induce a deterioration of postural stability in elderly subjects (Hijmans et al., 2009; Dankerl et al., 2016). In the light of these conflicting observations, we aimed to quantify the impact of these somatosensory orthoses on postural stability in a population with a specific impairment of the somatosensory system. Indeed, it seems plausible that, although the wearing of CG has probably no immediate impact on the damaged joint proprioceptive receptors, its compressive effect applied to subcutaneous connective tissue could allow better somatosensory transmission from cutaneous tactile mechanoreceptors. Hence, somatosensory deficit could be partially reduced by CG, which would compensate for joint proprioception impairment. Similarly, enhanced plantar cutaneous afferents induced by PI could increase the available sensory information for postural control.

The goal of the present study was to assess: (i) the impact of somatosensory deficit on subjective visual vertical (SVV) and postural stability; and (ii) the effects of somatosensory orthoses (i.e., CG and PI) on static postural control. We hypothesized that: (i) somatosensory impairments would modify SVV, strongly impair postural stability and increase the use of visual information; and (ii) enhancing somatosensory feedback with the orthoses would restore the balance in the use of sensory modalities, thus reducing the use of visual information, and consequently enhance postural stability.

MATERIALS AND METHODS

Study Population

Six patients with hEDS (6 females; mean age ± SD: 37 ± 10.41 years) and six healthy, age- and gender-matched control subjects (6 females; mean age ± SD: 36 ± 11.52 years) participated in this study. Patient selection was carried out in the Internal Medicine Department of Caen University Hospital. Inclusion criteria were based on the revised Villefranche criteria, including the presence of generalized joint hypermobility, skin hyperelasticity, chronic musculoskeletal pain, and/or a positive family history (Beighton et al., 1998). Additionally, patients must have reported hypersensoriality (e.g., a low hearing threshold). Exclusion criteria were: (i) wearing of somatosensory orthoses (i.e., PI and CG); (ii) inability to maintain a minimum of postural stability in static conditions (i.e., holding an upright stance during 1 min); (iii) treatment by a physical therapist; and (iv) other pathologies that directly impact postural control (e.g., Ménière's disease). Finally, patients were checked for vestibular disorders by ENT examination with otolithic myogenic evoked potentials, and videonystagmography. Healthy controls subjects were recruited by local phone call. Control subjects were excluded if they had a neurologic (with a special focus on vestibular disease using the Fukuda test; Fukuda, 1959) or orthopedic disorder (analysis of foot plantar pressure distributions using a podoscope) that could affect their postural stability, and a generalized disease affecting joints, or a Beighton score >4/9.

All subjects were treated in strict compliance with the Declaration of Helsinki. The protocol was approved by the CERSTAPS (Ethical Committee of Sport and Physical Activities Research), Notice Number: 2016-26-04-13, approved by the National Academic Commission (CNU) on April 26, 2016. Written informed consent was obtained from all participants.

Instrumentation

Somatosensory Orthoses

The CG and PI required in this study were customized based on the needs of each patient by orthotic and prosthetic practitioners (Novatex Medical). CG included pants, vest, and mittens, which covered the entire body of all participants (i.e., trunk, upper and lower limbs; **Figure 1**).

Postural Control

Postural sway was recorded using a motorized force platform (SYNAPSYS, France). Three strain gauges integrated into the force platform recorded the vertical ground reaction force component. The data were sampled at 100 Hz and transformed by computer-automated stability analysis software (i.e., Synapsys software) to obtain x-y coordinates of the center of pressure (COP).

Subjective Visual Vertical

Perception of the vertical was assessed by the SVV test using the Perspective System® (Framiral®, France).

FIGURE 1 | (A) Compression garments (CG) and **(B)** proprioceptive insoles (PI) worn by an Ehlers-Danlos syndrome hypermobility type (hEDS) patient during the experiment.

Experimental Procedure

In the first part of the experiment, participants underwent postural control assessment (duration: 1 h 45 min for patients, and 20 min for controls) followed by SVV assessment (duration: 15 min for all participants).

Subjective Visual Vertical Assessment

To assess the SVV, each participant, in a completely darkened room, was shown, in front of them, the projection of a luminous rod (laser line 2 m in length placed 3 m in front of them). Participants could rotate the rod around its center in the clockwise or counterclockwise directions using a transmitter, and were instructed to place the rod vertically with respect to the true gravitational vertical. All subjects performed the SVV test in three conditions: standing, sitting and lying on their right side. In this latter condition, participants lay in a standard position on a stretcher with an adjustable head-rest, which was positioned identically initially for each participant (body and head were tilted, respectively, at 90° and 72°). Subjects were asked to minimize their movements during the tests. Each condition comprised four trials: two with the rod initially oriented to the right side (i.e., 30° to the right—clockwise) and two to the left side (i.e., −30° to the left—counterclockwise). The tests and conditions were randomly distributed within each participant.

Postural Control Assessment

Postural sway was measured for 52 s while participants stood on a force platform. Participants were asked to stand still, barefoot, arms hanging freely, feet positioned at an angle of 30°, and to focus on a visual reference mark fixed 1.5 m in front of them in their individual line of vision. The assessment comprised four conditions with two tests each lasting 52 s, with a 20 s rest between each test, and 5 min between each condition. The start and stop signals were given 3 s before and 3 s after each acquisition. The four conditions were: (1) control condition (CC; without orthoses); (2) CG; (3) PI; and (4) the combination of CG and PI (CG-PI). Each condition was performed with either eyes open (EO) or eyes closed (EC). Participants also underwent dual-task (combining postural control with a cognitive task) and dynamic (sinusoidal translation of support) trials under the four above-mentioned conditions (results are not included in the present article). To minimize any order effects during testing, such as fatigue effects, all conditions and trials (EO/EC) were randomized among subjects. A training test was performed before testing (**Figure 2**).

Data Analysis

Subjective Visual Vertical Analysis

SVV evaluation error was scored in degrees of deviation from the vertical. Mean errors were calculated across conditions, according to the initial orientation of the rod. Errors were scored negatively when the subjective vertical was oriented to the left, and positively when it was oriented to the right.

Postural Control Analysis

Postural sway parameters calculated from the COP recordings were as follows: the anteroposterior and mediolateral sway standard deviation (SD-AP/SD-ML; mm) and the sway area (AREA-CE; mm^2) corresponding to the 95% confidence elliptic area included within the COP path.

Statistical Analysis

The SVV (angle of deviation from the vertical) and postural (AREA-CE, SD-AP and SD-ML) dependent variables failed to display an acceptable normal distribution (Shapiro-Wilk test). Consequently, non-parametric tests were used for statistical analysis.

The Mann-Whitney U-test was used to compare healthy controls to hEDS patients on verticality perception and postural stability. A Friedman test was used to determine differences between the performances carried out in each postural condition (CC, CG, PI and CG/PI) and each SVV condition (standing, seated, lying: right and left initial orientation). When the result of the Friedman test was significant, we subsequently used a Wilcoxon test for matched samples to determine the effects of vision (EO and EC) and somatosensory orthoses on postural stability. We used the Bonferroni method to correct for multiple comparisons. Statistical significance was set at 0.05. Statistica (version 10, Statsoft, Inc., Tulsa, OK, USA) was used to perform all analyses.

RESULTS

Subjective Visual Vertical

We first analyzed perception of the visual vertical in each position (standing, seated, lying on the right side) using the Mann-Whitney U-test. In standing condition, hEDS patients oriented the vertical more in left side than controls, when the initial orientation of the rod was also on the left ($U = 4$, $p = 0.026$). Simultaneously, in lying on the right condition, when the initial orientation of the rod was on the left, patients did not exhibit the substantial perceived tilt of the visual vertical in the direction of the body tilt (Aubert effect), and oriented their vertical closer to the real vertical compared to controls, ($U = 0$, $p = 0.002$). Interestingly, in sitting condition, perception of visual vertical was similar in both groups (**Figure 3**).

The Friedman test revealed significant differences in verticality perception according to the initial orientation of the rod (right and left) and body position (sitting, standing and lying on the right) in hEDS patients ($p = 0.0001$) and controls ($p = 0.00034$). As 30 side-by-side comparisons were carried out for each *post hoc* analysis, the Bonferroni method was used to correct the significance level at 0.0016. Consequently, all the results from the Wilcoxon test reported below with a $p > 0.0016$ have been used because of our small sample size, and thus have a descriptive vocation.

Regardless of the position, the initial orientation of the rod seems to influence the verticality perception of hEDS patients (sitting: $Z = 2.20$, $p = 0.027$; standing: $Z = 2.20$, $p = 0.027$;

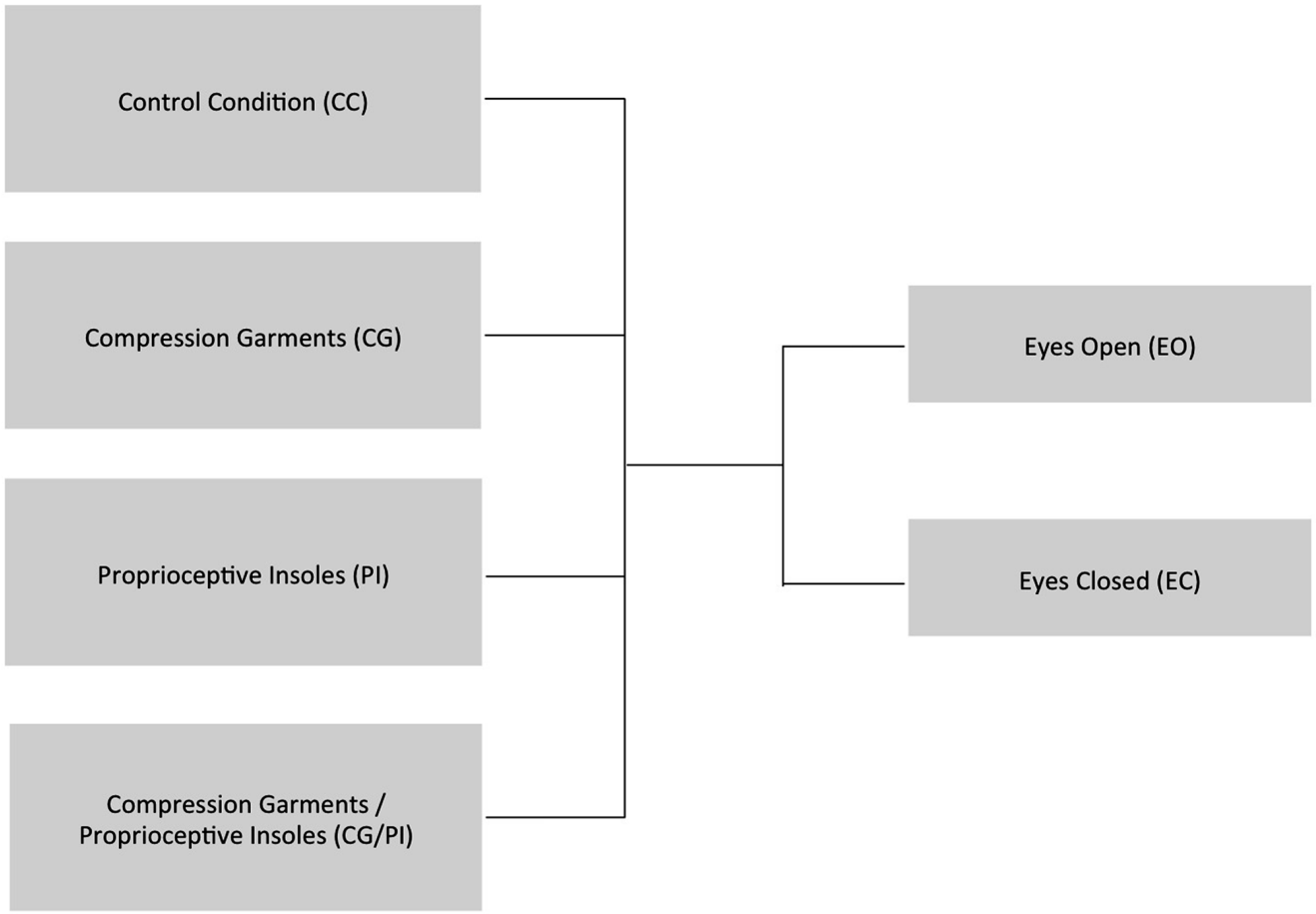

FIGURE 2 | Design of the postural control assessment.

lying: $Z = 2.20$, $p = 0.027$). When the initial orientation of the rod was to the right, patients showed a greater degree of deviation of verticality perception in standing compared to sitting ($Z = 2.20$, $p = 0.027$), and to a larger extent, when lying compared to sitting ($Z = 2.20$, $p = 0.027$) and standing ($Z = 2.20$, $p = 0.027$). In contrast, no difference was observed when the initial orientation of the rod was to the left. Likewise, in controls, the initial orientation of the rod did not influence verticality perception. In addition, controls presented a greater deviation of their verticality perception when lying as opposed to sitting and standing, regardless the initial orientation of the rod (right initial orientation: sitting vs. lying: $Z = 2.20$, $p = 0.027$, standing vs. lying: $Z = 2.20$, $p = 0.027$; left initial orientation: sitting vs. lying: $Z = 2.20$, $p = 0.027$, standing vs. lying: $Z = 2.20$, $p = 0.027$).

Postural Control without Somatosensory Orthoses

Compared with controls, hEDS patients showed impaired postural stability, as reflected by their increased sway area (EO, $U = 4$, $p = 0.052$) and increased AP sway SD (EO, $U = 3$, $p = 0.015$). These latter effects became more pronounced in the absence of visual information (AREA-CE: EC, $U = 2$, $p = 0.017$; SD-AP: EC, $U = 0$, $p = 0.004$). Furthermore, postural stability also deteriorated in the ML direction without vision ($U = 4$, $p = 0.052$). Besides, the Wilcoxon test comparing EO and EC revealed an increased sway area ($Z = 2.022$, $p = 0.043$) and an increased ML sway SD in hEDS patients ($Z = 2.022$, $p = 0.043$). Removal of vision had no effect on postural stability in controls (**Figure 4**).

Postural Control with Somatosensory Orthoses

The Friedman test was conducted to assess the effects of somatosensory orthoses on postural stability in hEDS patients in four conditions (control, PI, CG, and PI-CG), with (EO) and without (EC) vision. Then, as six side-by-side comparisons were carried out within each *post hoc* analysis, the significance threshold was set at 0.00833, as indicated by Bonferroni correction. Similar to the SSV, all the results from the Wilcoxon test reported below with a $p > 0.00833$ have a descriptive vocation.

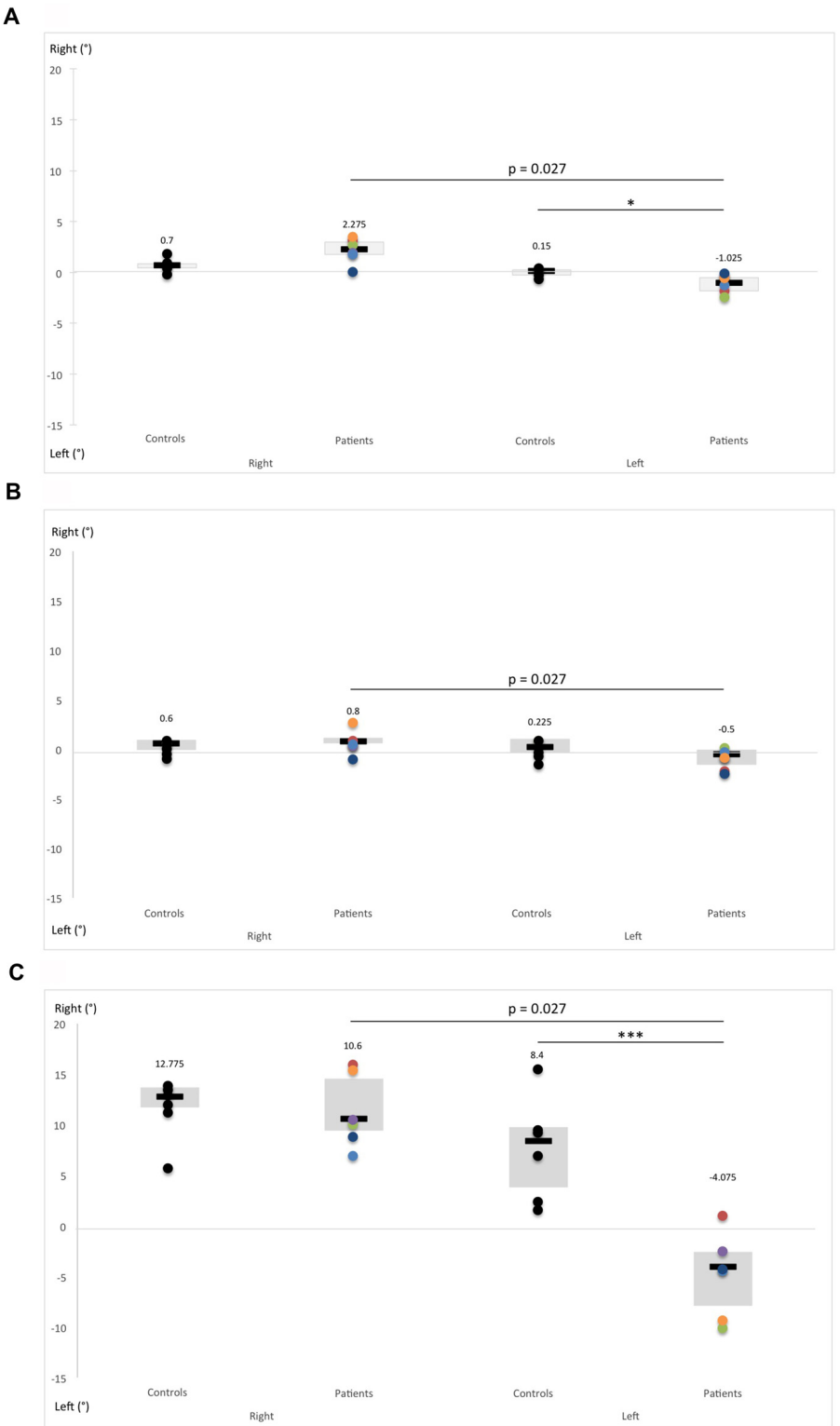

FIGURE 3 | Comparison of subjective visual vertical (SVV) performance between hEDS patients and controls in different body positions: **(A)** standing, **(B)** sitting and **(C)** lying on the right side. SVV was measured by presenting a laser rod 12 times in total darkness with a 30-degree deviation from the vertical alternately on the right and the left. Subjects were asked to reposition the rod vertically using a remote control. Box plots represent median and quartiles, and dots represent performance of each participant as follows: controls: black; patient 1: red; patient 2: green; patient 3: purple; patient 4: light blue; patient 5: orange; patient 6: dark blue. $*p < 0.05$, $***p < 0.005$.

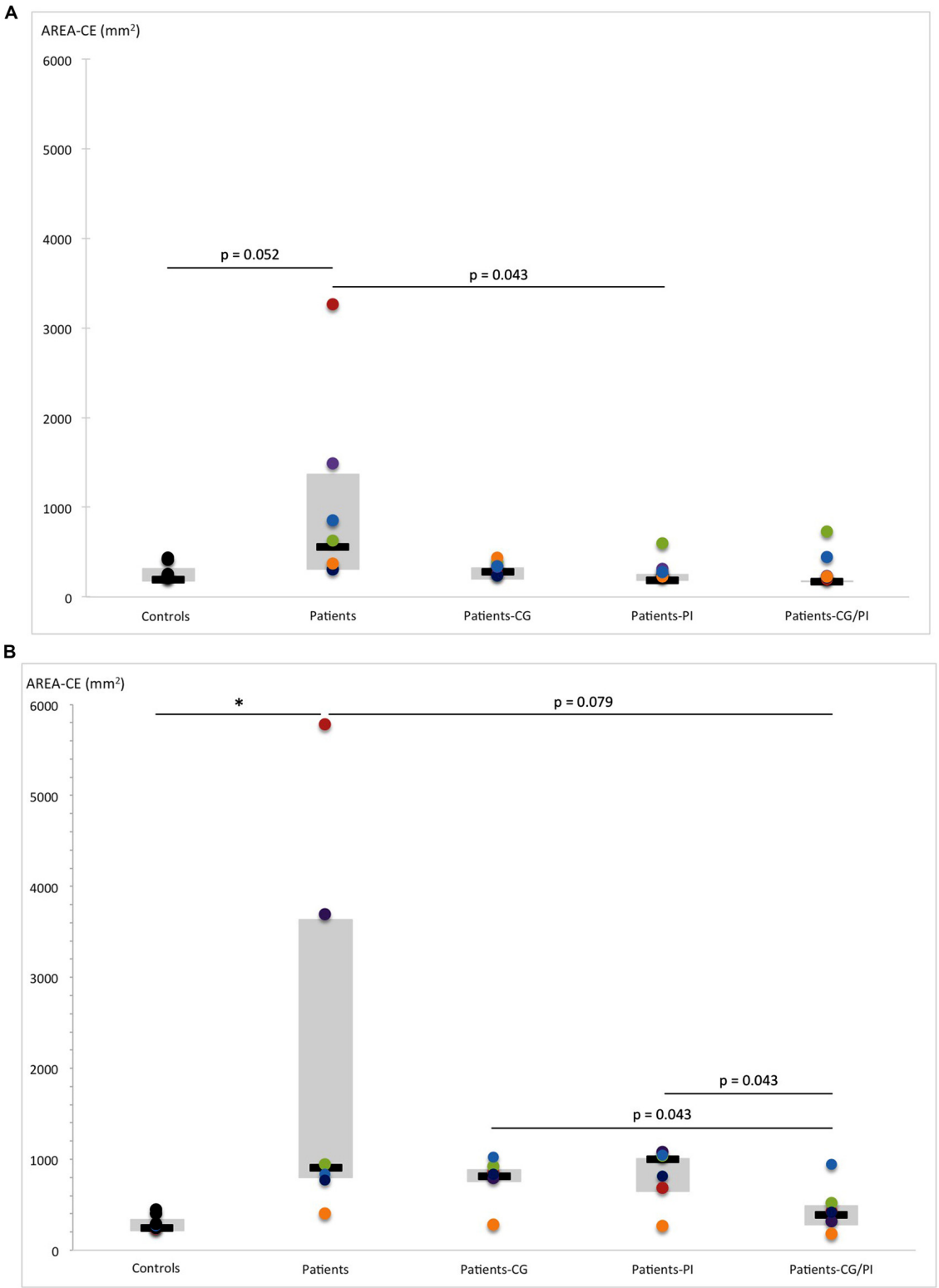

FIGURE 4 | Comparison of AREA-CE (area of 95% confidence circumference, mm^2) obtained by hEDS patients and controls, with and without somatosensory orthoses (CG, compression garments; PI, proprioceptive insoles; CG-PI, both somatosensory orthoses): in **(A)** eyes-open, and **(B)** eyes-closed conditions. Box plots represent median and quartiles, and dots represent performance of each participant as follows: controls: black; patient 1: red; patient 2: green; patient 3: purple; patient 4: light blue; patient 5: orange; patient 6: dark blue. $^*p < 0.05$.

With Vision

The Friedman test revealed that somatosensory orthoses tended to have a significant effect on sway area (p = 0.069), with an improvement in postural stability (decreased sway area) in the presence of PI compared to the CC (Z = 2.022, p = 0.043; **Figure 4A**). However, the patients' performance distribution within each orthosis condition indicates that this result may be due to a lower inter-individual heterogeneity than in CG/PI condition, and a median slightly lower than in CG condition (**Figure 4A**). Consequently, there is little evidence that the PI condition induced an improvement of postural stability greater than the other conditions (CG, CG/PI), which all seem to induce a beneficial but similar effect on postural stability. This effect appeared to be even more pronounced when the patient was unstable in the CC. On the other hand, somatosensory orthoses had no significant effect on AP and ML sway SD (**Figures 5A**, **6**).

Without Vision

The Friedman test revealed that somatosensory orthoses significantly impacted AP sway SD (p = 0.040), and tended to have a significant effect on sway area (p = 0.06). Importantly, the simultaneous wearing of the two orthoses seems to have induced further improvement on AP sway SD (Z = 2.022, p = 0.043; **Figure 5B**), compared to control, as opposed to the wearing of each orthosis separately. Indeed, the observed effects were more pronounced when the two orthoses were worn together rather than separately (AREA-CE: CG vs. CG/PI: Z = 2.022, p = 0.043; PI vs. CG/PI: Z = 2.022, p = 0.043; **Figure 4B**; SD-AP: CG vs. CG/PI: Z = 1.75, p = 0.079; PI vs. CG/PI: Z = 2.022, p = 0.043; **Figure 5B**). Also, the decreased AP sway SD induced by CG (Z = 2.022, p = 0.043) tended to be greater than that induced by PI (Z = 1.75, p = 0.079; **Figure 5B**). However, in light of patients' performance distribution under these two conditions, it is difficult to identify an additional effect of CG as compared to PI. In the ML direction, somatosensory orthoses did not show any significant impact on postural stability.

With vs. Without Vision

The increased sway area found in hEDS patients without vision and somatosensory orthoses (Z = 2.022, p = 0.043) persisted when they wore orthoses, alone (PI: Z = 2.022, p = 0.043; CG: Z = 1.75, p = 0.079) or in combination (Z = 2.022, p = 0.043). A similar result was observed for ML sway SD (PI: Z = 2.022, p = 0.043; CG: Z = 1.75, p = 0.079, PI/CG: Z = 1.75 p = 0.079; **Figure 6**). In contrast, visual removal did not appear to affect AP sway SD, regardless of the presence of somatosensory orthoses.

DISCUSSION

Subjective Visual Vertical in hEDS

In the standing condition, the results obtained by hEDS patients suggest a greater deviation from true gravitational vertical than controls. This effect seems to be less apparent in the sitting condition. These findings suggest that hEDS is associated with changes in the neural processing of somatosensory inputs, which could in turn alter judgment of the SVV (Trousselard et al., 2003). Moreover, one can speculate that, as previously observed in stroke patients, this specific alteration of verticality perception in the standing condition could be associated with postural instability in hEDS patients, and especially with lower limb asymmetry (Bonan et al., 2006, 2007). However, correlational analyses did not strongly confirm a direct link between these two factors. The small number of subjects included in this pilot study makes these analyses irrelevant due to pronounced heterogeneity between patients in both postural stability and verticality perception performances. In addition, certain technical limitations prevented us from computing parameters able to quantify postural asymmetry. Nevertheless, these observations provide preliminary data that should be explored further. More relevantly, when lying in the right condition, the Aubert or A-effect (i.e., SVV deviation from the true vertical in the same direction as the body tilt; Aubert, 1861) was found when the rod was tilted to the right in both groups, but absent when the rod was initially left-oriented in hEDS patients. In healthy controls, the A-effect is considered to result from the subject's tendency to shift the SVV toward the longitudinal body axis, independently of the initial orientation of the rod (Mittelstaedt and Glasauer, 1993). More specifically, it may result from changes in vestibular (i.e., otolithic organs; *gravitational vector*) and somatosensory (i.e., muscular and articulatory endocaptors, cutaneous exocaptors; interception *idiotropic vector*) inputs related to a body tilt in the dark (Bronstein, 1999). In their study, Bronstein et al. (1996) demonstrated that when patients with bilateral peripheral labyrinthine lesion are lying at approximately 90° on their right side, they presented an A-effect twice as large as controls. The authors suggested that tilt-mediated effect on the visual vertical is more likely to be of somatosensory rather than vestibular origin. The implication of the somatosensory system in verticality perception was confirmed by studies on SVV in somatosensory deficient populations (Yardley, 1990; Anastasopoulos and Bronstein, 1999). In these studies, the authors found a unilateral loss of A-effect when hemianesthetic patients were lying on the same side as their lesion, and a bilateral loss in patients with severe polyneuropathy. Thus, our results are consistent with those reported in the literature for healthy controls. A striking finding is that the perceived vertical of hEDS patients was not far from the true vertical when the rod was initially oriented to the left side. This finding is also consistent with earlier studies (Yardley, 1990; Anastasopoulos and Bronstein, 1999), and another study conducted by Barra et al. (2010), who found that the A-effect was markedly reduced in patients with somatosensory deficit (i.e., hemiplegia and paraplegia). The explanation advanced is that these patients cannot integrate somatosensory inputs. Hence, their SVV relies mainly on gravitational (vestibular) input. Another interesting finding is that this phenomenon did not appear when the rod was initially right-oriented. A plausible explanation is that, in this condition, the initial orientation of the rod was directly congruent with the joint combination of the idiotropic and gravitational vectors (internal representation of the vertical). This was not the case when

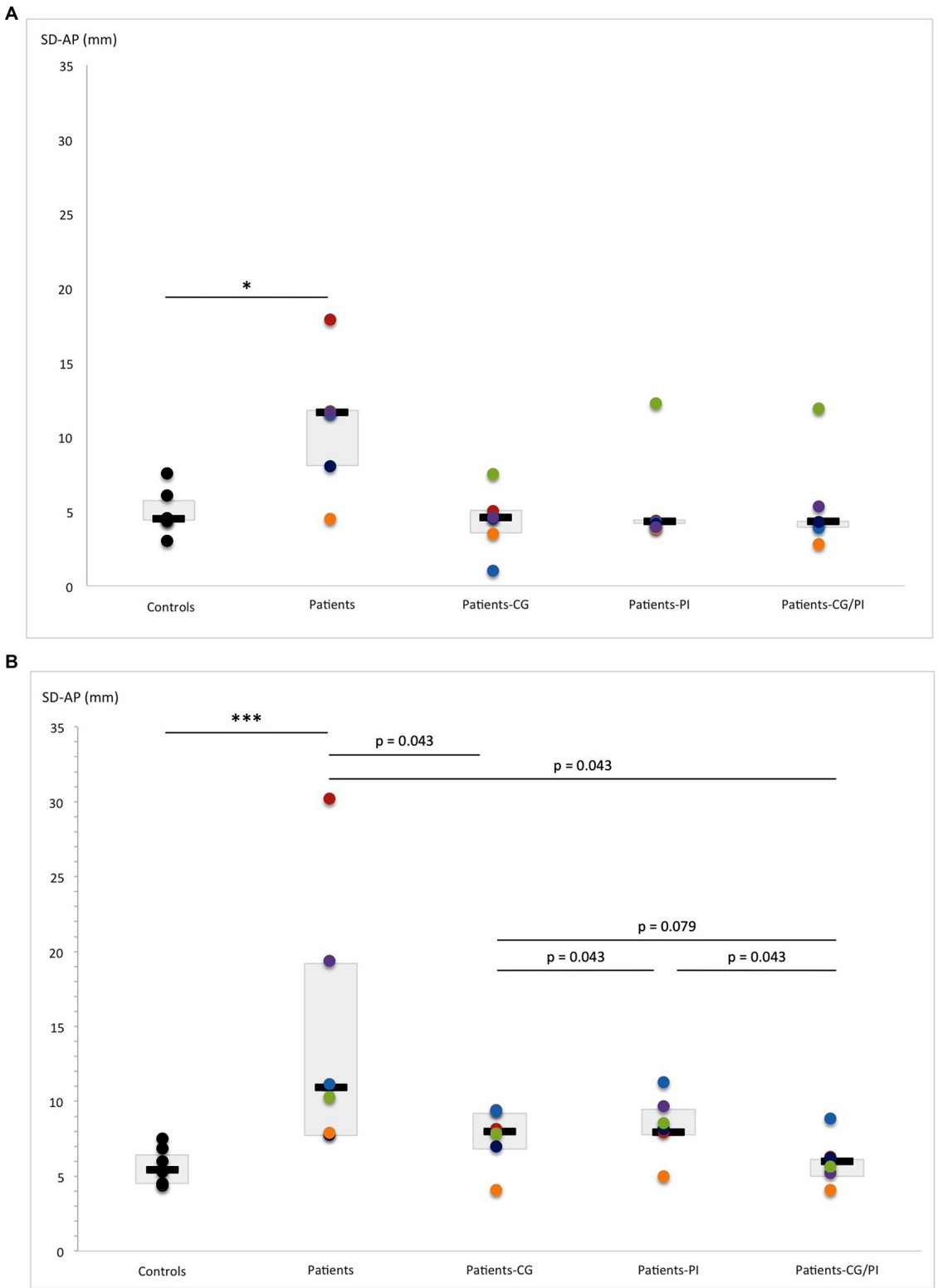

FIGURE 5 | Comparison of SD-AP (standard deviation of anteroposterior center-of-pressure (COP) displacement: mm) obtained by hEDS patients and controls, with and without somatosensory orthoses (CG, compression garments; PI, proprioceptive insoles; CG-PI, both somatosensory orthoses): in **(A)** eyes-open, and **(B)** eyes-closed conditions. Box plots represent median and quartiles, and dots represent performance of each participant as follows: controls: black; patient 1: red; patient 2: green; patient 3: purple; patient 4: light blue; patient 5: orange; patient 6: dark blue. $^{*}p < 0.05$, $^{***}p < 0.005$.

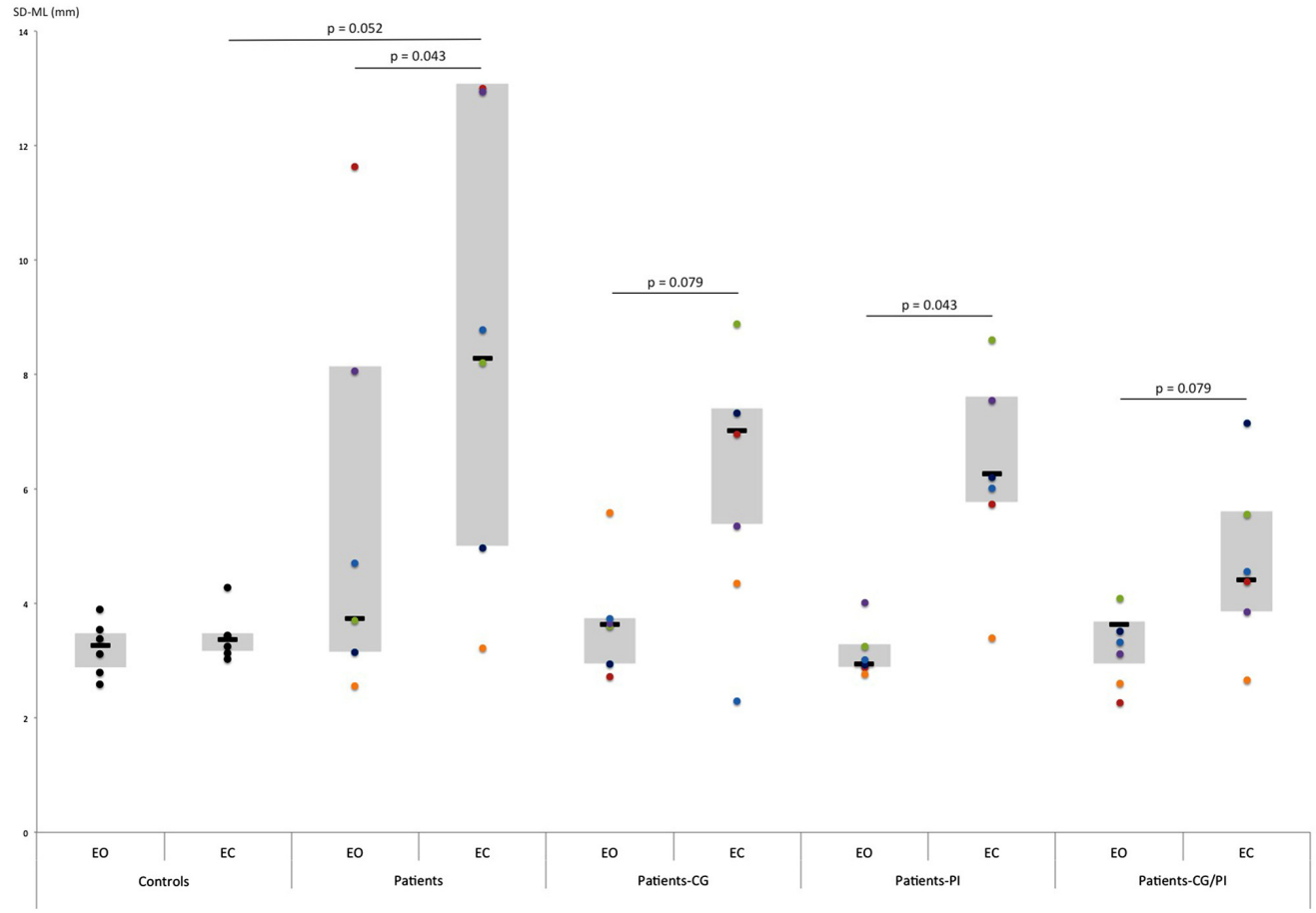

FIGURE 6 | Comparison of SD-ML (standard deviation of mediolateral COP displacement: mm) obtained by hEDS patients and controls, with eyes open (EO) and eyes closed (EC) depending on the somatosensory orthoses worn (CG, compression garments; PI, proprioceptive insoles; CG-PI, both somatosensory orthoses). Box plots represent median and quartiles, and dots represent performance of each participant as follows: controls: black; patient 1: red; patient 2: green; patient 3: purple; patient 4: light blue; patient 5: orange; patient 6: dark blue.

the rod was initially left-oriented (i.e., rotated in a direction opposite to the longitudinal body axis). This may be due to the greater complexity of the task that led patients to preferentially rely on gravitational (vestibular) input. Indeed, to adjust the rod with their verticality perception when it was initially left-oriented, the rod systematically passed through the true vertical. Consequently, one can postulate that the predominance of vestibular input relative to somatosensory input led patients to perceive as vertical the position where the rod converged with gravitational vector. This finding is consistent with the fact that somatosensory input is not absent, but is compromised by damage to its receptors and the poor pressure transmission induced by degraded connective tissue. Hence, we could suggest that somatosensory input is also present, but its contribution to perception could be inhibited or reduced due to its lack of reliability. Finally, taken together, these findings highlight changes in the relative contributions of somatosensory and vestibular inputs to verticality perception in hEDS patients (i.e., central adaptation in somato-vestibular perceptual systems).

Baseline Characteristics of Postural Control in hEDS

In line with previous studies, hEDS patients showed significant difficulties in controlling COP displacements (i.e., increased sway area—confidence ellipse area), especially when visual information was absent (Galli et al., 2011; Rigoldi et al., 2013). Interestingly, controls did not show any difference in their postural stability between EO and EC conditions as observed in other studies (e.g., Lacour et al., 1997; Błaszczyk et al., 2014). This result is not surprising given the fact that the healthy controls included in this study were fairly young (approximately 37 years old) and presented no orthopedic and sensory disorders. In addition, it is also possible that postural parameters used in this study were not the most sensitive to assess the effect of visual removal in healthy young subjects (Prieto et al., 1996). However, our result suggests that hEDS patients (especially the most unstable cases) relied on vision for postural stability. Marigold and Eng (2006) found that the removal of vision in stroke patients increased postural instability, particularly in the ML direction, and all the more so in presence of

postural asymmetry. To explain this observation, the authors suggested that, in stroke patients, the body schema formed by the CNS may lack appropriate somatosensory information due to altered supraspinal centers (Niam et al., 1999). In hEDS patients, impairment of somatosensory receptors would induce a down-weighting of this sensory modality, compensated by an up-weighting of visual modality (slow dynamic; Chiba et al., 2015). The balance between the contributions of each sensory modality is essential in continuous sensory reweighting (fast dynamic), which permits the maintenance of efficient and adaptable postural control (Nashner, 1976; Asslander and Peterka, 2014; Chiba et al., 2015). Furthermore, hEDS patients also had great difficulty in maintaining their ML postural stability when vision was withdrawn. Therefore, ML stability appears to depend upon two factors: reliance on vision and asymmetry in postural control. Our results tend to confirm an overreliance on visual information, but suggest only the presence of postural asymmetry in hEDS patients. It would be interesting to investigate this question in future studies. Regardless of visual condition, the intergroup difference in sway SD was more pronounced in the AP direction. Increased AP sway was also found in stroke patients when somatosensory information was altered (Marigold et al., 2004). To interpret these results, the authors hypothesized that the ability to integrate information from cutaneous sensation can reduce the contribution of ankle proprioception in controlling postural sway. Consequently, the increased AP sway observed in stroke patients in whom ankle proprioception was compromised would be due to their inability to compensate by using cutaneous plantar information (Marigold et al., 2004; Marigold and Eng, 2006). However, the authors found no correlation between cutaneous plantar foot sensation and postural sway. Thus, it is still unclear how somatosensory information affects AP postural sway in stroke patients. This finding, also observed in hEDS patients with specific somatosensory impairment, suggests that AP stability results, at least in part, from accurate somatosensory information. Moreover, a previous study conducted in healthy young subjects showed that the neuromuscular system must allocate 50 percent more effort to control AP stability in the upright stance (Błaszczyk et al., 2014). Thus, the greater AP sway SD in hEDS patients suggests that they may have difficulty generating sufficient neuromuscular effort to maintain their postural stability. However, this hypothesis needs to be confirmed as Błaszczyk et al. (2014) used COP velocity (sway ratio and sway directional index) to quantify postural stability. Technological limitations prevented us from computing this parameter. Hence, we posit that the greater neuromuscular effort allocated for controlling AP stability may produce higher recruitment of the somatosensory system. Therefore, somatosensory impairment could prevent hEDS patients from producing sufficient neuromuscular effort to stabilize their balance in the AP direction. To summarize, specificities of postural control in hEDS patients appear to result from both their somatosensory impairment and the adoption of postural compensatory strategies. This imbalance in multisensory integration complicates control of the upright stance and, therefore, is at least partly responsible for their postural instability. Finally, this process seems to be relatively variable between participants. This finding was not surprising given that considerable variability in clinical expression is commonly observed in hEDS patients. Consequently, it has recently been proposed to consider hEDS as a spectrum of pathogenetically-related manifestations of joint hypermobility (Malfait et al., 2017). Hence, it would be interesting to further investigate the link between severity of clinical expression of hEDS and the evolution of the sensori-motor strategy adopted by these patients.

Effects of Somatosensory Orthoses on Postural Control in hEDS

In hEDS patients (notably the most unstable cases), the wearing of somatosensory orthoses seems to reduce their postural instability (i.e., sway area) to such an extent that their performances became comparable to those of controls in eyes-open condition. However, further investigations will be required to confirm these preliminary observations with a larger sample. Interestingly, this effect turned out to be even more pronounced in the absence of visual information. Wearing the two orthoses in combination seems to help patients stabilize their balance and minimize their AP sway SD. Thus, the combined wearing of orthoses could induce a synergetic effect. Indeed, it seems to improve postural stability more than the wearing of the CG or PI separately in the eyes-closed condition for both sway area and AP sway SD. Therefore, one can reasonably hypothesize that the increased cutaneous plantar sensation applied by pressure on sole receptors from PI could be concurrent with the increased cutaneous sensation and joint position sense promoted by CG. Hence, the combination of CG and PI could possibly enhance the available somatosensory information and, consequently, balance, even without vision. In addition, it is noteworthy that removal of visual information increases the impact of somatosensory orthoses on postural stability, especially in the AP direction. We thus suggest that, in the EO condition, visual information compensates for the lack of somatosensory information. Consequently, the removal of vision obliges patients to rebalance their use of sensory modalities in favor of somatosensory information, thus reinforcing the somatosensory input provided by orthoses. In contrast, ML stability appears to be scarcely affected by the somatosensory orthoses and remained sensitive to visual input. This result supports our previous hypothesis, which assumed that visual information was, at least in part, responsible for ML stability. Besides, our results showed no effect of somatosensory orthoses on overreliance on visual input in hEDS patients. Also, their postural strategy, which consists in compensating their lack of somatosensory information by ample use of visual information, appears to have persisted although the somatosensory input was enhanced. It is thus legitimate to assume that, in order to modify the strategy adopted by these patients, prolonged wearing of somatosensory orthoses would be necessary. The long-term use of somatosensory orthoses would both stimulate and preserve somatosensory receptors and thus develop and consolidate the neural network, supporting a more balanced sensory-motor

strategy. Lastly, unlike previous studies which found no effect for PI and CG, our study suggested their efficacy on postural stability in hEDS patients (Hijmans et al., 2009; Dankerl et al., 2016). Indeed, in healthy controls, it is possible that the improved somatosensory input provided by CG actuate more information than needed to control their posture. Hence, the wearing of CG may induce noise in the somatosensory input in healthy subjects, whereas it helps adjust the somatosensory threshold in hEDS patients (Hijmans et al., 2009). Likewise, PI did not induce any effect on postural stability in healthy subjects, probably because no proprioceptive enhancement was required (Dankerl et al., 2016).

Study Limitations

This pilot study presents a number of limitations. First, the study was conducted on a small sample. Second, the methodology used to investigate SVV could be improved in several respects: (i) the number of trials performed (Piscicelli et al., 2015: a minimum of six trials are required); (ii) the subject's head should be fixed to their support to prevent any speculative movements; (iii) the head could be placed in the same alignment as the body; and (iv) the lying position could also be performed on the left side.

Conclusions

Collectively, the functional explorations performed on hEDS patients, using posturography and SVV, suggest an imbalance in the integration of sensory inputs. The results tended to show that somatosensory impairment modifies both verticality perception (Aubert effect) and postural instability. More specifically, results from postural assessment suggest a re-weighting of multisensory integration in favor of visual input. This compensatory strategy, adopted by the patients in order to maintain their balance, may diminish their adaptability, which could, at least in part, account for their postural instability. In contrast, our findings suggest an enhancement of somatosensory feedback induced by the orthoses, thus facilitating postural control, which in turn tends to become more stable. Lastly, this is the first investigation assessing the effect of somatosensory orthoses in hEDS patients, providing new perspectives for improving medical care. However, the observations in this pilot study need to be confirmed by further investigations with a larger number of subjects. Yet, they strongly suggest that postural and SVV assessments are potentially useful tools for the diagnosis and monitoring of this pathology.

AUTHOR CONTRIBUTIONS

LMD and EGD designed the study. LMD, EGD and PL carried out the experiment. EGD, LMD and CC analyzed the data. EGD and LMD conceived the figures. EGD, LMD, SB, BB and PD interpreted the results and drafted the manuscript. BB, AS and EV screened potential participants to determine their eligibility for the study. All authors revised the manuscript and approved its final version.

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Influence of the Plantar Cutaneous Information in Postural Regulation Depending on the Age and the Physical Activity Status

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The aim was to compare the balance control adaptation to different supporting surfaces depending on the age and the physical activity status. The balance control of two groups of young ($n = 17$) and old ($n = 17$) participants who practiced regular physical activity (active groups) and two groups of young ($n = 17$) and old ($n = 17$) participants who did not practice physical activity (non-active groups) was compared on a firm surface and on a foam surface. The parameters of the center of foot pressure (COP) displacement were compared between the groups. The two older groups were more disturbed than the two younger groups when they stood on a foam surface and there was no difference between active and non-active groups. This result may be linked to the structural and functional involutions of the plantar cutaneous sole and foot that occur with age advancement. The participants' physical activity practice might be not specific enough to generate a more efficient postural adaption to the foam condition for the active groups than the non-active groups within their respective age groups.

Keywords: balance, aging, physical activity, foam, cutaneous, postural control

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INTRODUCTION

The skin is a highly complex interface, innervated by a wide array of specialized sensory neurons sensitive to heat, cold, pressure, irritation, itch and pain (McGlone and Reilly, 2010). Tactile information provides feedback about the environment that contributes to balance control (Massion, 1994; Palluel et al., 2008). Indeed, as the feet interface directly with the ground, the cutaneous afferents, emanating from the soles of the feet, provide sensory information on force distribution during upright stance. Thereby, the plantar sole may be considered as a "dynamometric map" (Kavounoudias et al., 1998). To maintain an upright stance, the central nervous system (CNS) integrates cutaneous afferents with other sensory afferents emanating from visual, vestibular and proprioceptive systems (Massion, 1994). An efficient balance control requires availability and accuracy of the sensory afferents (Maitre et al., 2013a). In the context of exogenous perturbation that alters postural segment positions and compromise upright stance, the CNS triggers compensatory postural strategies (Horak and Nashner, 1986) and sensory reweighting (Oie et al., 2002) to preserve balance. Nevertheless, with increasing age, individuals undergo involutions, which result in balance disorder and reduce the ability to compensate for unreliable or discordant sensory input (Sturnieks et al., 2008). These involutions may decrease the efficiency of the central processing mechanisms (Hay et al., 1996) and the neuromuscular function (Aagaard et al., 2010). Moreover, the

functional ability of the sensory systems may be reduced with increasing age (Sturnieks et al., 2008).

Although aging has deleterious effects on balance control, the iterative stimulations of the visual, vestibular and proprioceptive systems, induced by the regular practice of physical activity, are known to preserve their functional abilities (Gauchard et al., 2001, 2003; Ribeiro and Oliveira, 2007) and can even improve their contribution in the postural regulation (Quarck and Denise, 2005; Jafarzadehpur et al., 2007; Aman et al., 2015). Moreover, the beneficial effects of the physical activity can also contribute to enhance the ability to detect the plantar pressure distributions (Schlee et al., 2007; Li and Manor, 2010).

It is known that foot problems may occur with aging and are associated with impaired balance and functional ability and increased risk of falls (Menz et al., 2006). With increasing age, the foot undergoes structural and functional involutions, which may result in flatter feet, reduced range of motion of the ankle joint, a higher prevalence of hallux valgus, toe deformities and toe plantarflexor weakness, and reduced plantar tactile sensitivity (Scott et al., 2007). Since the physical activity appears to have opposite effects to the age-related involutions in terms of balance control, it would be interesting to clarify the resultant between the benefits induced by the physical activity and the involutions induced by aging in an ecological context. The use of a foam-supporting surface appears to be a relevant tool to challenge balance control and produces a substantial and multi-directional balance perturbation (Patel et al., 2008a,b) to detect age-related changes (Choy et al., 2003) and exercise (Hue et al., 2004) effects on the postural function. Static standing on a foam surface would change the multiple biomechanical variables in the foot, resulting in an alteration of the distribution of the plantar pressures (Chiang and Wu, 1997). Consequently, the aim of this study was to compare the balance control adaptation to different characteristics of the supporting surface (i.e., firm surface and foam surface) between young and old participants in relation to their physical activity status (i.e., active and non-active). We hypothesized that physically active participants would demonstrate better postural control in context of an altered support surface (i.e., foam surface) than non-active participants whatever the age considered.

MATERIALS AND METHODS

Participants

Recruitment for this study involved the participation of 68 women who gave their informed consent. The experiments received the approval of the local committee for the protection of human participants. All the participants were free from any disorder after medical examination (i.e., neurological, motor and metabolic disorders). The cutaneous sensations under the feet were screened with a pencil and participants were free from any foot disorders and lesion of the foot skin support surface. Four groups were made up according to the age (i.e., young and old) and the physical activity status (i.e., active and non-active). The inclusion criteria in each group were previously described (Maitre et al., 2013b). The young active group ($n = 17$; age: 20.5 ± 1.1 years; height: 164.8 ± 5.7 cm; weight: 60.5 ± 7.1 Kg; foot size: 26.0 ± 0.9 cm) was formed with sports science students who have practiced sports (for 3 h or more each week, at least at regional level; i.e., swimming, gymnastics, handball, basketball, athletics). The young non-active group ($n = 17$; age: 20.0 ± 1.3 years; height: 162.3 ± 5.4 cm; weight: 56.2 ± 9.2 Kg; foot size: 25.5 ± 0.8 cm) was formed with students who have not practiced physical activities for at least 3 years. The old active group ($n = 17$, age: 74.0 ± 3.8 years; height: 156.6 ± 4.2 cm; weight: 63.2 ± 6.9 Kg; foot size: 25.6 ± 0.8 cm) was formed with healthy older women who practice (for 3 h or more each week) and have regularly practiced (for at least 3 years) physical activity in a sports club (i.e., gymnastics, walking, dancing, aquarobics). The old non-active group ($n = 17$, age: 74.7 ± 6.3 years; height: 155.8 ± 5.7 cm; weight: 62.4 ± 9.0 Kg; foot size: 25.3 ± 0.7 cm) was formed with healthy older women who have not practiced any physical activity (for at least 3 years) except for daily tasks.

Measurements

The participants were tested on a force platform with three strain gauges (Techno Concept^{TM} Mane, France; 40 Hz frequency, 12 bit A/D conversion) in two bipodal conditions with eyes open (i.e., eyes fixed straight ahead on a target at 1.5 m). They were asked to take an upright stance (i.e., barefoot, 30° of feet angle, inter-malleolar distance of 9 cm), as still as possible, with their arms at their side in a "reference condition" (REF condition, i.e., stance on a firm surface) and in a "Foam condition". During the Foam condition, the participants were asked to take an upright stance on a foam surface (15 mm, 70 $kg.m^{-3}$; TG700, Domyos®, Villeneuve d'Ascq, France) fitted on the force platform to modify the contribution of plantar cutaneous information in postural regulation (Chiang and Wu, 1997). The main objective of the foam condition was to alter plantar cutaneous sensory information in order to determine the reliance attributed to this input in postural regulation. Each condition lasted 20 s. Before the two condition tests, participants benefited from at least 2 min of familiarization with the force platform (as still as possible with eyes open and eyes closed).

The acquisition of the center of foot pressure (COP) displacements was done using Posturowin software (Techno Concept^{TM}, Mane, France) to calculate the parameters that give features of the balance control: the postural stability (i.e., COP surface, mm^2; Caron et al., 2000) and the postural control (i.e., the COP velocity, $mm.s^{-1}$; Caron et al., 2000). The COP velocity may be calculated for the frontal (COP_X velocity, $mm.s^{-1}$) and the sagittal (COP_Y velocity, $mm.s^{-1}$) directions. The smaller these parameters (i.e., velocity and surface) the better the balance control.

Statistical Analysis

Statistical treatment of data was achieved using Statistica software. The one-factor analysis of variance (ANOVA) was used to test the mean differences among the four groups for the

anthropometrical data and for the COP displacement parameters in the reference condition. A three factor ANOVA with repeated measures was used to test the condition (reference and foam condition), the age (young and old) and the activity (active and non-active) effects. The differences among means were tested using the Newman-Keuls *post hoc* analysis when significant main effect was found. The results were considered significant at the level of 5%.

RESULTS

Age and Anthropometrical Data

The results indicated significant age differences between the younger and older groups ($F = 1158.7$, $p < 0.001$). The young active and non-active groups were respectively younger than the old active ($p < 0.001$ and $p < 0.001$) and non-active ($p < 0.001$ and $p < 0.001$). Furthermore, there were significant height differences between the younger participant groups and the older participant groups ($F = 11.8$, $p < 0.001$). The young active and non-active groups were respectively taller than the old active ($p < 0.001$ and $p < 0.01$) and non-active ($p < 0.001$ and $p < 0.01$).

Center of Foot Pressure Displacement Parameters

The COP displacement parameters for the reference and the foam condition is presented in the **Figures 1**–**3**.

Reference Condition

The results concerning the reference condition comparisons indicated that the COP surface ($F = 4.6$, $p < 0.01$) and the COP_Y velocity ($F = 9.3$, $p < 0.001$) differed significantly between the four groups. The *post hoc* analyses indicate that the COP surface (**Figure 1**) and the COP_Y velocity (**Figure 3**) were lower for the young active group than for the two older groups (i.e., the active and non-active groups) in the reference condition. Furthermore, the COP_Y velocity (**Figure 3**) was lower for the young non-active group than the two older groups (i.e., the active and non-active groups).

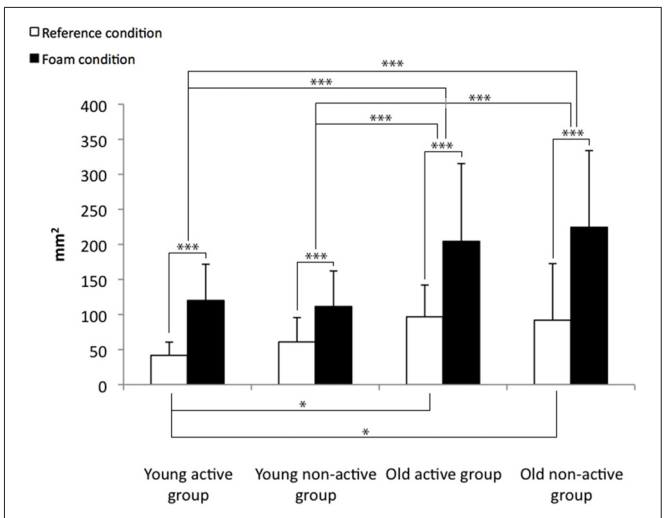

FIGURE 1 | Means and standard deviations for the center of foot pressure (COP) surface for the reference and the foam conditions. $^*p < 0.05$, $^{***}p < 0.001$.

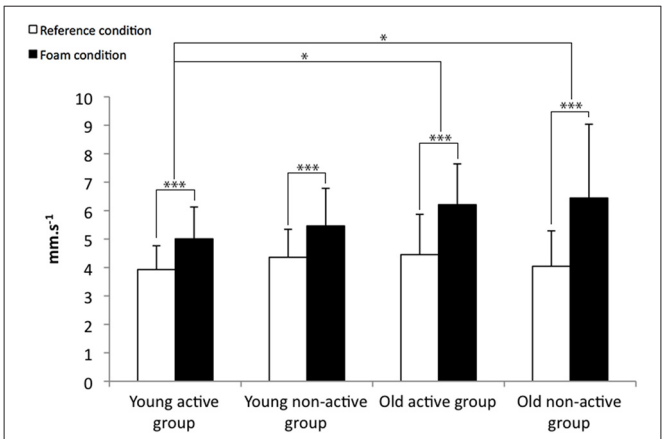

FIGURE 2 | Means and standard deviations for the COP_X velocity for the reference and the foam conditions. $^*p < 0.05$, $^{***}p < 0.001$.

Differences Between the Firm and Foam Condition

All the COP displacement parameters presented significant condition effects for the COP surface ($F = 82.4$, $p < 0.001$), the COP_X velocity ($F = 77.5$, $p < 0.001$) and the COP_Y velocity ($F = 110.4$, $p < 0.001$). These results indicate that the COP displacement parameters increased for all the groups (**Figures 1**–**3**). Otherwise, there is a significant condition × age interaction for the COP surface ($F = 7.5$, $p < 0.01$), the COP_X velocity ($F = 7.5$, $p < 0.01$) and the COP_Y velocity ($F = 25.0$, $p < 0.001$). These results indicate that the balance control was more altered for the older participants than for the younger participants, particularly on the Y-axis. The COP surface and the COP_Y velocity increased less for the two younger groups (i.e., the active and non-active) than for the two older groups

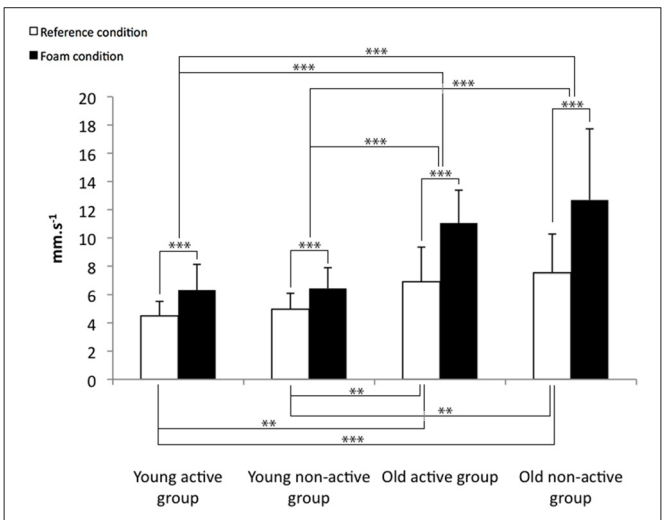

FIGURE 3 | Means and standard deviations for the COP_Y velocity for the reference and the foam conditions. $^{**}p < 0.01$, $^{***}p < 0.001$.

(i.e., the active and non-active; **Figures 1**, **3**). In addition, the COP_X velocity increased less for the young active group than the two older groups (i.e., the active and non-active groups; **Figure 2**).

DISCUSSION

The aim of this study was to compare the balance control adaptation to different characteristics of the supporting surface (i.e., firm surface and foam surface) between young and old participants in relation to their physical activity status (i.e., active and non-active). We did not find support for our hypothesis. The main result of this study indicated that there is no difference between active and non-active participants within their respective age groups for the reference and the foam conditions. The older participants demonstrated less efficient balance control on the firm surface (i.e., reference condition) than the younger participants. Moreover, balance control was disturbed for all the participants when they stood on a foam surface, but the older participants were more disturbed than the younger participants.

As suggested by previous results, aging alters balance control even for a simple postural task (i.e., bipedal stance with eyes open on a firm surface; Choy et al., 2003). In the present study, the COP_Y velocity differences between the younger and older groups indicated that older participants demonstrated a poorer postural control than the younger participants, in the anteroposterior direction. This result is supported by the literature (Du Pasquier et al., 2003) and may be due to the unavoidable involutions of the postural function (i.e., alteration of the sensory, central processing, and muscular functions; Sturnieks et al., 2008). Furthermore, the postural differences between younger and older individuals may be more highlighted in the context of challenged postural task (Maitre et al., 2013a,b).

In the present study, when participants stood on the foam surface the COP surface and the COP velocities on the X and Y axes increase significantly as compared to the firm surface. The disturbing effects of standing on a foam surface have been investigated previously in several studies (Chiang and Wu, 1997; Patel et al., 2008a,b). Static standing on a foam surface would change the multiple biomechanical variables in the foot, resulting in an alteration of the distribution of the plantar pressures (Chiang and Wu, 1997). Foam condition would affect the input of both joint and cutaneous mechanoreceptors. The foam condition would alter the spatial configuration of the cutaneous mechanoreceptors in the foot, thereby reducing the ability to sense pressure distribution and body orientation (Chiang and Wu, 1997). Moreover, the mechanical properties of the compliant surface may also alter the postural behavior. The elastic characteristics of the foam enable smaller opposing mechanical resistance than a firm surface that could cushion the foot movements produced by the ankle musculature, which reduces the motor output generated for postural stabilization (Horak and Hlavacka, 2001; Patel et al., 2008b). Consequently, the balance control is altered on a foam-supporting surface.

Relative to the reference condition, the COP surface and the COP_Y velocity increased significantly more for the older groups than the younger groups while standing on the foam. This result corroborates previous work (Choy et al., 2003), which indicated that older participants demonstrated poorer balance control on a foam-supporting surface than younger participants. The poorer postural control achieved by the older groups compared to the younger groups could be explained in two ways. Firstly, it could be linked to a plantar tactile sensitivity malfunction in the older groups in comparison with the younger groups. Although participants of this study were free from any foot disorders and lesion of the foot skin support surface, we cannot exclude that the plantar tactile sensitivity differs between the younger and older groups. Indeed, it is known that foot and ankle undergo involutions with aging that may alter balance function (Menz et al., 2006). Older individuals may exhibit flatter feet, reduced range of motion of the ankle joint, a higher prevalence of hallux valgus, toe deformities and toe plantarflexor weakness, and reduced plantar tactile sensitivity (Perry, 2006; Scott et al., 2007). Cutaneous mechanoreceptors decrease in number and have a progressive structural deterioration with ageing (Shaffer and Harrison, 2007; Decorps et al., 2014). These elements may contribute to decrease the ability of the older groups to accurately detect foot pressure distribution and correctly regulate posture (Menz et al., 2006). Indeed, several authors (Simmons et al., 1997; Horak and Hlavacka, 2001) showed that when somatosensory information is reduced postural control might be altered. Secondly, the poorer postural control achieved by the older groups compared to the younger groups could be linked to the inability of the older groups to take advantage of the non-altered sensory information as effectively as the younger groups. Indeed, in a context of a sensory alteration, the balance control mechanism requires the availability as well as the accuracy of information emanating from the non-altered sensory systems to enable the CNS to integrate the information and to initiate a compensatory motor strategy limiting the postural disturbance related to the foam surface (Massion, 1994; Peterka, 2002). When cutaneous information is reduced, individuals are compelled to rely more on other sensory systems (i.e., visual, vestibular and proprioceptive systems) to maintain their stability (Lord and Menz, 2000; Horak and Hlavacka, 2001; Paillard et al., 2007). Although, Meyer et al. (2004) suggested that, in a context of plantar cutaneous anesthesia, plantar sensation is of moderate importance for the maintenance of normal standing balance, the impact of reduced plantar sensitivity on postural control increases with the loss of additional sensory modalities. With increased age, there is a progressive loss of functioning of visual, vestibular and proprioceptive systems, which can contribute to balance deficits (Sturnieks et al., 2008). In addition, the ability to correctly reweight sensory information may be altered with aging (Horak et al., 1989). Thereby, in the present study, the older participants may be less able to counteract postural disruption due to the foam-supporting surface than the younger groups.

The main result indicated that there is no difference between active and non-active participants within their respective age

groups for the reference and foam conditions, yet, previous studies have demonstrated that regular practice of physical activity may enhance balance control for young (Kiers et al., 2013) and old (Howe et al., 2007) individuals. In the present study, several elements could explain this lack of significant results. Firstly, as suggested by Kiers et al. (2013), the reference condition (i.e., bipedal stance with eyes open on a firm surface) probably constitutes a too simple postural task to produce evidence of differences between active and non-active participants. Secondly, the active participants might have improved their ability to maintain dynamic balance more than static balance with their physical practice. Indeed, the ability to maintain balance is likely to be specific to the training tasks (Hrysomallis, 2011). In this study, the postural tasks were statics and the active participants mainly practiced dynamic physical activities. Thirdly, the rubber of foam used in the foam condition was probably too thin to sufficiently challenge the balance control in order to demonstrate difference in relation to the physical activity status. Patel et al. (2008a,b) have suggested that thin rubber of foam enables closer contact with the rigid surface beneath the foam, which allows plantar tactile sensory feedback and ankle movements to be more effective. In addition, the deformation properties of the foam surface matched to the participants' weight (Gosselin and Fagan, 2015). The heavier participants might be in closer contact with surface beneath the foam. In the present study, the foam characteristics were relevant to highlight differences in relation to the age, but probably not appropriate to highlight difference in relation to the physical activity status. Caution should be taken when using foam pads on force platforms during balance assessments. To evidence a postural control difference in relation to the physical activity status, the postural task difficulty has to be accurately calibrated, since the foam properties (Patel et al., 2008a,b) and the anthropometric characteristics of the participant (Gosselin and Fagan, 2015) may alter posturographic data.

This study suggests that the ability to detect the distribution of the plantar pressure contributes to the balance control. Although foot problems may occur with increasing age (Menz et al., 2006), previous studies have demonstrated that augmenting tactile sensory information from the sole of the foot may improve balance in older people (Palluel et al., 2008). Furthermore, the regular practice of physical activity may improve the tactile sensitivity (Schlee et al., 2007; Kerr et al., 2008; Li and Manor, 2010; Kattenstroth et al., 2013). Nevertheless, in the present study, the effect of the regular practice of physical activity appeared to be not strong enough and/or appropriate to generate postural difference between active and non-active participants within their respective age groups. It is known that physical activity induces specific postural adaptation (Hrysomallis, 2011). In the present study, it could be construed that the characteristics of the physical activities practiced by the participants might not be specific enough to generate a more efficient postural adaption to the foam condition for the active groups than the non-active groups within their respective age groups (Paillard et al., 2010). Most of the participants in the active groups do not practice barefoot physical activities that specifically stimulate cutaneous mechanoreceptors. Specific training that stimulates plantar cutaneous sensory mechanoreceptors improves postural function (Morioka et al., 2011). Practiced barefoot, physical activity could enhance plantar cutaneous sensitivity (Schlee et al., 2007). Hence, the data of the present study suggest that the practice of barefoot exercises could be recommended to improve efficiency of the postural function on altered support surface.

CONCLUSION

This study corroborates that, with increased age, there is an alteration of the contribution of plantar cutaneous information. This loss of functioning was present for a simple postural task (i.e., upright stance with eyes open on a firm surface) and for a more complex postural task (i.e., upright stance with eyes open on a foam surface). Relative to the reference condition, when the cutaneous sensory information was altered by the use of a foam-supporting surface, the balance control was more disrupted for the older participants than the younger participants. The inability to counteract this sensory alteration might be linked to the unavoidable structural and functional involutions of the plantar cutaneous sole and foot that occur with age advancement. The main result of this study suggests that there is no difference between active and non-active participants within their respective age groups in the foam conditions. Physical activity traditionally practiced with shoes might not sufficiently stimulate the cutaneous mechanoreceptor to counteract the effects of aging on the plantar skin sensitivity. In order to extend the analysis of the effects of physical activity on the cutaneous sensitivity in relation to the age and the physical activity status, participants should be compared according to the type of sports (i.e., with shoes or barefoot) and the cutaneous sensitivity should be analyzed by the use of specific tests (e.g., vibrotactile or monofilament sensitivity). Identifying influence of barefoot physical activity would enable clinician to prevent loss of plantar skin sensitivity and so improve postural control in older people.

AUTHOR CONTRIBUTIONS

JM and TPP contributed to the conception and design of the work; and the acquisition, analysis, and interpretation of data.

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frontiers in Human Neuroscience

METHODS
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Sample Entropy, Univariate, and Multivariate Multi-Scale Entropy in Comparison with Classical Postural Sway Parameters in Young Healthy Adults

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The present study aimed to compare various entropy measures to assess the dynamics and complexity of center of pressure (COP) displacements. Perturbing balance tests are often used in healthy subjects to imitate either pathological conditions or to test the sensitivity of postural analysis techniques. Eleven healthy adult subjects were asked to stand in normal stance in three experimental conditions while the visuo-kinesthetic input was altered. COP displacement was recorded using a force plate. Three entropy measures [Sample Entropy (SE), Multi-Scale Entropy (MSE), and Multivariate Multi Scale Entropy (MMSE)] describing COP regularity at different scales were compared to traditional measures of COP variability. The analyses of the COP trajectories revealed that suppression of vision produced minor changes in COP displacement and in the COP characteristics. The comparison with the reference analysis showed that the entropy measures analysis techniques are more sensitive in the incremented time series compared to the classical parameters and entropy measures of original time series. Non-linear methods appear to be an additional valuable tool for analysis of the dynamics of posture especially when applied on incremental time series.

Keywords: center of pressure, sample entropy, multi-scale entropy, multivariate multi-scale entropy, visuo-kinesthetic effect

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INTRODUCTION

Postural control is of paramount importance to ensure safe completion of complex tasks such as locomotion or simpler tasks such as standing. Postural control in healthy subjects is strongly affected by spatial orientation (Isableu et al., 1998) which in turn is based on both vestibulo-proprioceptive and visual cues (Asch and Witkin, 1948). Some subjects show an increased visual dependency (Guerraz et al., 2001) and therefore closing the eyes or introducing distorted visual feedback (e.g., wearing translucent goggles) increases the difficulty of standing tasks (Bronstein, 1986). A diminished postural control may result in a loss of equilibrium and consequently in falling (Carroll and Freedman, 1993; Collins and De Luca, 1993). This diminution may either be

due to normal ageing (Pascolo et al., 2005, 2006) or due to a neurodegenerative disorder such as Parkinson's disease (Sabatini, 2000; Duarte and Zatsiorsky, 2001).

Usually, the quantification of postural control is included in clinical assessments but this strongly depends on the technology available. Either the postural control is rated based on clinical rating scales (Bloem et al., 2016) e.g., Tinetti Balance Scale, Rating Scale for Gait Evaluation, or on specific equipment such as force plates (Yamada, 1995; Newell et al., 1997) to measure body sway. The displacement of the center of pressure (COP) (the point of application of the vertical resultant force acting on the body from the supporting surface, dos Santos, 2008) is commonly measured when evaluating the postural control of a person (Carroll and Freedman, 1993; Collins and De Luca, 1993). The COP is highly irregular and non-stationary which has led multiple studies to characterize the functional effects of conditions such as disease, aging, cognitive task and visual perception on the postural stability (Ramdani et al., 2009).

Techniques for quantifying the displacement of the COP vary from descriptive measures (mean or standard deviation) to techniques taken from signal processing (root-mean-square and frequency analyses). The non-linear deterministic methods allow for the exploration of the randomness or predictability of the COP fluctuations. Those methods were used in studies investigating the deterministic features of COP dynamics (Myklebust et al., 1995; Riley et al., 1999; Doyle, 2004; Doyle et al., 2005), and their potentially chaotic behavior (Cavanaugh, 2005; Costa et al., 2005; Roerdink et al., 2006; Cavanaugh et al., 2007) but also on the quantification of the complexity of COP time series (Ramdani et al., 2009). Entropy family, as a non-linear measure of time series, has been widely applied to study features of COP displacement in different situations.

Entropy family quantifies the regularity (predictability) of a signal, with predictable (e.g., periodic) signals resulting in low entropy, or completely unpredictable signals, resulting in high entropy. A more regular COP pattern indicates that the postural behavior is more rigid (Donker et al., 2007), suggesting that the regularity of COP displacements and the amount of attention paid to postural control are dependent (Donker et al., 2007; Vuillerme and Nafati, 2007). Complexity on the other hand is associated with meaningful structural richness (Grassberger, 1991) incorporating correlations over multiple spatio-temporal scales. A decrease of complexity is related with a functional decline; and a more rigid postural behavior results in dysfunctional balance control during perturbations (Schniepp et al., 2013).

For instance, the Sample Entropy (SE) (Roerdink et al., 2006) has been used to investigate the effect of visual perception (Sabatini, 2000), cerebral concussion (Cavanaugh, 2005; Cavanaugh et al., 2007) and cognitive tasks (Wei et al., 2012) on postural dynamics. Multi-scale Entropy (MSE) and Multivariate Multi-Scale Entropy (MMSE) (Ahmed and Mandic, 2011) are both able to represent the complexity of non-linear time series in different scales (Ahmed and Mandic, 2011). They measure and quantify the intrinsic complexity (Costa et al., 2005) of single and multi-channel signals and then provide a meaningful measure of regularity in biological signals as e.g., COP measurements (Ahmed and Mandic, 2012).

To extract additional features of the COP displacement, the analysis of incremented time series of original signals may be useful (Ramdani et al., 2009) and this approach provides extra information compared to other approaches (Huang et al., 2013). Incremented time series, equivalent to the velocity of the COP displacements have been shown to be effective in the analysis of physiological signals (Costa et al., 2007). In this study two types of incremented time series were computed and studied, the relationship between anterior-posterior (A/P) and medio-lateral (M/L) COP displacement while using univariate and bivariate entropy measures. Although previous studies (Costa et al., 2007; Ramdani et al., 2009) applied incremental time series in their COP analysis, no proof has been provided to determine its performance and advantage.

The working hypothesis was to test if non-linear entropy family methods quantify COP displacement better when using incremented time series during three standing conditions with varying visuo-kinesthetic input. In addition to the entropy measures, classical posturographic methods were also used to assess the COP displacement. The classical methods were then compared with the entropy measures of the original time series.

METHODS EXPERIMENTS AND SUBJECTS

Eleven healthy subjects (Mean age: 25.6 years; Mean bodyweight 73.76 kg) voluntarily participated in the experiment after signing a statement of informed consent as required by the Helsinki declaration and the Paris-Saclay STAPS (Sciences and Techniques of Sports and Physical Activities) local Ethics Committee. Subjects stood upright looking forward, on a force plate (AMTI OR6001200, Watertown, MA, USA) with their arms hanging loosely by their sides and feet separated by a self-selected distance (typically approximately 10 cm) for 30 s. Foot position was marked with an erasable marker to ensure the position was maintained if subjects needed to step off the force plate between trials or conditions. Subjects performed three trials of stationary bipedal standing in three different sensory conditions, eyes open (EO), eyes closed (EC) and perturbed vision (PV) by wearing translucent goggles, resulting in a total of nine trials. The trials for each condition were averaged accordingly.

In the PV condition, even though the eyes were opened, the visual input did not constitute a valid and meaningful source (i.e., neither self-motion nor self-orientation cues) of spatial referencing for postural balance, and cannot be integrated together with proprioception in an optimal manner (Jeka et al., 2000; Oie et al., 2001). Conditions were presented in a random order for each participant. Subjects were instructed to stand as still as possible with either the eyes open, eyes closed or wearing translucent goggles. The COP trajectories were recorded in both A/P and M/L directions at a sampling frequency of 250 Hz as shown in **Figure 1**. Rest periods of 60 s were provided between trials. The resulting data was low-pass filtered at 5 Hz using an 8th order Butterworth filter with a zero-phase digital filter (filtfilt.m) in the Matlab (MathWorks, Inc., USA) environment.

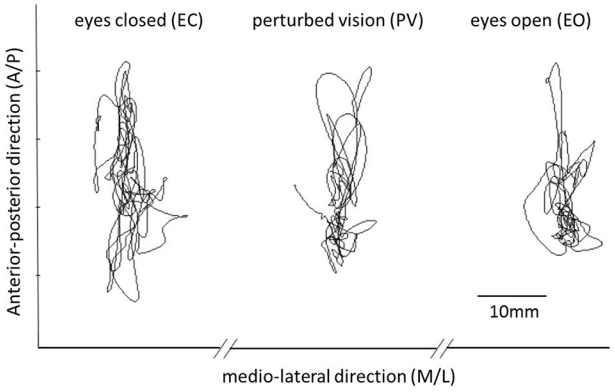

FIGURE 1 | This figure shows representative time series of COP data in each of the three experimental conditions (EO, EC, PV). Differences between conditions are explored using both classical parameters and entropy based methods.

ANALYSIS

Classical Methods

To quantify differences between the conditions (EC, PV, EO), the following variables were calculated from the postural sway: the root-mean square (RMS), mean velocity (MV), path length (PL), mean frequency (MF) and the surface area (SA) of COP displacements in A/P and M/L directions. The RMS was defined as the quadratic mean and is a measure of the postural sway displacement in both the A/P and M/L directions [mm]. The mean velocity defines the mean velocity of the postural sway representing the path length divided by the trial duration [mm/s]. The path length was defined as the length of the COP trajectory displacements on the platform surface [mm]. The MF is the mean frequency of the power spectrum of the postural sway in both the A/P and M/L directions. The SA is the surface area given by the 95% confidence ellipse representing the smallest ellipse that covers 95% of the points of the postural sway [mm^2] (Paillard et al., 2006).

Non-linear Methods

Three non-linear methods were used to measure the regularity of COP signals and compare their sensitivity between the incremented time series and the original time series. Sample Entropy is essentially a negative logarithm of conditional probability of the sequences of a data vector. If a vector of length N has repeated itself in tolerance γ for m points, it will also do so for m+1 points. The conditional probability means the ratio of counts of repeated time of m+1 points to that of m points. Thereby, high SE arises from a low probability of repeated sequences in the data. Higher SE means lower regularity and more complexity in the data. On the basis of SE, MSE is a method to evaluate the complexity of signals over different time-scales while MMSE generalizes the analysis to the multivariate case (Wei et al., 2012).

The SE is mathematically computed as follows:

First, from a vector $X_N = \{x_1, x_2, \cdots, x_N\}$, two sequences of m consecutive points $X_m(i) = \{x_i, \ldots, x_{i+m-1}\}$ and $X_m(j) = \{x_j, \ldots, x_{j+m-1}\}$ $(i, j \in [1, N-m], i \neq j)$ are selected to compute the maximum distance and compared to tolerance γ for repeated sequences counting, according to Equation (1). For the sequence $X_m(i)$, its count is defined as $B_i^m(\gamma)$.

$$d\left[X_m(i), X_m(j)\right] = \max[|x_{i+k}, x_{j+k}|] \leq \gamma(k \in [0, m-1], \gamma \geq 0) \quad (1)$$

1 where the tolerance γ equals to 0.1∼0.2*SD (Richman and Moorman, 2000), SD is the standard deviation of X_N.

$B^m(\gamma)$ is the average amount of $B_i^m(\gamma)$ for $i \in [1, N-m]$, and $B^{m+1}(\gamma)$ is the average of $m+1$ consecutive points. Thus, SE is obtained using the Equation (2).

$$SE(N, m, \gamma) = -ln\left[\frac{B^{m+1}(\gamma)}{B^m(\gamma)}\right] = -ln\left[\frac{(N-m-1)^{-1}\sum_{i=1}^{N-m-1} B_i^{m+1}(\gamma)}{(N-m)^{-1}\sum_{i=1}^{N-m} B_i^m(\gamma)}\right] \quad (2)$$

MSE has a coarse-grain procedure for the data vector X_N before SE computation, which is the main computation difference between MSE and SE. Due to this procedure, MSE is able to measure the distribution of complexity on multiple time-scales, which is fundamentally different from SE. The coarse-grain procedure averages each τ points to generate a new sequence from the data. It is similar to a non-overlapping mean filter with a window length τ. Changing τ leads to sequences in different time-scales. Higher τ means lower frequency components in the sequences. MSE generates the complexity distribution of the data through the sequences in different time-scales, and MSE is equal to SE when $\tau = 1$. The parameter m is the length of repeated mode in the data vector, which is defined by the data itself; and the tolerance γ decides the limitation condition of repeated mode. In biological time-series analysis, m is typically set at 2 or 3 and γ is 0.15*standard deviation (SD) (X_N) (Costa et al., 2005).

To calculate MSE, the following steps have to be computed: the first step is to form a sequence $y_j^{(\tau)}$ based on the scale factor τ, which can be found using the Equation (3):

$$y_j^{(\tau)} = \frac{1}{\tau}\sum_{i=(j-1)\tau+1}^{j\tau} x_i \quad (3)$$

The equation to compute MSE can be expressed as follows:

$$MSE(N, m, \tau, \gamma) = -\ln\left[\frac{A^{m+1}(\gamma)}{A^m(\gamma)}\right] \quad (4)$$

where both $A^m(\gamma)$ and $A^{m+1}(\gamma)$ are the average repeated amount of two *sequences* $Y_m(i)$ and $Y_{m+1}(i)$ [see Equations (1, 2)] to calculate $B_i^m(\gamma)$) and tolerance γ is also for the formed sequences $y_j^{(\tau)}$ with the length $N' = N/\tau \in [10^m, 30^m]$ (Pincus and Goldberger, 1994). Therefore, τ is defined by length of N of X_N and m. For example, N = 10,000 and m = 2,500 as the median of $[10^2, 30^2]$ could be selected to calculate the τ_{max} = 10,000/500 = 20 and $\tau \in [1, 20]$.

MMSE provides a complexity distribution too, not for a data vector but for the matrix vector from multichannel or multivariate data, which is more adaptive to multi-dimension or multi-parameter time series that are routinely measured in experimental and biological systems.

Given the matrix $X(p, N)$, p is the number of channels or variates, N is the original length, so that the first step for this matrix is just transforming it into a new matrix $X'(p, N')$, based on scale factor τ regardless of m, which gives the new matrix in a new time scale like the coarse-grain procedure in MSE. In the second step, m and ε are extended to an embedding vector and a time lag vector for a p -variate embedded reconstruction respectively. For the consistence of each variate in the matrix, the values of m and ε are identical, e.g., $m =$ [3,3,3]; $\varepsilon = [1, 1, 1]$. That means three MSE computations with the embedding dimension $m = 3$ for three variates and the time delay $\varepsilon = 1$. The time delay $\varepsilon = 1$ is the best choice when the minimum embedding dimension for each of the time series is 3 (Cao et al., 1998).

In practice its first step is to define temporal scales of the increased length by coarse-graining the *p-variate* $\left\{x_{k,i}\right\}_{i=1}^{N}, k = 1, 2, \ldots, p$. For a scale factor τ, the multivariate coarse-grained time series $y_{k,j}^{(\tau)}$ is calculated [see Equation (5)], where $1 \leq j \leq N/\tau$.

$$y_{k,j}^{(\tau)} = \frac{1}{\tau} \sum_{i=(j-1)\tau+1}^{j\tau} x_{k,i} \tag{5}$$

In order to obtain the MMSE, the multivariate embedded vectors $Y_m(i) \in \mathbb{R}^p$ must be constructed firstl, which is shown as:

$$\begin{aligned} Y_m(i) = [&y_{1,i}, y_{1,i+\varepsilon_1}, \ldots, y_{1,i+(m_1-1)\varepsilon_1}, y_{2,i}, y_{2,i+\varepsilon_2}, \ldots, \\ &y_{2,i+(m_2-1)\varepsilon_2}, \ldots, y_{p,i}, y_{p,i+\varepsilon_p}, \ldots, y_{p,i+(m_p-1)\varepsilon_p}] \end{aligned} \tag{6}$$

where $1 \leq i \leq \mathrm{N}' - n$ and $\mathrm{N}' = N/\tau$, $n = max\{M\} \times max\{\varepsilon\}$. $M = \left[m_1, m_2, \ldots, m_p\right] \in \mathbb{R}^p$ is the embedding vector, while $\varepsilon = \left[\varepsilon_1, \varepsilon_1, \ldots, \varepsilon_p\right]$ is the time lag vector and $M = \sum_{k=1}^{p} m_k$. Then the maximum norm is defined by Chebyshev distance between any two composite delay vectors $Y_m(i)$ and $Y_m(j)$, that is expressed as:

$$\begin{aligned} d\left[Y_m(i), Y_m(j)\right] = &max_{l=1,\ldots,m} \\ &\left\{\left|y\left(i + l - 1\right) - y(j + l - 1)\right|\right\} \end{aligned} \tag{7}$$

where $j \in [1, \mathrm{N}' - n], j \neq i$. For a given $Y_m(i)$, $\mathrm{P_i}$ is the number of vector pairs that meets $d\left[Y_m(i), Y_m(j)\right] \leq \gamma$, so that $A_i^m(\gamma) = P_i/(\mathrm{N}' - n - 1)$, where $n = max\{M\} \times max\{\tau\}$. And for all i, $A^m(\gamma) = (\mathrm{N}' - n)^{-1} \sum_{i=1}^{\mathrm{N}'-n} A_i^m(\gamma)$.

Finally, the average similarity $A^m(\gamma)$ over all $i \in [1, \mathrm{N}' - n]$ and the $A^{m+1}(\gamma)$ over all $i \in [1, \mathrm{p} * (\mathrm{N}' - n)]$ are used to gain the MMSE, as shown in Equation (8).

$$MMSE(N', M, \tau, \gamma) = -ln\left[\frac{A^{m+1}(\gamma)}{A^m(\gamma)}\right] \tag{8}$$

where γ is the tolerance level and N' is the length of the time series $y_{k,j}^{(\tau)}$.

The embedding vector $M = \left[m_1, m_2, \ldots, m_p\right] \in \mathbb{R}^p$ and the tolerance level γ in MMSE have the equivalent values with parameters m and γ in MSE (Wei et al., 2012).

The three non-linear entropy methods are effective to measure complexity of time series, specifically the SE for the univariate vector, MSE for the univariate vector in multiple time-scale, and MMSE for the multivariate matrix in multiple time-scale respectively. Moreover, it is crucial to have the original time series filtered as all entropy methods are extremely sensitive to random noise. Therefore, our COP data was filtered by a low-pass filter before the computation of entropy.

Incremental Time Series

The postural sway was analyzed in the A/P and the M/L direction, COP (A/P) and COP (M/L) respectively. Additional to the original COP data, its increments were calculated 2-fold: First $\Delta_{inc}\mathrm{x} = [\mathrm{x(t + 1) - x(t - 1)}]$, defined as the ***Increment***; second $\Delta_{diff}\mathrm{x} = [\mathrm{x(t + 1) - x(t)}]$, defined as ***Difference***. Since mean velocity is a classical parameter of COP estimation, the increments of original COP data, as its equivalent velocity, were created from the original data to remove long-range correlations and avoid potential masking of the complexity of the COP time series.

Simulation

In the simulation, both the original and incremental time series are used to evaluate differences by means of SE, MSE, and MMSE. White noise and 1/f noise are prominent signals to test entropy family measures because of their short-term and long-term correlated properties (Richman and Moorman, 2000; Costa et al., 2005; Ahmed and Mandic, 2011; Wei et al., 2012). To illustrate the behavior of incremental time series and its influence on entropy measures, we considered six time series with a length of $N = 20{,}000$ (meeting the range minimum $10^m \times \tau_{max}$ when $m = 3$ and $\tau_{max} = 20$) of each data vector corresponding to 80 s (near to the sum of 30 s in trail and 60 s in rest) of data acquisition at 250 Hz: 1/f noise, 1/f noise ***Increment***, 1/f noise ***Difference***, white noise, white noise ***Increment***, white noise ***Difference***. ***Increment*** and ***Difference*** are computed from both the 1/f noise and the white noise data through $\Delta_{inc}\mathrm{x} = [\mathrm{x\,(t + 1) - x\,(t - 1)}]$ and $\Delta_{diff}\mathrm{x} = [\mathrm{x(t + 1) - x(t)}]$ respectively. MSE and MMSE were calculated with m = 2 and 3, $\gamma = 0.15$*SD (Costa et al., 2005) and a scale factor of $\tau = 1$ to 20 (**Figure 2**) (meeting the range minimum, Richman and Moorman, 2000).

The results of the simulations show decreasing complexity with increasing scale factor except for the 1/f noise series. To understand the differences between $m = 2$ & 3 on the entropy values, **Table 1** shows individual differences as a function of the scale factor for the six considered time series. The simulation results show differences between scale factors 11 and 15 with an absolute deviation of 0.01, indicating that SE is more sensitive on a larger scale with a pattern length of $m = 3$ (**Figure 2**). The MMSE analysis of bivariate time series shows similar patterns but larger entropy values in the correlated bivariate time series (**Figure 3**). When computing MSE and MMSE for short-term

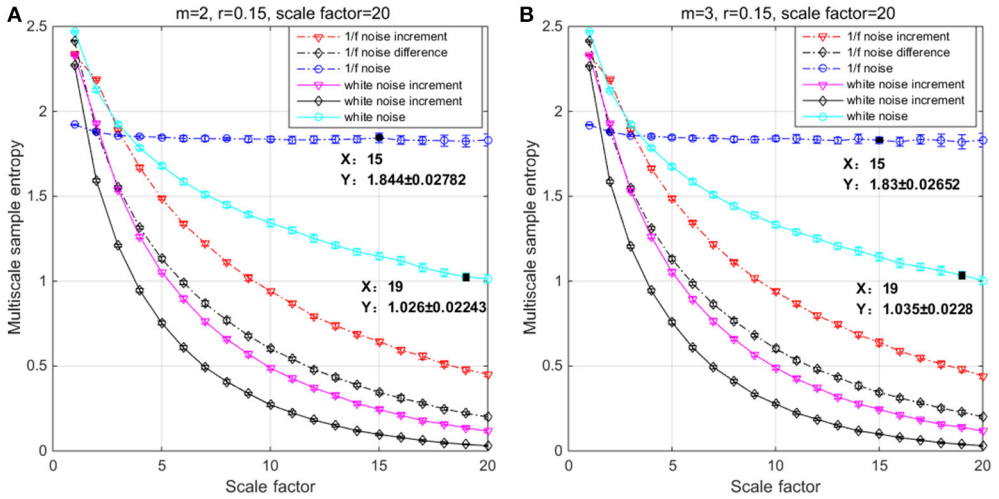

FIGURE 2 | Multiscale entropy (MSE) analysis of white noise, 1/f noise and their Increment and Difference using (A) $m = 2$, $r = 0.15$, and $\tau = 20$ and **(B)** $m = 3$, $r = 0.15$, and $\tau = 20$. Each channel has 20 000 data points, and the plots represent an average of 20 independent groups and error bars the standard deviation (SD).

TABLE 1 | Differences between the SE calculated with $m = 2$ and $m = 3$ for different scales and noises.

Scale factor	1/f noise			White noise		
	Original	Increment	Difference	Original	Increment	Difference
1	0.0010	0.0020	0.0010	0.0000	0.0010	0.0050
2	−0.0020	0.0010	0.0010	0.0010	0.0020	0.0070
3	0.0010	0.0000	−0.0015	0.0010	0.0060	0.0060
4	−0.0020	0.0050	0.0020	0.0010	−0.0010	0.0013
5	0.0020	0.0000	0.0020	0.0040	0.0000	−0.0036
6	−0.0020	−0.0050	0.0057	0.0000	0.0038	0.0010
7	−0.0030	0.0050	0.0045	0.0040	−0.0024	−0.0030
8	0.0020	0.0010	0.0025	0.0080	−0.0010	−0.0025
9	0.0050	0.0010	−0.0027	0.0030	0.0042	0.0056
10	−0.0030	0.0019	0.0000	0.0011	−0.0021	−0.0052
11	−0.0070	0.0028	0.0074	−0.0091	0.0028	0.0017
12	0.0000	−0.0039	−0.0011	−0.0010	0.0000	−0.0046
13	0.0080	−0.0064	0.0000	0.0050	0.0070	−0.0020
14	−0.0010	0.0038	0.0035	−0.0050	0.0018	0.0010
15	0.0140	0.0051	−0.0090	0.0030	−0.0040	−0.0024
16	0.0090	0.0059	−0.0080	0.0015	−0.0070	0.0093
17	−0.0060	0.0010	−0.0019	−0.0030	−0.0050	−0.0022
18	−0.0030	0.0030	−0.0045	−0.0013	0.0022	0.0020
19	0.0030	−0.0070	−0.0059	−0.0090	−0.0035	−0.0038
20	0.0000	0.0011	−0.0017	0.0010	−0.0016	−0.0020

correlated signals (white noise), a reduction in complexity occurs with larger scale factors in contrast to long-term correlated signals (1/f noise).

When computing MSE and MMSE for incremented time series with white noise and 1/f noise, reductions of complexity with increasing scales occur. The incremental time series removes the long-term correlated components from the original time series and represent short-term complexity. Compared to the MSE, the MMSE analysis shows lower entropy values per scale and seems to detect signal divergence faster and can, therefore, be considered more suitable for complexity detection.

Based on the simulation results indicating that SE is more sensitive on larger scales, while m was set to three, $\gamma = 0.15$*SD and a scale factor ranging from 1 to 20. A larger scale factor

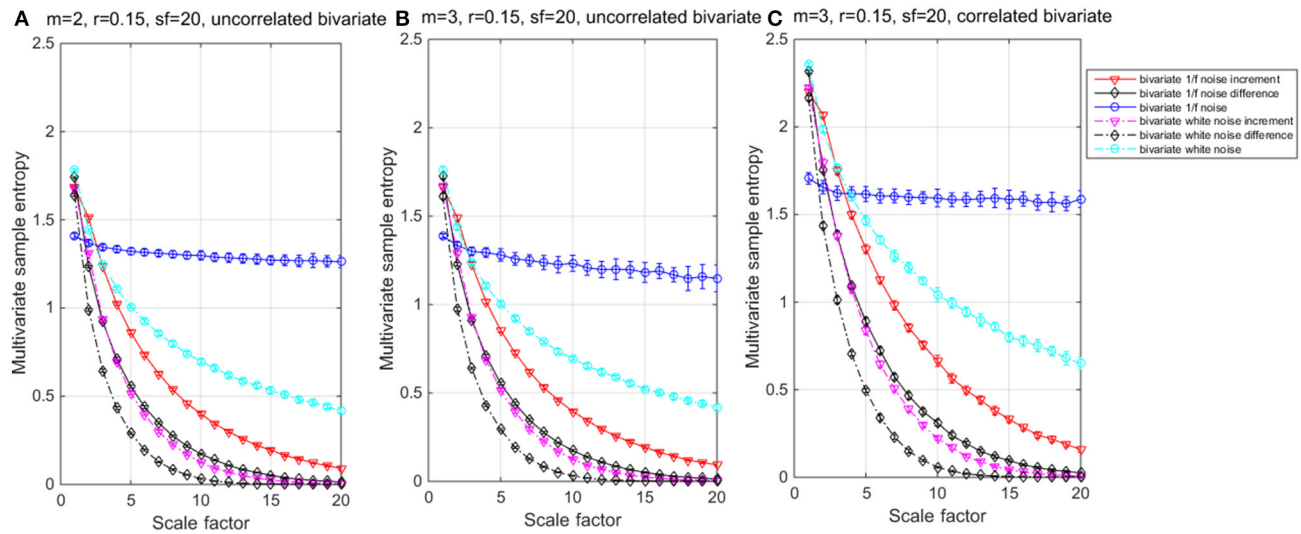

FIGURE 3 | Multivariate multiscale entropy (MMSE) analysis for uncorrelated bivariate 1/f noise, white noise and their Increment and Difference within $m = 2$ (A) and 3 **(B)** respectively; and for **(C)** correlated bivariate 1/f noise, white noise and their Increment and Difference within $m = 3$.

provides a higher resolution of complexity in the time domain and visuo-vestibular regulation is related to low frequencies (0–0.5 Hz) of the COP displacement (Dichgans et al., 1976; Paillard et al., 2006).

Statistical Analysis

Friedman tests were used to examine the effect of condition (i.e., EO, EC, PV) on all postural parameters. The complexity index (CI), defined as the integral of the MSE or MMSE curve, was used for the statistical analysis of the entropy measures (MSE, MMSE). The normality of the data sets was verified using the Kolmogorov-Smirnov test. *Post-hoc* pairwise comparisons (between-conditions) were performed when needed using Wilcoxon's tests with a Bonferroni adjustment. The effect size values were described by the magnitude of change expressed as Cliff's delta ($|r|$). All tests were performed using IBM SPSS Statistics version 16 with a level of significance set at $p < 0.05$.

RESULTS

The Kolmogorov-Smirnov tests indicated non-parametric distribution of the data sets and therefore the data is reported using median (*Med*) and inter-quartile range (*IQR*). For the classical parameters, Friedman tests indicated significant differences in path length, mean velocity and mean frequency (A/P), depending on the condition (**Table 2**). The *post-hoc* Wilcoxon's analyses revealed a statistically significant difference between the EO and EC conditions for path length, [EC ($Med = 230.95$, $IQR = 120.52$) and EO ($Med = 184.19$, $IQR = 53.62$), $z = 2.934$, $p \leq 0.01$], mean velocity [EC ($Med = 7.7$, $IQR = 4.02$) and EO ($Med = 6.14$, $IQR = 1.78$), $z = 2.934$, $p \leq 0.01$], and mean frequency [EC ($Med = 0.52$, $IQR = 0.31$) and EO ($Med = 0.45$, $IQR = 0.30$), $z = 2.934$, $p \leq 0.01$]. The small effect size calculation for the tree parameters with Cliff's delta values ($r < 0.35$) suggests minimal practical significance. For the 95% confidence ellipse, mean frequency (M/L), root-mean-square in A/P, or M/L direction (**Table 2**) no differences were found.

The analysis for ***Original*** time series showed a significant effect of condition on CI_MSE (A/P) and CI_MMSE (**Table 2**). The *post-hoc* Wilcoxon's analyses revealed a statistically significant difference between the EO and PV conditions for CI_MMSE, [EO ($Med = 13.98$, $IQR = 1.15$) and PV ($Med = 13.58$, $IQR = 1.12$), $z = 2.401$, $p \leq 0.05$]. The large effect size calculation with a Cliff's delta value ($r > 0.80$) suggests high practical significance.

For the ***Incremented*** time series, significant differences between conditions were found in three of the five parameters (**Table 2**). The *post-hoc* Wilcoxon's analyses revealed a statistically significant difference between the EC and EO conditions for CI_MSE (A/P) [EC ($Med = 18.91$, $IQR = 1.14$) and EO ($Med = 17.99$, $IQR = 1.73$), $z = 2.934$, $p \leq 0.01$], CI_MSE (M/L) [EC ($Med = 20.29$, $IQR = 1.37$) and EO ($Med = 19.00$, $IQR = 0.95$), $z = 2.490$, $p \leq 0.05$], and CI_MMSE [EC ($Med = 9.03$, $IQR = 0.40$) and EO ($Med = 8.46$, $IQR = 0.71$), $z = 2.934$, $p \leq 0.01$]. The small effect size calculation for the tree parameters with Cliff's delta values ($r < 0.35$) suggests minimal practical significance.

When comparing the EC and PV conditions, the *post-hoc* Wilcoxon's analyses revealed a statistically significant differences for CI_MSE (A/P) [EC ($Med = 18.91$, $IQR = 1.14$) and PV ($Med = 18.29$, $IQR = 1.35$), $z = 2.401$, $p \leq 0.05$], CI_MSE (M/L) [EC ($Med = 20.29$, $IQR = 1.37$) and PV ($Med = 19.94$, $IQR = 0.84$), $z = 2.701$, $p \leq 0.01$], and CI_MMSE [EC ($Med = 9.03$, $IQR = 0.40$) and PV ($Med = 8.83$, $IQR = 0.43$), $z = 2.667$, $p \leq 0.01$]. The large effect size calculation for the three parameters with Cliff's delta values ($r > 0.95$) suggests large practical significance.

When comparing the PV and EO conditions, the *post-hoc* Wilcoxon's analyses revealed statistically significant differences for CI_MSE(A/P) [PV ($Med = 18.29$, $IQR = 1.35$) and EO (Med

TABLE 2 | Results of non-parametric statistical tests (median ± IQR) on differences between the three experimental conditions (EC, PV, EO) on classical and non-linear complexity parameters.

					Friedman tests		Wilcoxon's *post-hoc* comparisons					
	Classical parameters						EC vs. EO		EC vs. PV		PV vs. EO	
	EC	PV	EO	Trend	$\chi^2(2)$	*p*	*z*	|r|	*z*	|r|	*z*	|r|
Path Length	230.95 ± 120.52	208.14 ± 76.33	184.19 ± 53.62	■■■	14.73	**0.001**	2.934	0.273**				
Mean Velocity	7.7 ± 4.02	6.94 ± 2.54	6.14 ± 1.78	■■■	14.73	**0.001**	2.934	0.273**				
Confidence Ellipse	75.77 ± 61.27	84.32 ± 120.52	77.81 ± 43.34	■■■	0.55	0.761						
Mean Frequency (A/P)	0.52 ± 0.31	0.42 ± 0.33	0.45 ± 0.3	■■■	10.36	**0.006**	2.934	0.339**				
Mean Frequency (M/L)	0.26 ± 0.13	0.2 ± 0.08	0.15 ± 0.11	■■■	5.09	0.078						
RMS (A/P)	1.11 ± 0.66	1.19 ± 0.85	1.3 ± 0.5	■■■	0.55	0.761						
RMS (M/L)	3.79 ± 2.22	3.34 ± 2.38	4.4 ± 2.44	■■■	0.55	0.761						
	Original time series				$\chi^2(2)$	*p*	*z*	|r|	*z*	|r|	*z*	|r|
SE (A/P)	1.28 ± 0.16	1.30 ± 0.15	1.32 ± 0.13	■■■	0.55	0.761						
SE (M/L)	0.76 ± 0.28	0.72 ± 0.16	0.77 ± 0.46	■■■	2.91	0.234						
CI_MSE (A/P)	18.99 ± 2.4	19.4 ± 2.26	19.14 ± 1.47	■■■	6.73	**0.035**						
CI_MSE (M/L)	12.49 ± 4.26	11.46 ± 2.09	11.07 ± 6.13	■■■	1.27	0.529						
CI_MMSE	13.98 ± 1.15	13.58 ± 1.12	14.17 ± 0.56	■■■	6.73	**0.035**					2.401	0.818*
	Incremented time series				$\chi^2(2)$	*p*	*z*	|r|	*z*	|r|	*z*	|r|
SE (A/P)	2.35 ± 0.02	2.34 ± 0.01	2.34 ± 0.01	■■■	5.09	0.078						
SE (M/L)	2.36 ± 0.01	2.35 ± 0.01	2.35 ± 0.02	■■■	4.55	0.103						
CI_MSE (A/P)	18.91 ± 1.14	18.29 ± 1.35	17.99 ± 1.73	■■■	18.727	**0.000**	2.934	−0.025**	2.401	1.000*	2.934	0.669**
CI_MSE (M/L)	20.29 ± 1.37	19.94 ± 0.84	19 ± 0.95	■■■	8.419	**0.015**	2.490	0.124*	2.701	0.950**		
CI_MMSE	9.03 ± 0.4	8.83 ± 0.43	8.46 ± 0.71	■■■	14.727	**0.001**	2.934	0.008**	2.667	0.967**	2.578	0.752*
	Difference time series				$\chi^2(2)$	*p*	*z*	|r|	*z*	|r|	*z*	|r|
SE (A/P)	2.27 ± 0.01	2.27 ± 0.01	2.27 ± 0.01	■■■	7.47	**0.024**						
SE (M/L)	2.27 ± 0.01	2.27 ± 0.01	2.26 ± 0.01	■■■	3.82	0.148						
CI_MSE (A/P)	12.29 ± 0.84	11.94 ± 0.85	11.62 ± 1.14	■■■	17.636	**0.001**	2.934	−0.074**			2.934	0.686**
CI_MSE (M/L)	13.2 ± 0.99	12.88 ± 0.69	12.03 ± 0.65	■■■	8.727	**0.013**	2.534	−0.074*	2.667	0.950**		
CI_MMSE	5.24 ± 0.23	5.15 ± 0.19	5 ± 0.23	■■■	16.233	**0.000**	2.934	−0.091**	2.497	1.000*	2.801	0.669**

*EC, eyes closed condition; PV, perturbed vision; EO, eyes open condition. A/P, anterior-posterior; M/L, medio-lateral. SE, Sample Entropy; CI_MSE, complexity index of Multi-Scale Entropy; CI_MMSE, complexity index of Multivariate Multi-Scale Entropy. *$p < 0.05$ (after Bonferroni correction, $p < 0.017$), **$p < 0.01$. Bold values shows significantly different among three conditions.*

= 17.99, $IQR = 1.73$), $z = 2.934$, $p \leq 0.01$], and CI_MMSE [PV ($Med = 7.7$, $IQR = 4.02$) and EO ($Med = 6.14$, $IQR = 1.78$), $z = 2.578$, $p \leq 0.05$]. The medium effect size calculation for the two parameters with Cliff's delta values ($r > 0.65$) suggests high practical significance.

In the ***Difference*** time series, four of the five non-linear parameters significantly changed between conditions (**Table 1**). The *post-hoc* Wilcoxon's analyses revealed statistically significant differences between the EO and EC conditions for CI_MSE (A/P) [EC ($Med = 12$, 29 $IQR = 0.84$) and EO ($Med = 11.62$, $IQR = 1.14$), $z = 2.934$, $p \leq 0.01$], CI_MSE (M/L) [EC ($Med = 13.20$, $IQR = 0.99$) and EO ($Med = 12.03$, $IQR = 0.65$), $z = 2.534$, $p \leq 0.05$], and CI_MMSE [EC ($Med = 5.24$, $IQR = 0.23$) and EO ($Med = 5.00$, $IQR = 0.23$), $z = 2.934$, $p \leq 0.01$]. The small effect size calculation for the tree parameters with Cliff's delta values ($r < 0.35$) suggests minimal practical significance.

When comparing the EC and PV conditions, the *post-hoc* Wilcoxon's analyses revealed a statistically significant differences for CI_MSE (M/L), [EC ($Med = 13.20$, $IQR = 0.99$) and PV ($Med = 12.88$ $IQR = 0.69$), $z = 2.667$, $p \leq 0.01$], and CI_MMSE [EC ($Med = 5.24$, $IQR = 0.23$) and PV ($Med = 5.15$, $IQR = 0.19$), $z = 2.497$, $p \leq 0.05$]. The large effect size calculation for the three parameters with Cliff's delta values ($r > 0.90$) suggests large practical significance.

When comparing the PV and EO conditions, the *post-hoc* Wilcoxon's analyses revealed statistically significant differences for CI_MSE (A/P), [PV ($Med = 11.94$, $IQR = 0.85$) and EO ($Med = 11.62$, $IQR = 1.14$), $z = 2.934$, $p \leq 0.01$], and CI_MMSE [PV ($Med = 5.15$, $IQR = 0.19$) and EO ($Med = 5.00$, $IQR = 0.23$), $z = 2.801$, $p \leq 0.01$]. The medium to large effect size calculation for the two parameters with Cliff's delta values ($r > 0.60$) suggests large practical significance.

DISCUSSION

In this experiment, classical parameters were tested against non-linear complexity parameters to reveal differences between the COP displacements during three standing conditions. Non-linear entropy family methods resulted in better uncovering of postural displacement differences when compared to the classical posturographic methods. Only three of the seven classical parameters [i.e., PL, MV, MF (A/P)] were able to differentiate between conditions (EO, EC, PV). Amongst the five studied entropy measures, only two showed significant differences between conditions [i.e., CI_MSE (A/P) and CI_MMSE] using the ***Original*** time series, and in the ***Incremented*** and ***Difference*** time series CI_MSE (A/P), CI_MSE (M/L) and CI_MMSE showed higher sensitivity to the condition effect. Between-conditions differences in the ***Original*** time series were only revealed for the CI_MMSE parameter. In the ***Increment*** and ***Difference*** time series between-conditions differences were found for CI_MSE (A/P), CI_MSE (M/L) and CI_MMSE parameters. The most consistent parameter for the three time series is the CI_MMSE and could therefore be considered as the most reliable parameter in detecting between-conditions differences.

For visual feedback, the results show that the complexity quantified by MSE, and MMSE statistic in ***Increment*** and ***Difference*** is lower in the EC condition compared to EO and PV. Even though the statistical analysis has not shown significant differences on the COP displacement related to the effect of visual feedback, the entropy values for SE (A/P) of the ***Original*** is lowest in the EC condition. Higher entropy values are related to more irregularity, something that may be associated with a functional decline of the postural control system resulting in maladaptive responses to perturbations and thereby destabilizing the balance control (Vaillancourt and Newell, 2002; Schniepp et al., 2013). This finding is consistent with previous research (Roerdink et al., 2011) showing that physical and physiological visual parameters affect postural control during quiet standing and therefore the COP displacement (cf. Stins et al., 2009; Vuillerme and Pinsault, 2009). The sample size and the choice of young healthy participants that were recruited from the Sports Science department may have influenced the results as they may have higher postural capacities compared to age matched subjects. Working with healthy young adults increases the difficulty to distinguish between EO and EC compared to older adults (Prieto et al., 1996). Taking this into account the relation between COP regularity and the amount of attention invested in posture (Donker et al., 2007; Stins et al., 2009), are in line with the findings of our study. The COP regularity in the ***Original*** time series showed no differences between conditions by means of sample entropy while in the ***Difference*** time series such differences were uncovered. This confirms previous work showing that a decrease of the complexity of the physiological and behavioral systems is observed when the kinesthetic cues are reduced (Newell et al., 1997) but also that incremented time series provide short-term correlated components containing more information about the non-linear system (Ramdani et al., 2009).

Using entropy measures allows us to deal with highly irregular and variable signals like postural sway (Prieto et al., 1996). However, limitations of the particular parameters and properties of the entropy measures have to be discussed. MSE is an entropy measure for univariate time series and MMSE is extended to multivariate cases. Even though the results of MSE and multivariate MSE analysis are promising, some problems still have to be resolved when working with postural data. Entropy measures assess the complexity of physiological time series signals rather than measure motor performance. The creation of one complexity index summing all twenty scales needs to be addressed in future research as it is currently unknown which time-scale is more important or related to postural control. Data length affects entropy measures but it depends on the experiment and therefore a high sampling rate of 250 Hz was chosen to obtain the necessary data length. The COP signal does not contain high frequency signals and the use of a low-pass filter (cut-off 5 Hz) is common. This may create an oversampling issue and the first several scales may not have physiological meaningful information related to dynamical COP changes. Furthermore, the coarse-graining procedure reduced the input data length to half its original size for each successive data scale and therefore potentially changed the intrinsic dynamical scales defined by the signal-generating system.

The reduction of MSE with increasing time-scale is based on the tolerance settings (i.e., constant fraction of the variance of the

original time series) and the conventional γ*SD tolerance could be replaced by the variance of each coarse grained time series (Humeau-Heurtier, 2015).

Previous research from our laboratory has shown those MSE characteristics and a possible solution could be the use of diverse empirical mode decomposition techniques (Shih et al., 2015). Decomposing the ***Original*** time series into intrinsic mode functions when testing different combinations of frequency bands with relevant complexity indexes has been shown to be efficient and promising in studies on elderly subjects exposed to slight vibrations under their feet (Wei et al., 2012). Empirical mode decomposition and Hilbert–Huang transformation can also be used to observe the physiological signals in instantaneous frequency and instantaneous amplitude through intrinsic mode functions, and then transformed inversely into the time domain to observe the changes in different conditions (Shih et al., 2015). However, the ***Increment*** and ***Difference*** time series approaches also seem appropriate as they removed trends from the original time series and showed changes in the COP displacements. Other approaches (Yeh et al., 2016) such as the above-mentioned empirical mode decomposition also provide useful data-driven scale factor and intrinsic entropy calculation of complex time series showing the possibility to explore the dynamical complexity of postural control in the future by combining incremented time series and empirical mode decomposition methods.

CONCLUSIONS

The current work supports the notion that some measures of non-linear entropy discriminate postural displacement better than classical measures when using incremented time series. Future studies should look to extend applied methods by examining other populations with impaired motor control. We also suggest that future research should consider empirical mode decomposition in combination with incremented time series across different clinical conditions to establish the reliability and validity of this new approach.

AUTHOR CONTRIBUTIONS

CH, LM, PF, and BI designed and conducted the experiment, QW and JS conducted the analysis and simulations, CH, QW, and JS wrote the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
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Regularity of Center of Pressure Trajectories in Expert Gymnasts during Bipedal Closed-Eyes Quiet Standing

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We compared postural control of expert gymnasts (G) to that of non-gymnasts (NG) during bipedal closed-eyes quiet standing using conventional and nonlinear dynamical measures of center of foot pressure (COP) trajectories. Earlier findings based on COP classical variables showed that gymnasts exhibited a better control of postural balance but only in demanding stances. We examined whether the effect of expertise in Gymnastic can be uncovered in less demanding stances, from the analysis of the dynamic patterns of COP trajectories. Three dependent variables were computed to describe the subject's postural behavior: the variability of COP displacements (A_{CoP}), the variability of the COP velocities (V_{CoP}) and the sample entropy of COP (SEn_{CoP}) to quantify COP regularity (i.e., predictability). Conventional analysis of COP trajectories showed that NG and G exhibited similar amount and control of postural sway, as indicated by similar A_{CoP} and V_{CoP} values observed in NG and G, respectively. These results suggest that the specialized balance training received by G may not transfer to less challenging balance conditions such as the bipedal eyes-closed stance condition used in the present experiment. Interestingly, nonlinear dynamical analysis of COP trajectories regarding COP regularity showed that G exhibited more irregular COP fluctuations relative to NG, as indicated by the higher SEn_{CoP} values observed for the G than for the NG. The present results showed that a finer-grained analysis of the dynamic patterns of the COP displacements is required to uncover an effect of gymnastic expertise on postural control in nondemanding postural stance. The present findings shed light on the surplus value in the nonlinear dynamical analysis of COP trajectories to gain further insight into the mechanisms involved in the control of bipedal posture.

Keywords: balance, entropy

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INTRODUCTION

Posture can be defined as the spatial organization of the body segments (e.g., Winter, 1995). Postural regulation is a complex skill that requires coordinating and controlling subtle rotational movements of hundreds of joints by means of several hundreds of muscles to maintain the center of mass within the base of support. The multisensory consequences of the kinematics and kinetic variations

patterns of postural movements, i.e., the dynamics of postural balance, would be informative of the direction of balance (DOB, Riccio et al., 1992) and preferred modes of spatial referencing (Streepey et al., 2007a,b; Isableu et al., 2010; Slaboda and Keshner, 2012). To maintain a bipedal posture stable, central processing factors are known to play a major role insofar as the central nervous system has to process information from various sensory cues (visual, somesthetic and vestibular), and weight them in proportion to their reliabilities (Oie et al., 2002). Analysis of the center of pressure (COP) in various upright stance tasks is widely used to characterize postural control and to understand the underlying motor control mechanisms during challenging experimental conditions. Force platform is typically used to assess the location and the dynamics of the COP. COP dynamics are likely due to complex control process associated with the maintenance of postural control, as well as the inherent noise within the human neuromotor system. COP is widely used to assess the health of the postural control system, but also to learn about the effect of athletic expertise (Lion et al., 2009; Herpin et al., 2010; Paillard et al., 2011; Zemková, 2014a,b). Previous studies investigated postural control during quiet standing in expert gymnasts (G), a sport requiring high balance abilities (Vuillerme et al., 2001a,b; Asseman et al., 2004, 2008; Vuillerme and Nougier, 2004; Gautier et al., 2008). Interestingly, these studies reported no significant difference between gymnasts and non-gymnasts (NG) under relatively non-challenging conditions (bipedal eyes-open posture). Authors suggested that expertise in gymnastics only has an effect on the control of specific postures for which the practice is specifically related to (see also, Henry, 1968; Schmidt and Young, 1987). However, standing posture during an eyes-closed bipedal standing task is known, as a test condition that increases reliance on vestibular (and proprioceptive) input (Rougier, 2003; Isableu and Vuillerme, 2006; Isableu et al., 2010), but also to require attention demands in gymnast and NG (Vuillerme and Nougier, 2004). At this point, however, the common observation from these studies is that the use of conventional measures of the center of foot pressure (COP; e.g., COP surface area, COP velocity) to quantify postural control in expert gymnasts may have yielded an incomplete picture of postural control in expert gymnasts (Asseman et al., 2004; Vuillerme and Nougier, 2004). Analyses carried out on nonlinear dynamic features of the COP revealed that variability in the motor output is not randomness but structured. Further insight into the underlying dynamics of bipedal eyes-closed postural control in expert gymnasts could be obtained through the recourse to nonlinear dynamical analysis of the COP regarding its regularity (i.e., predictability) using sample entropy measures (SEn_{CoP}; Borg and Laxåback, 2010). Interestingly, a more irregular COP trajectory, as assessed by higher SEn_{CoP}, has been suggested to be associated with more automaticity and has been proposed to be viewed as a reduction of the amount of attention invested in the control of posture (e.g., Roerdink et al., 2006, 2009, 2011; Donker et al., 2007; Stins et al., 2009a,b; Manor et al., 2013; Biec et al., 2014; Wayne et al., 2014).

The present experiment was designed to address the relationship between attention invested in posture and COP regularity by comparing postural control of expert gymnasts to that of NG during bipedal eyes-closed standing using both conventional and nonlinear dynamical measures of the COP trajectories. The two underlying hypotheses are: (A) The extensive postural control training that gymnasts receive over the years changes the requirements on their postural control system in such a way that for the same balance task they require less attentional resources than NG; and (B) If more attentional resources are invested in a postural control task, then the COP movement becomes more regular, if, on the other hand, the postural task is controlled more by automated processes, then the COP movement characteristics become more irregular or complex (e.g., Roerdink et al., 2006, 2009, 2011; Donker et al., 2007; Stins et al., 2009a,b; Manor et al., 2013; Wayne et al., 2014).

From these two hypotheses, the following prediction can be derived: if both hypotheses are correct, then the sample entropy, a measure of irregularity of a time series, calculated for the COP of gymnasts should be higher than the SEn_{CoP} of NG. Hence, the purpose of the current study was to test the two hypotheses by confirming or refuting this prediction.

As a result, taking into account the above-mentioned results (Vuillerme et al., 2001a,b; Asseman et al., 2004, 2008; Vuillerme and Nougier, 2004), no significant difference between conventional measures of the COP measured in gymnasts and those measured in NG were expected. On the other hand, and more *originally*, considering: (1) the decreased attentional demand required for regulating postural sway during quiet standing previously reported in gymnasts relative to NG using a dual-task paradigm (Vuillerme and Nougier, 2004); and (2) the proposed relationship between the amount of attention invested in posture and COP regularity (e.g., Roerdink et al., 2006, 2009, 2011; Donker et al., 2007; Stins et al., 2009a,b; Manor et al., 2013; Wayne et al., 2014), gymnasts were expected to exhibit more irregular COP trajectories, operationalized with higher SEn_{CoP}, values, than NG.

MATERIALS AND METHODS

Subjects

Two groups of athletes voluntarily participated in the experiment. They were naïve as to the purpose of the study. This study was carried out in accordance with the recommendations of the local Ethics Committee with written informed consent from all subjects. All subjects gave written informed consent to the experimental procedure in accordance with the Declaration of Helsinki. The protocol was approved by the local Ethics Committee.

The group of expert gymnasts (G) consisted of 10 males having more than 10 years of experience (8 h/week) in gymnastics competition at the regional level or higher. Females were not considered in this study to remove potential bias due to: (i) known influence of anthropometric factors and gender on postural balance in adults (Chiari et al., 2002; Farenc et al., 2003; Alonso et al., 2012); but also because (ii) mechanical, and skeletal differences known to produce different neuromuscular control of the knee joint (Shultz and Perrin, 1999) on body sway resulting in a different postural response

(Schmitz et al., 2007; Ku et al., 2012) to sensory alteration (Raffi et al., 2014); and (iii) sensory integration difference with men favoring visual dependency (Raffi et al., 2014; Persiani et al., 2015). Since our findings may originate simply from the practice of sports in general, gymnasts' performance was compared to the performance of a control group composed of 10 NG males who were also experts in sport (soccer, handball, or tennis). We also adjusted the composition of the two groups such that there was no significant difference either in age, weight and height (**Table 1**) because body properties have been demonstrated to be determinant for postural task (Chiari et al., 2002; Ruhe et al., 2010).

Experimental Procedure

Subjects stood barefoot on the force platform (Dynatronic, France) in a standardized position (feet abducted at 30°, heels separated by 3 cm), their arms hanging loosely by their sides with eyes closed. This closed eyes condition has been chosen to avoid visual information interfering with the control of bipedal posture. Indeed, given the crucial role of visual information (for a review, see Redfern et al., 2001), earlier studies provided evidence that the eyes-closed condition in evaluating postural control helps to improve the discrimination between healthy people (see Isableu and Vuillerme, 2006; Isableu et al., 2010), and patients with sensory (e.g., vestibular; Horak et al., 1990; Allum et al., 2001), somesthetic (Oppenheim et al., 1999; Nardone et al., 2001) or sensory-motor (Marigold and Eng, 2006; Blaszczyk et al., 2007) impairments. In fact, the availability of visual information allows individuals to compensate for their postural deficits (for a review, see Redfern et al., 2001) limiting the use of the eyes-open condition as a normative based clinical protocol for objective evaluation of postural control, particularly if vestibular or somesthetic functions have to be assessed (Hlavačka, 2003). As a consequence, the eyes-open condition was not measured in this study. Subject's task was to stand as still as possible during the trial.

Three 30 s trials were performed. Rest periods of 60 s were provided between successive trials during which subjects were allowed to sit down.

Data were recorded at a sampling frequency of 40 Hz which is large enough for capturing the physiological content of the postural signal localized below 5 Hz and which is equal or larger than the sampling frequency used in others studies (Cavanaugh et al., 2007; Ramdani et al., 2009, 2011; Borg and Laxåback, 2010; Rhea et al., 2011).

Collected data were protected by the MedSafe technology by the IDS Company (Montceau-les-Mines, France). IDS Company is an approved hosting provider in personal health data by the French Ministry for Social Affairs and Health.

TABLE 1 | Age, weight, height of Non-gymnasts (NG) and Gymnasts (G) groups.

	Non gymnasts (n = 10)	Gymnasts (n = 10)	T-test ($P < 0.05$)
Age (years)	22.0 ± 1.3	21.9 ± 1.0	Ns
Weight (kg)	68.3 ± 2.9	67.5 ± 2.0	Ns
Height (cm)	173.9 ± 3.3	170.9 ± 3.1	Ns

Values are means and standard deviation (±); Ns = non-significant difference between the two groups.

Data Analysis

The anteroposterior and mediolateral COP time series were centered on zero mean before constructing the resultant distance COP time series. Specifically, the resultant distance is the vector distance from the center of the posturogram to each point in the posturogram and hence it is not sensitive to the orientation of the base of support on force platform (Prieto et al., 1996).

Three dependent variables computed from the resultant distance COP were used to describe the subject's postural behavior using a similar methodology as recently proposed by Roerdink et al. (2009, 2011). The "amount of sway" and the "sway control" were quantified using two conventional, scale-dependent measures (see Prieto et al., 1996; Donker et al., 2007):

(1) the variability of COP displacements (A_{CoP} in mm, expressed as the root mean square of the COP time series),
(2) the variability of the COP velocities (V_{CoP} in mm/s, expressed as the root mean square of the COP velocities time series);

To examine the dynamical structure of COP trajectories and index its regularity independent of the size or scale. To this end, the RD time series was normalized to zero mean and unit variance resultant distance by subtracting its mean from this time series and dividing it by its standard deviation. Subsequently,

(3) the sample entropy of COP (SEn_{CoP}, dimensionless) was quantified for RD distance time series (Roerdink et al., 2009, 2011). Note that sample entropy was not calculated for the resultant distance differenced time series as suggested by Ramdani et al. (2009) to eliminate the inherent non-stationary nature of COP trajectories. Indeed, Roerdink et al. (2011) showed that it yields similar results. Algorithms of Lake and colleagues (Lake et al., 2002; Richman et al., 2004) were used to estimate corresponding sample entropy values. The sample entropy in a set of data points is the negative natural logarithm of the conditional probability (CP = A/B) that a sequence of data points with length N, having repeated itself within a tolerance r for m points, will also repeat itself for $m + 1$ points, without allowing self-matches (Richman and Moorman, 2000; Lake et al., 2002). Accordingly, B represents the total number of matches of length m while A represents the subset of B that also matches for $m + 1$. Sample entropy thus follows from $-\log$ (A/B), with a low sample entropy value arising from a high probability of repeated template sequence in the data. In this context, entropy is the rate of generation of new information and the lower the entropy, the greater the regularity (predictability) of the time series in question.

The reliability of the sample entropy estimation depends on the parameter choice of m and r. Sample entropy is best estimated with m as large and r as small as possible (Roerdink et al., 2009, 2011). Lake et al. (2002) introduced a statistical criterion to optimize the parameter choice, which is based on the maximum of the relative error of sample entropy and the conditional probability estimates. This metric simultaneously penalizes the conditional probability near 0 and

near 1 (Lake et al., 2002) and represents the tradeoff between accuracy and discriminative capability. The criterion was set to be no higher than 0.05, implying that the 95% confidence interval of the sample entropy estimate is maximally 10% of its value (Lake et al., 2002). Ramdani et al. (2009, 2011) recently proposed a practical graphical method based on a convergence criterion to optimize the choice of the parameter values. This optimization procedure was notably used by Roerdink et al. (2011) who found ($m = 3$, $r = 0.05$) to be the optimal couple (see Rhea et al., 2011; Hansen et al., 2017). This result is comparable to other couple of parameters previously obtained from the original optimization procedure proposed by Lake et al. (2002) for the resultant distance times series too (Donker et al., 2007; Roerdink et al., 2009). Therefore, this couple was also used in this study to perform the calculation of sample entropy (Hansen et al., 2017).

Statistical Analysis

The mean of ACoP, VCoP and SEnCoP values obtained for each of three trials were averaged for statistical analysis. COP data being normally distributed, A_{CoP}, V_{CoP} and SEn_{CoP} obtained in the NG group were compared with those obtained in the G group using *t*-tests for independent measures. Statistical analyses were performed using Statistica 10. Level of significance was set at 0.05.

RESULTS

Statistical difference between the NG and the G was observed neither for the A_{CoP} ($t = -1.20$, $P = 0.25$, **Figure 1A**) nor for the V_{CoP} ($t = -0.83$, $P = 0.42$, **Figure 1B**). Conversely, SEn_{CoP} was significantly higher in G than in NG ($t = -2.48$, $P = 0.023$, **Figure 1C**).

DISCUSSION

Regarding the conventional posturographic analysis of COP trajectories, our results showed that NG and G exhibited similar amount and control of postural sway, as indicated by similar A_{CoP} (**Figure 1A**) and V_{CoP} values (**Figure 1B**) observed in NG and G, respectively. These results confirmed previous observations (Vuillerme et al., 2001a,b; Asseman et al., 2004, 2008) supporting the general idea according to which, the postural control capacities are specific to the training program and the requirements of each discipline. The specialized balance training received by gymnasts may not transfer to less challenging balance conditions such as the bipedal eyes-closed stance condition used in the present experiment (see also, Henry, 1968; Schmidt and Young, 1987). However, Vuillerme and Nougier (2004), using a stimulus-responses reaction time paradigm to assess attentional investment, reported a smaller attentional involvement in balance control for expert gymnasts than for NG. Interestingly, in this study, the main effect of expertise assessed via classical COP variables was not significant. These results suggested that some variables used in conventional posturographic analysis of COP trajectories did not capture the amount of attention invested to control postural balance. One reason is that most variables used in conventional posturographic analysis of COP trajectories are *a priori* more suited to capture linear stationary processes (i.e., additive phenomenon) hidden in signal fluctuations (Wayne et al., 2014; Gow et al., 2015), and as a consequence fail to capture complex central interaction that result from the combination of both additive and multiplicative processes (Huang et al., 2016). The results mentioned above suggest that attentional mechanisms likely involve complex neural interaction and nonlinear processes (i.e., a mixture of additive and multiplicative phenomenon). Hence, attentional-based interactions and the amount of attentional investment in postural control seem better captured in the COP fluctuations by using nonlinear (multiplicative) variables.

Regarding the nonlinear dynamical posturographic analysis of COP trajectories regarding COP regularity, our results showed indeed that G exhibited more irregular COP fluctuations relative to NG, as indicated by the higher SEn_{CoP} values observed for the G than for the NG (**Figure 1C**). This result shows that nonlinear variables (SEn_{CoP}) are more appropriate to capture nonlinear multiplicative processes in the COP signal. Following the proposed relation between COP regularity and the amount of attention invested in the control of posture (e.g., Stins et al., 2009a), these results and ours suggest less attentional investment, i.e., a more fully automatized form of balance, in experts in sports requiring fine postural control (i.e., dancers and gymnasts) than controls. Our results are in accordance with those of Vuillerme and Nougier (2004) who, using a stimulus-responses reaction time paradigm to operationalize attentional investment, reported a smaller attentional involvement in balance control for expert gymnasts than for NG. Although to the best of our knowledge, no previous study has assessed regularity of COP trajectories in expert gymnasts during bipedal eyes-closed quiet standing, our observation is in line with a recent result obtained in experts in dance (Stins et al., 2009b), a sport that also require high balance abilities. Stins et al. (2009b) reported higher SEn_{CoP} in preadolescent pre-professional dancers than age-matched non-dancers. An alternative explanation of our findings could be drawn from the Borg and Laxåback's (2010) study. The higher COP entropy observed in gymnasts relative to nongymnasts suggests they exhibited a more automatic balance control. Within this view, higher COP entropy could indicate that they deployed a more efficient balancing. The efficiency with which postural balance (low COP variability and low attentional investment) is controlled is closely tied to the selection of an appropriate mode of spatial referencing (generally proprioceptive-based; Berthoz, 1991; Paillard, 1991; Kluzik et al., 2005; Streepey et al., 2007b; Isableu et al., 2010, 2011; Mergner, 2010; Slaboda et al., 2011a,b; Brady et al., 2012; Scotto Di Cesare et al., 2015). Several authors showed that these modes of spatial referencing are known to impact the attentional investment (Goodenough et al., 1987; Marendaz et al., 1988; Marendaz, 1989; Bailleux et al., 1990; Yan, 2010; Agathos et al., 2015). Following this rationale, it is likely that with the selection of the adequate frame of reference, attentional investment should decrease, and accounts for the emergence of more irregular (more complex) COP time series (Vuillerme and Nougier, 2004), even in nondemanding stance.

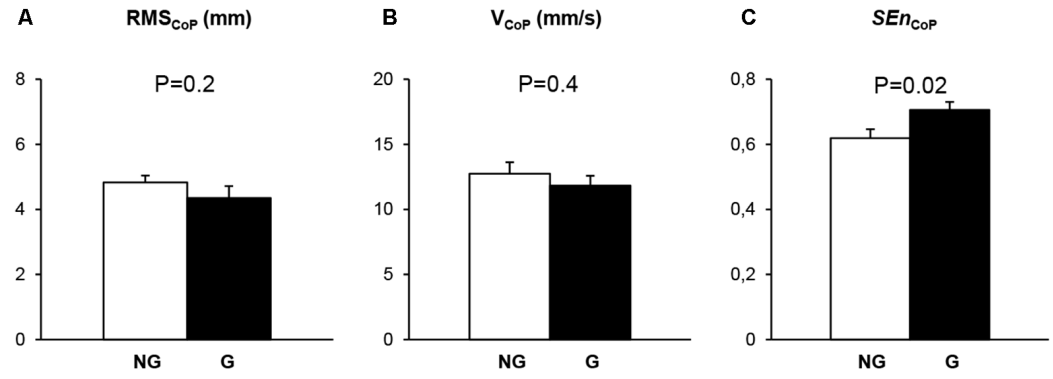

FIGURE 1 | Mean and standard error of mean of the variability of the displacements (A_{CoP}; **A**), the velocity (V_{CoP}; **B**) and the regularity (SEn_{CoP}; **C**) of the center of foot pressure (COP) trajectories obtained in the two groups of Non gymnasts (NG; *white bars*) and Gymnasts (G; *black bars*). The *P* values for comparisons between postural parameters computed from the NG and those computed from the G are reported.

Finally, two main conclusions can be drawn from the differential effect of expertise in gymnastics observed on the conventional (**Figures 1A,B**) and the nonlinear dynamical measure of the COP trajectory (**Figure 1C**) during bipedal eyes-closed quiet standing. First, these results suggest that, under mild challenging postural condition such as bipedal eyes-closed stance, postural control in expert gymnasts is *qualitatively*, but not *quantitatively*, different than that of controls. Although the expert population is different, the present findings are in line with those of Manor et al. (2013) and Wayne et al. (2014) on the impact of short- and long-term Tai Chi exercise training. These authors also reported that the effect of Tai Chi on postural control may be better characterized by quantifying its effects on the degree of complexity associated with the system output (i.e., COP dynamics) than by the traditional sway parameters (Manor et al., 2013; Wayne et al., 2014). Indeed, using both standard measures of postural sway and recurrence quantification analysis, these authors (Manor et al., 2013; Wayne et al., 2014) observed that trained ballet dancers exhibited similar variability and amount of postural sway, but more irregular sway and thus complex patterns than physically fit control group. Second, the observation that the balance skills of gymnasts were observed in the dynamic patterns of COP displacements (**Figure 1C**), but not in the control (**Figure 1A**) and the amount of postural sway velocity (**Figure 1B**) shed light on the surplus value in nonlinear dynamical analysis of COP trajectories to gain further insight into the mechanisms involved in the control of bipedal eyes-closed posture. Along these lines, some limitations of our study can be pointed. Nonlinear dynamics features of the COP displacements could have been explored in more depth using Multi-Scale Entropy (MSE), and Multivariate Multi-Scale Entropy (MMSE). These methods are particularly suitable to quantify the degree of regularity or predictability over multiple scales of time (see Costa et al., 2005; Gow et al., 2015). Our analyses were mainly carried out on the original time series. Additional information can be obtained from the analysis of the decremented time series (which removes the long-term correlated components from the original time series and represent short-term complexity). Hansen et al. (2017), showed that MMSE analysis performed on the decremented time series is particularly suitable to detect signal divergence faster and can, therefore, be considered more suitable for complexity detection. Further experiments are currently performed to assess the relationship between variation of attentional ressources allocated to control potural balance and complexity of the COP at different scales, but also whether and how characteristics other than sportive expertise, such as anthropometry, neuromuscular state or preferred modes of spatial frames of reference (Streepey et al., 2007b; Isableu et al., 2010, 2011; Slaboda and Keshner, 2012; Agathos et al., 2015), that have been shown to affect balance control, could also modify the dynamical structure of the COP trajectories in terms of their regularity and complexity at different scales and frequency bands (by decomposing the original time series into intrinsic mode functions via empirical mode decomposition techniques (Costa et al., 2005; see Wei et al., 2012; Shih et al., 2015; Hansen et al., 2017).

AUTHOR CONTRIBUTIONS

BI, PH, BD and NV conceived and designed the experiment, performed the experiment, analyzed the data, contributed reagents/materials/analysis tools, wrote the article, prepared figures and/or tables, reviewed drafts of the article.

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The Spatial Distribution of Ankle Muscles Activity Discriminates Aged from Young Subjects during Standing

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During standing, age-related differences in the activation of ankle muscles have been reported from surface electromyograms (EMGs) sampled locally. Given though activity seems to distribute unevenly within ankle muscles, the local sampling of surface EMGs may provide a biased view on how often and how much elderly and young individuals activate these muscles during standing. This study aimed therefore at sampling EMGs from multiple regions of individual ankle muscles to evaluate whether the distribution of muscle activity differs between aged and young subjects during standing. Thirteen young and eleven aged, healthy subjects were tested. Surface EMGs were sampled at multiple skin locations from tibialis anterior, soleus and medial and lateral gastrocnemius muscles while subjects stood at ease. The root mean square amplitude of EMGs was considered to estimate the duration, the degree of activity and the size of the region where muscle activity was detected. Our main findings revealed the medial gastrocnemius was active for longer periods in aged (interquartile interval; 74.1–98.2%) than young (44.9–81.9%) individuals ($P = 0.02$). Similarly, while tibialis anterior was rarely active in young (0.7–4.4%), in elderly subjects (2.6–82.5%) it was often recruited ($P = 0.01$). Moreover, EMGs with relatively higher amplitude were detected over a significantly wider proximo-distal region of medial gastrocnemius in aged (29.4–45.6%) than young (20.1–31.3%) subjects ($P = 0.04$). These results indicate the duration and the size of active muscle volume, as quantified from the spatial distribution of surface EMGs, may discriminate aged from young individuals during standing; elderlies seem to rely more heavily on the active loading of ankle muscles to control their standing posture than young individuals. Most importantly, current results suggest different conclusions on the active control of standing posture may be drawn depending on the skin location from where EMGs are collected, in particular for the medial gastrocnemius.

Keywords: postural control, standing, aging, electromyography, muscle activity

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INTRODUCTION

Different mechanisms have been suggested to account for the control of human, standing posture. Of recent interest is the notion that bodily sways are arrested by timely, triggered bursts of calf muscles' activity (Loram et al., 2005; Vieira et al., 2012; Héroux et al., 2014). The physiological mechanism underpinning timed activation in standing is controversial; some suggest there is an

internal clock triggering calf muscles' activation (Loram et al., 2009) while others believe activation is event-triggered (Bottaro et al., 2008). In spite of the potential sources accounting for such intermittent, postural activation, alternating periods of muscle activation with silencing seems advantageous. Periodically silencing postural muscles during standing may: (i) allow the nervous system to sense joint angles without interference from muscle contraction (Loram et al., 2011); (ii) compensate for intrinsic, feedback delays (Cabrera and Milton, 2002); (iii) reduce metabolic costs (Bottaro et al., 2008); (iv) not increase postural instability (Cabrera and Milton, 2002). In this view, the assessment of muscle activation may therefore reveal pivotal features of the control of standing posture, especially e.g., in persons with balance impairments.

Surface EMGs revealed, indeed, key differences in the activation of postural muscles with aging. From bipolar surface EMGs collected from the plantar flexor muscles, for example, previous studies reported that elderlies tend to stand with a more continuous and higher degree of activation than young individuals (Laughton et al., 2003; Nagai et al., 2011; Baudry et al., 2012). Moreover, while tibialis anterior is typically silent in young subjects during standing (Di Giulio et al., 2009; Masani et al., 2013), in aged individuals it is often recruited (Laughton et al., 2003). From the point of view of muscle activation, it seems therefore standing becomes progressively more demanding with aging. A crucial question arising from previous studies is whether the greater, prolonged activation observed locally (i.e., with bipolar EMGs) in plantar and dorsal flexors of aged subjects reflects the activation of the muscle as a whole.

The spatial distribution of surface EMGs over the whole muscle rather than the local sampling of surface EMGs with bipolar electrodes seems to more likely provide a genuine indication on the duration and degree of muscle activity. EMGs with different amplitudes have indeed been observed when sampled from different regions of a single muscle (Brown et al., 2007; Farina et al., 2008), suggesting activity does not distribute uniformly within the muscle volume. This uneven distribution of activity has been often observed for the calf muscles and for a number of circumstances, including standing (McLean and Goudy, 2004; Hodson-Tole et al., 2013; Reffad et al., 2014). Methodologically, these results suggest the local sampling of surface EMGs may not provide a representative view of the degree and duration of calf muscles' activation. Physiologically, the differential distribution of activity within the calf muscles may indicate a key mechanism contributing to the control of muscle force and thus of the standing posture. It is therefore possible that differences in the activation of postural muscles with aging are more expressive than previously appreciated.

This study questions, for the first time, whether the distribution of muscle activity differs between aged and young subjects during standing. Differently from previous studies, here we use arrays of surface electrodes to sample EMGs from different regions of individual, ankle muscles. More specifically, from surface EMGs collected serially from ankle plantar and dorsal flexors we ask: do young and aged subjects activate an equal proportion of their muscles for a similar duration during standing? If aging is associated with greater muscular effort for standing control (Nagai et al., 2011; Baudry et al., 2012), we therefore expect to observe EMGs with greater amplitude for a longer duration and in a larger muscle region in aged than young individuals.

MATERIALS AND METHODS

Participants

Thirteen young male volunteers provided written informed consent before participating in the study (mean ± SD; age: 26 ± 3 years; body mass: 72.4 ± 10.1 kg; height: 1.75 ± 0.06 m) and 11 aged (70 ± 6 years; 72.9 ± 12.5 kg; 1.72 ± 0.08 m). All participants were classified as minimally active according to the international physical activity questionnaire (IPAQ); short self-administered version (Tomioka et al., 2011). All community-dwelling older adults lived independently. We decided to include participants without a sedentary lifestyle because physical inactivity may further broaden the between-subjects variability often reported for stabilometric descriptors (Chiari et al., 2002). The experimental procedures considered in this study conformed with the *Declaration of Helsinki* and were approved by the Regional Ethics Committee (Commissione di Vigilanza, Servizio Sanitario Nazionale—Regione Piemonte—ASL 1—Torino, Italy). Volunteers did not report any balance impairments, neurological disorders, muscular injuries, or the intake of medications that could affect their standing balance at the occasion of experiments.

Experimental Protocol

Participants were instructed to stand upright barefoot on a force-plate, with eyes open and arms alongside the body. They positioned their feet at a comfortable orientation and distance, while keeping heels and toes at the same position along the force plate anterior-posterior axis (**Figure 1A**). Prior to starting experiments, the contour of both feet was marked on the force plate to ensure participants would keep the same feet position throughout the standing tests.

Two standing tasks were applied. In the first task, participants were provided with visual feedback of their CoP position in the anterior-posterior axis and were instructed to keep it at 65% of the longitudinal size of their support base for 60 s (**Figure 1B**). The size of the support base in the anterior-posterior axis was defined as the distance between the tip of the third metatarsal head and the tip of the calcaneus bone projected in the anterior-posterior direction (**Figure 1A**). The 65% figure corresponds roughly to 80% of the distance between the heels and the anterior limit of stability of healthy, young subjects (Duarte and Zatsiorsky, 2002); this figure was selected to ensure a somewhat high degree of calf muscles active loading while not threatening stability, in particular for the aged individuals. All elderly subjects tested could stand with their CoP at the target value without losing balance. This postural task was considered for the normalization of EMGs, as described below. In the second task, volunteers were asked to stand at ease for 60 s. Subjects were engaged in active conversation to ensure they would take their mind off the test and thus avoid any voluntary change in muscle activity (Loram and Lakie, 2002b). The trial started over in the

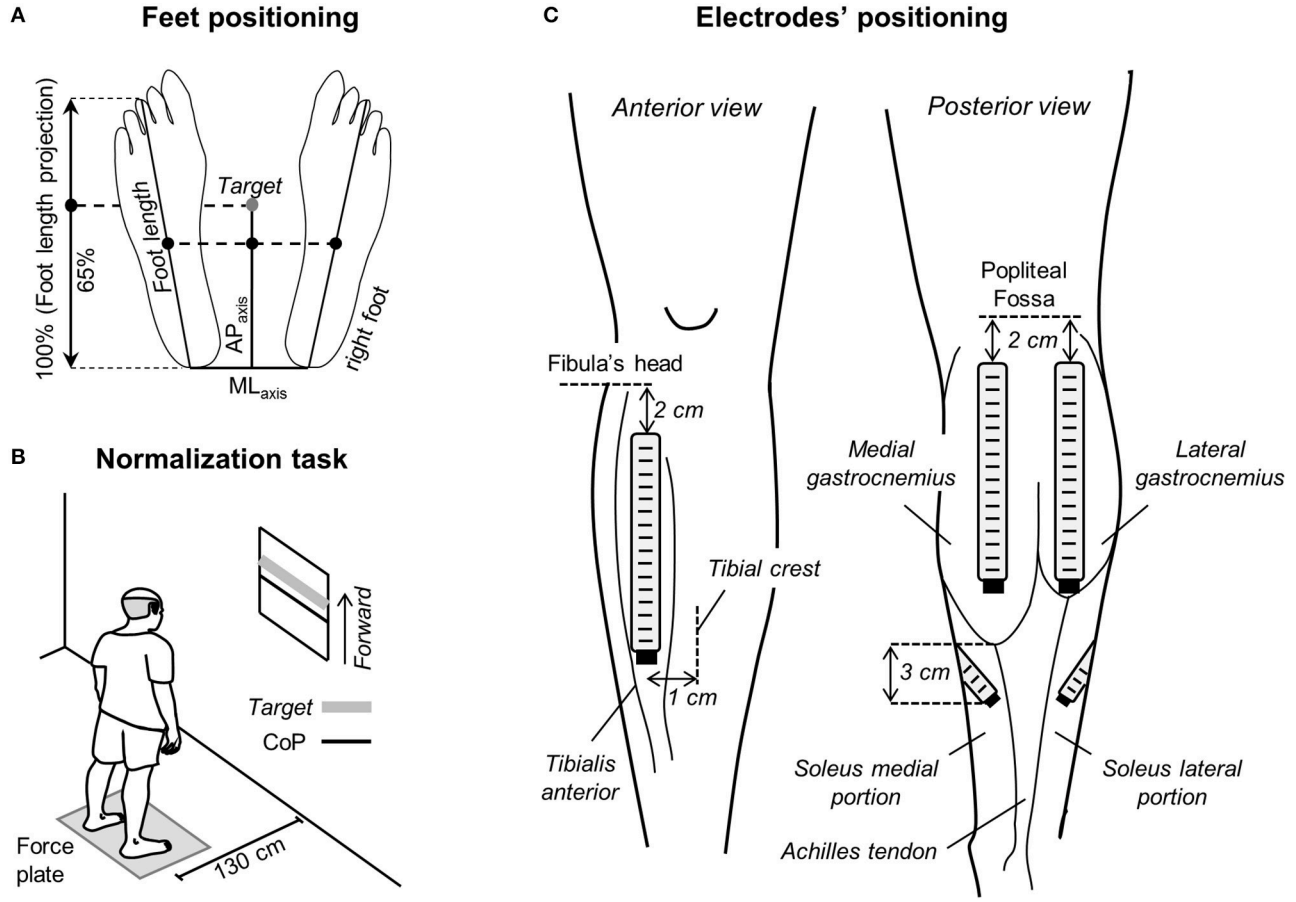

FIGURE 1 | Standing protocol and feet and electrode positioning. (A) Schematic illustration showing the procedure considered to measure feet length. The midpoint between the tip of left and right calcaneus bones was considered as the origin of the reference system for center of pressure (CoP) and foot length measurements. The target value, corresponding to 65% of the foot length projected on the anterior-posterior axis (AP_{axis}), was calculated and then considered for the normalization task shown in **(B)**. In such task, participants were asked to keep their CoP position in the AP_{axis} (black line) within 10% (±5%) of the target value (thick, gray line). **(C)** The positioning of electrode arrays is shown for the tibialis anterior muscle (left), for the medial and lateral gastrocnemius heads and for the soleus medial and lateral portions (right).

case gross body movements were noticed by the experimenter. The standing at ease task was applied three times, in accordance with previous evidence on excellent reliability of stabilometric descriptors (Pinsault and Vuillerme, 2009). Similarly, good-to-excellent reliability has been recently reported for EMGs detected from the calf muscles in aged individuals during standing (Gallina et al., 2016). Five minute intervals were applied between trials and their order was randomized.

Electrodes' Positioning

Linear arrays of surface electrodes were used to sample the distribution of ankle muscles' activity. Arrays were positioned over the plantar and dorsal flexors of both legs. Two arrays of 16 electrodes (10 mm inter-electrode distance) were used to detect surface EMGs from the medial and lateral gastrocnemius muscles. The most proximal electrode was located 2 cm distally to the popliteal fossa and arrays were aligned parallel to the longitudinal axis of each gastrocnemius' head (**Figure 1C**). Such positioning maximizes the representation of action potentials from muscle units residing in different, proximo-distal gastrocnemius' regions (Vieira et al., 2011). EMGs were sampled with one array of 16 electrodes (10 mm inter-electrode distance) from the tibialis anterior muscle, aligned 1 cm laterally and parallel to the tibial crest and with the most proximal electrode located 2 cm distally to the fibula's head (**Figure 1C**). Given the in-depth pennate architecture of tibialis anterior, as for gastrocnemius, such positioning is expected to provide EMGs representative of different, proximo-distal fibers. Two arrays with four electrodes each (10 mm inter-electrode distance) were used to sample EMGs from the soleus medial and lateral portions. For each soleus portion, arrays were aligned ∼45 degree outward to the line connecting the junction between gastrocnemius' heads and the calcaneus tip. The lower border of both the medial and lateral arrays was positioned 3 cm distally to the medial gastrocnemius myotendinous junction (**Figure 1C**; Reffad et al., 2014). Gastrocnemii junction and their myotendinous junction

were identified with ultrasound imaging (cf. Supplementary Material in Vieira et al., 2010b). Arrays were positioned after cleaning the skin with abrasive paste.

Electromyographic and Stabilometric Recordings

EMGs were recorded in single-differential derivation. All 51 single-differential EMGs were amplified by a between-individuals variable factor—from 5,000 to 10,000—to ensure the highest signal-to-noise ratio without saturation (10–750 Hz bandwidth amplifier; EMG-USB, OTBioelettronica and LISiN, Politecnico di Torino, Turin, Italy). CoP coordinates in the sagittal and frontal planes were computed from the ground reaction forces supplied by a piezoelectric force-plate (9286AA Kistler, Zurich, Switzerland). Reaction forces and surface EMGs were sampled synchronously at 2,048 Hz using a 12-bit A/D converter (±2.5 V input dynamic range).

Quantifying Muscle Activity during Standing

Raw surface EMGs were visually inspected. Whenever any channel in the array presented contact problems, likely due to high skin-electrode impedance, or massive power line interference, the corresponding channel was disregarded. Occurrences of low quality EMGs were infrequent (17 out of 1,224 EMGs detected in total) and were observed mainly in one channel per array. After controlling for signal quality, EMGs from tibialis anterior and gastrocnemius muscles were inspected for the identification of propagating potentials. Propagating potentials may be observed in the distal muscle region, where surface electrodes and muscle fibers may run in parallel direction. In such case, different electrodes sample from the same group of fibers rather than from different, proximo-distal fibers (cf. Figure 1 in Hodson-Tole et al., 2013). Channels providing propagating potentials were therefore excluded from analysis; from 0 to 8 channels per array were excluded for the 24 participants tested.

After visual inspection, EMGs were band-pass filtered with a fourth order Butterworth filter (15–350 Hz cutoff; zero lag, bidirectional filter). Then, the Root Mean Square (RMS) was computed over 40 ms epochs (Laughton et al., 2003), providing a total of 1,500 RMS values per channel. From these RMS values, three indices were considered to assess for how long, how diffusely and how much elderly and young activated their ankle muscles during standing.

Instants of activation were estimated by comparing the RMS values obtained during standing with the background activity. The background activity was defined from the RMS amplitude of EMGs collected with the ankle muscles at rest (Laughton et al., 2003). More specifically, for each channel in each array of electrodes we: (i) computed the RMS values over 40 ms epochs for EMGs detected during 3 s while participants were in supine position, providing a total of 75 RMS values; (ii) calculated the mean and the standard deviation for these RMS values; (iii) set the threshold defining the background noise level as the mean value plus three standard deviations; (iv) assigned Active or Inactive state to RMS samples respectively exceeding or not exceeding the background threshold. This procedure provided a series of Active-Inactive state values per channel. Given the EMGs detected by consecutive electrodes in the array sample from different fibers along the muscle proximo-distal axis, concurrent Active-Inactive events were often not observed between channels (**Figure 2A**). For this reason, to provide a global indication on the duration of muscle activity during standing, the muscle was deemed active whenever an Active state was observed across channels (cf. shaded areas in **Figures 2A,B**). The global series of Active-Inactive states indicates how long the ankle muscles were active throughout standing, regardless of where activity was observed in the muscle.

Based on the instants of activation, the spatial distribution and the intensity of muscle activity were computed. First, the number of channels detecting surface EMGs with RMS amplitude greater than 70% of the highest RMS amplitude in the array was identified. The 70% amplitude threshold was selected because it has been shown to provide a robust identification of channels located over active fibers within muscles pennate in the depth direction (Vieira et al., 2010a). The number of segmented channels multiplied by the inter-electrode distance was then normalized with respect to the muscle length (see below). Second, the degree of muscle activity was estimated by averaging the RMS values across all segmented channels for each muscle tested. This average RMS amplitude was then normalized with respect to the RMS amplitude averaged across channels identified during the normalization, standing task (**Figure 1B**), to compensate for the effect of anatomical differences between participants on the surface EMGs (Farina et al., 2002). It should be noted here the normalization of EMGs collected in a given condition with respect to that collected in a reference condition compensates for the effect of inter-individual differences on their amplitude though not on the spatial distribution of their amplitude. Finally, the size of the active region in the proximo-distal direction and the degree of activity were considered for analysis whenever any given muscle was active for at least 10% of the total, standing duration. Following previous evidence, occurrences of such sporadic activity was regarded as of marginal relevance for the control of standing posture (Héroux et al., 2014). Given we observed medial gastrocnemius was active for different durations (∼20%) between legs in both aged and young subjects, the electromyographic indices and architectural muscle parameters (see below) computed from the subject's leg active for longer durations (left side for 10 young and 8 elderly subjects) were used for comparisons between groups.

Measurements of Ankle Muscles' Length and Subcutaneous Thickness

Parasagittal images from tibialis anterior and gastrocnemii were taken with a linear, ultrasound probe (10 MHz, 4 cm length; Echo Blaster 128, Telemed Ltd., Vilnius, Lithuania), with participants lying comfortably on a padded bed. Initially, the myotendinous junction was identified and marked on the skin. The length of tibialis anterior was then quantified as the distance between its myotendinous junction and the head of the fibula, whereas the

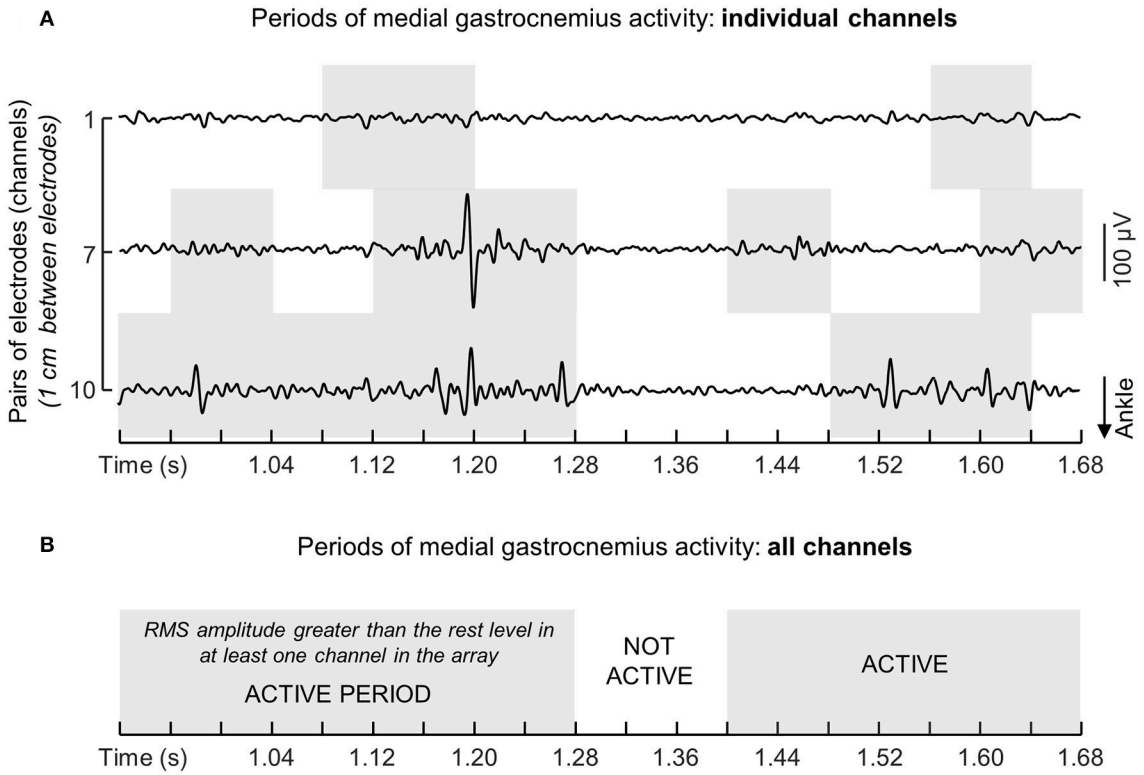

FIGURE 2 | Computation of instants of muscle activation. (A) Shows examples of single-differential EMGs detected by channels 1, 7, and 10 from the medial gastrocnemius muscle of a single participant. Note action potentials do not appear with equally high amplitude in the three channels. The muscle was considered active whenever for any given instants the RMS amplitude exceeded the background activity in at least one channel. Light gray rectangles in the grid denote periods within which the RMS amplitude of EMGs in each channel exceeded the background activity computed with the muscle at rest (see text). The resulting series of instants of muscle activity for this representative example is illustrated with a succession of white (Inactive state; muscle at rest) and gray (Active state; muscle active) rectangles **(B)**.

length of each gastrocnemius head was defined as the shortest distance between the myoetendinous junction and the popliteal fossa. Subcutaneous thickness and pennation angle were further quantified to assist in the interpretation of potential proximo-distal differences in the distribution of activity with aging. Subcutaneous thickness was computed as the distance between the skin/fat layer over the muscle and its superficial aponeurosis from parasagittal images obtained with the probe centered halfway the muscle length. Thickness measurements were taken from the central region of the proximal, central and distal thirds of the ultrasound images and then averaged, providing a representative indication on the general subcutaneous thickness per subject (Onambele et al., 2006). Finally, the pennation angle was estimated as the angle between a clearly visible fascicle in the image and the muscle deep aponeurosis (Avancini et al., 2015). Thickness and pennation angle values were obtained with the muscle at rest.

Quantifying the CoP Sway Area

The CoP sway area was considered to assess how largely young and elderly individuals swayed during the whole standing tests. The overall size of postural sways was estimated from the elliptic area conveying almost 85% of the total CoP samples during standing (Oliveira et al., 1996). The CoP elliptic area, as well as the EMG descriptors, were averaged across the three standing trials and considered for between-group comparisons. CoP data was 50 Hz low-pass filtered with a second order Butterworth filter to remove high-frequency noise.

Statistical Analysis

Non-parametric statistics were applied to compare the distribution of ankle muscles' activity between young and aged individuals, after ensuring the data distribution was not Gaussian (Shapiro-Wilk's W-test, $P < 0.03$ in all cases). The Mann-Whitney U-test was used to verify whether, during standing and for each muscle independently, the duration of the active period, the degree of activity, the relative size of the active region and the CoP elliptic area were different between groups. The same statistics was applied to assess regional differences in activity within soleus, by comparing the normalized RMS amplitude obtained for the muscle medial and lateral aspects. The level of statistical significance was set at 5% and data were reported using non-parametric, descriptive statistics.

RESULTS

Representative Examples of Variations in Ankle Muscles' Activity during Standing

Different ankle muscles were activated differently when young and aged individuals stood at ease. Descriptive considerations on these differences are summarized in this section based on the data shown in **Figure 3** for one young and one aged, representative participant. Lateral gastrocnemius was active for 6 and 17% of the whole standing trial for the young and aged subjects respectively. For the tibialis anterior muscle, the amplitude of EMGs remained below the background activity for the young subject during the whole standing duration while, for the elderly, bursts of activity were observed and provided an active duration of 36%. Conversely, EMGs with remarkably high amplitude in the soleus medial and lateral portions were observed consistently for both subjects (cf. shaded areas in **Figure 3**).

The medial gastrocnemius showed a somewhat different pattern of activity when compared with the other ankle muscles. Differently from lateral gastrocnemius, soleus and tibialis anterior, medial gastrocnemius was not completely silenced, was not activated almost continuously and did not show sporadic bursts of activity. For both participants whose data is shown in **Figure 3**, alternate periods of medial gastrocnemius activation and silencing were observed consistently during standing (**Figure 4A**). When considering the distribution of activity within medial gastrocnemius, EMGs with relatively high amplitude were detected by six channels in the young and by nine channels in the aged subject (cf. gray circles in **Figure 4B**).

Ankle Muscles' Activation in Elderly and Young Individuals during Standing

When considering group data, differences in the duration of ankle muscles' activity were observed between elderly and young subjects. The Mann-Whitney *U*-test revealed the medial gastrocnemius was activated for longer periods in aged (median, interquartile interval; 81.2, 74.1–98.2%) than young (58.8, 44.9–81.9%) individuals (**Figure 5A**; $P = 0.02$; $N = 24$; 13 young × 11 aged subjects). Similarly, notwithstanding the marked variability in the duration of active periods for the elderly, aged participants activated their tibialis anterior muscle during standing for a significantly longer duration than young subjects ($P = 0.01$; $N = 24$); tibialis anterior was rarely active in young (1.3, 0.7–4.4%) though not in the elderly (29.1, 2.6–82.5%). No group differences were observed in the duration of lateral gastrocnemius ($P = 0.07$) and soleus medial ($P = 0.90$) and lateral ($P = 0.26$) portions.

The degree and the distribution of activity within ankle plantar flexors varied differently between groups. The RMS amplitude of EMGs collected from the medial gastrocnemius

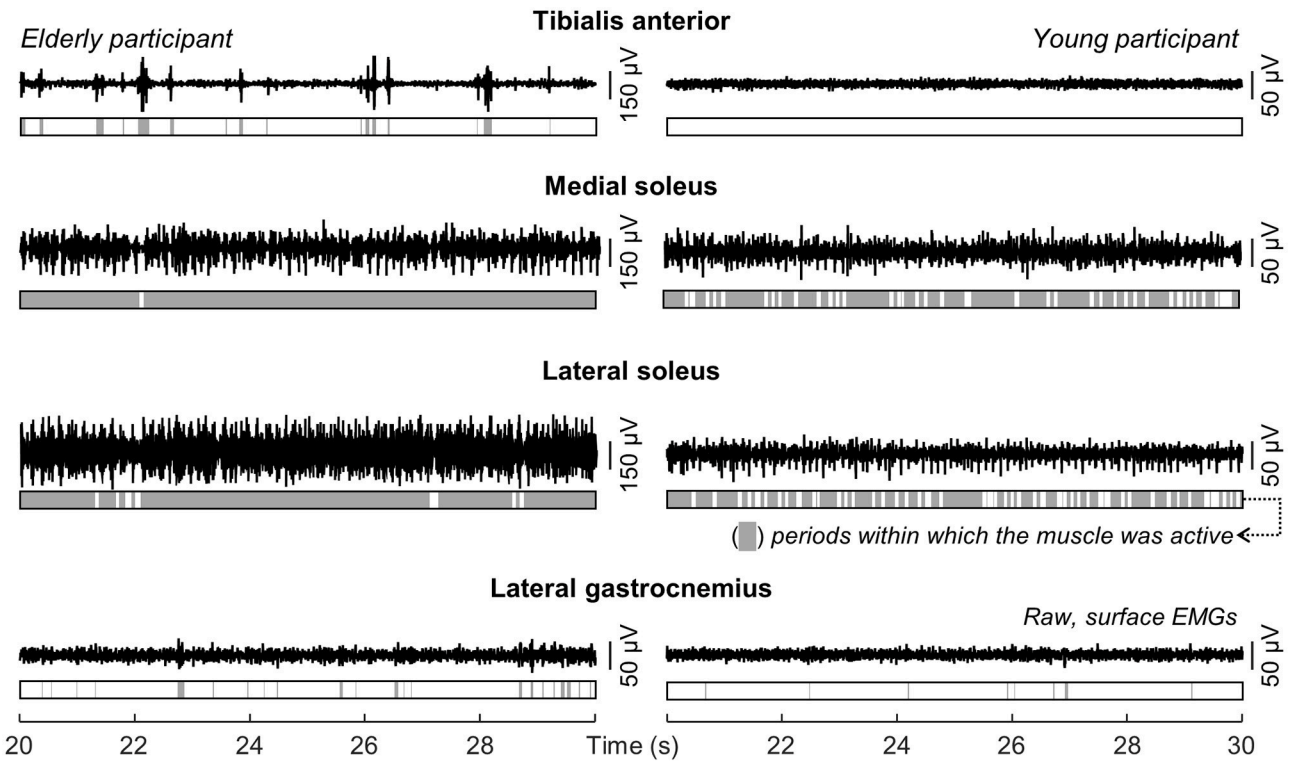

FIGURE 3 | Modulations in ankle muscles' activity during standing. Single-differential EMGs collected for a representative channel from the tibialis anterior, the soleus medial and lateral portions and from the lateral gastrocnemius of a representative young and elderly participant are shown for 10 s of standing at ease. Light gray areas in the bars indicate periods within which the RMS amplitude exceeded the background activity (i.e., Active state).

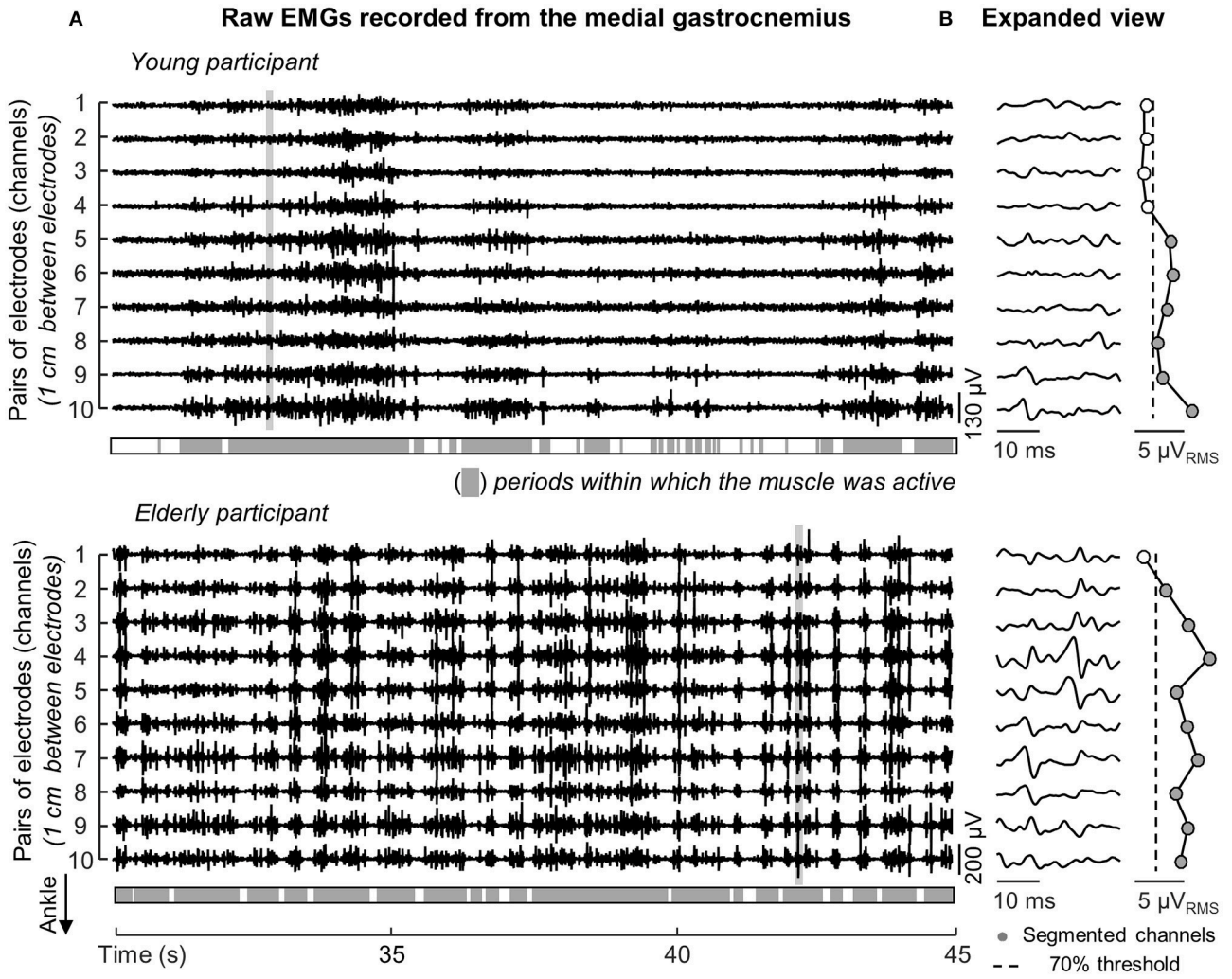

FIGURE 4 | Duration and distribution of medial gastrocnemius activity during standing. Raw EMGs detected by channels located over the gastrocnemius superficial aponeurosis, from channel 1 to 10, are shown in **(A)** for a young and elderly representative participant. Light gray areas indicate periods within which the RMS amplitude exceeded the background activity. **(B)** Shows an expanded view of all EMGs. Note different action potentials appear in different channels for each subject. Note also there is no delay between potentials detected by consecutive channels (e.g., channels 1–6 for the aged participant). The distribution of RMS amplitude across channels is represented from circles, with gray circles indicating the *segmented channels*; that is, channels detecting largest EMGs in the array (see text).

and from the medial and lateral soleus portions did not differ between elderly and young (**Figure 5B**; $P > 0.40$ in all cases; $N = 24$). No differences were observed between the RMS amplitude for EMGs collected medially and laterally from soleus muscle, both for young and elderly ($P > 0.70$ in both cases). In contrast, for medial gastrocnemius, EMGs with relatively higher amplitude were detected over a significantly wider proximo-distal region in aged (32.5, 29.4–45.6%) than young (29.8, 20.1–31.3%) subjects (**Figure 5C**; $P = 0.04$; $N = 24$). Given the lateral gastrocnemius and tibialis anterior of young individuals were active for a somewhat short period during the whole standing tests (less than 10% on average; **Figure 5A**), these muscles were disregarded from further consideration.

Medial Gastrocnemius' Subcutaneous Thickness and Pennation Angle

No differences in subcutaneous thickness were observed between groups ($P = 0.58$). Thickness values ranged from 1.6 to 2.7 mm for young and from 1.6 to 3.5 for aged participants. Similarly, the pennation angle did not differ significantly ($P = 0.37$) between young (range: 19.6–24.0 degrees) and aged subjects (17.2–25.0 degrees).

Differences in CoP Sway Area with Age

While aged participants stood at ease, their CoP occupied an area roughly twice (median, interquartile interval; 4.4, 3.8–9.6 cm^2) as large as that (2.3, 1.6–4.5 cm^2) confining the CoP of young participants ($P = 0.052$).

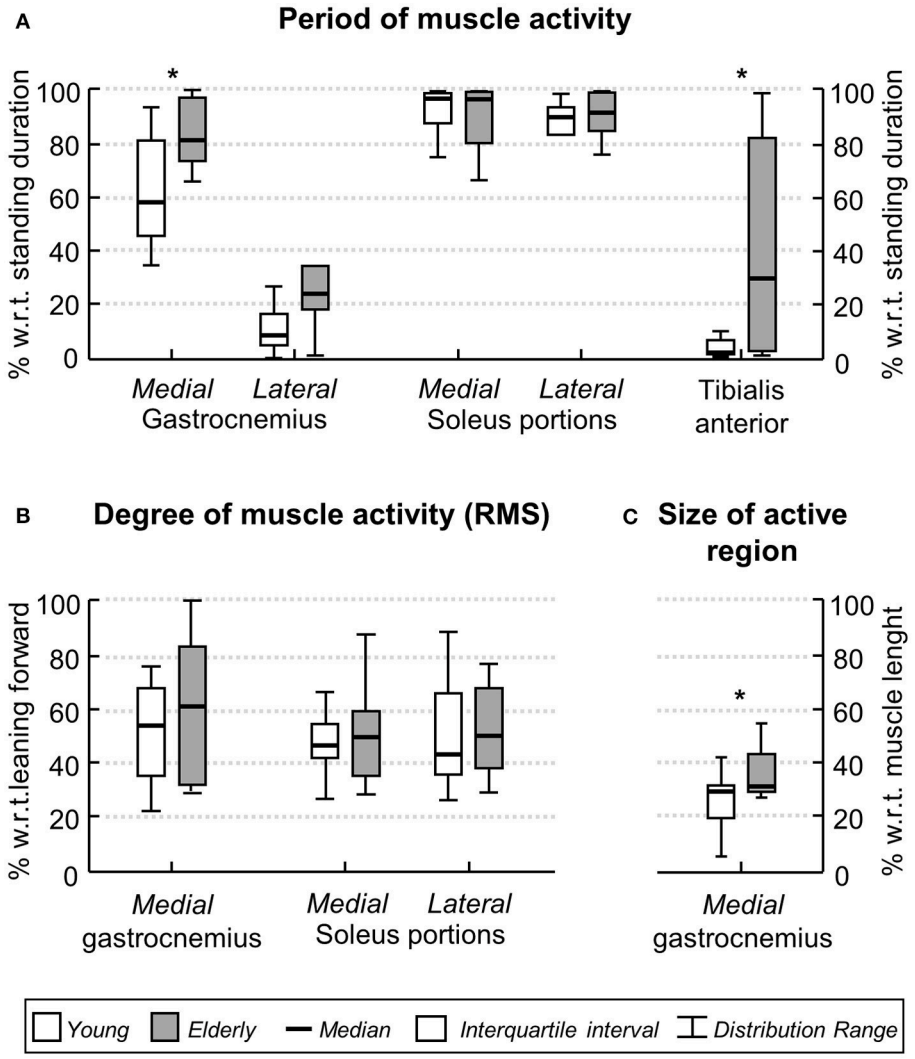

FIGURE 5 | Age-related differences in the ankle muscles' activity during standing. Boxplots in **(A)** show the relative period within which, during standing, young (white boxes) and elderly (gray boxes) individuals activated their ankle muscles. Group data in **(B)** corresponds to the normalized, RMS amplitude obtained for both groups from the medial gastrocnemius and from the medial and lateral soleus portions. The proximo-distal size of medial gastrocnemius region over which largest EMGs were detected in both groups is shown in **(C)**. Asterisks indicate significant differences between groups ($P < 0.05$).

DISCUSSION

In this study we used arrays of electrodes to investigate whether the temporal and spatial distributions of ankle muscles' activity differ between elderly and young individuals during standing. We hypothesized that elderlies would present greater EMGs, distributed over a larger muscle region and for a longer duration than young individuals. Surface EMGs from different regions of the ankle muscles were collected while subjects stood at ease to test this hypothesis. Our key results indicate that during standing: (i) tibialis anterior and medial gastrocnemius muscles were active for a longer duration in aged than young subjects; (ii) a greater proportion of medial gastrocnemius volume was active in elderlies. Collectively, these results indicate elderlies rely more heavily on the active loading of ankle muscles to control their standing posture than young individuals.

Preliminary, Methodological Considerations on Surface EMG Detection

Differently from previous studies, here we sampled surface EMGs with arrays of electrodes (**Figure 1C**). Our decision to sample activity from multiple locations of individual ankle muscles was motivated by recent evidence suggesting different muscle regions may be activated differently (Brown et al., 2007; Farina et al., 2008), in particular for pennate muscles (McLean and Goudy, 2004; Staudenmann et al., 2009; Vieira et al., 2011; Hodson-Tole et al., 2013); EMGs sampled locally (i.e., with a single pair of shortly spaced electrodes) may not provide a representative

view of muscle activation. Indeed, as shown in **Figure 2**, EMGs in different locations may provide different estimations for the duration of gastrocnemius activity. Considering EMGs were represented with different amplitude in different muscle regions (**Figures 2**, **4**), the duration of muscle activity would have been likely underestimated if we had not considered EMGs detected at different skin regions (cf. shaded areas for individual and all channels in **Figure 2**). Similarly, biased estimations on the degree of each calf muscles' activity would have been obtained if we had considered the RMS amplitude of EMGs detected locally. Depending on where EMGs were detected from, in particular for young individuals (**Figure 4**), their corresponding RMS values would provide either under- (white circles in **Figure 4B**) or over- (gray circles in **Figure 4B**) estimates of the degree of activity in the whole muscle. Through arrays of surface electrodes, we were able to obtain estimates of the duration and degree of activity presumably more representative of individual ankle muscles' volumes than previously appreciated. As discussed below, new insights have been gained into age-related differences in postural activation from such a high-density, surface EMG approach.

Are the Ankle Muscles Activated for a Similar Duration in Aged and Young Subjects?

The differences between aged and young individuals reported here were muscle dependent. When considering the duration of activity for lateral gastrocnemius and soleus muscles, statistic differences were not observed between groups. Both groups recruited lateral gastrocnemius for less than ∼20% of the total, standing duration (**Figures 3**, **5A**). The soleus muscle, on the other hand, was activated for periods roughly longer than 80% of standing. These results corroborate previous findings on the duration of calf muscles' activity, extensively reported for young subjects. Indeed, while the absence of activity in lateral gastrocnemius has been observed in some subjects (Masani et al., 2013; Héroux et al., 2014), it seems well-documented that soleus is recruited at almost all time during standing (Laughton et al., 2003; Héroux et al., 2014). Even though the temporal activation of postural muscles is not as commonly assessed for elderlies as it is for young individuals, Laughton et al. (2003) observed age similarities for the duration of soleus activity during standing. Extending the observation of Laughton et al. (2003), our current results suggest the duration of activity of the lateral gastrocnemius and soleus regions accessed by our surface electrodes is unlikely sensitive to aging.

Age differences emerged however in the duration of medial gastrocnemius and tibialis anterior activity during standing. Aged individuals activated their medial gastrocnemius muscle for a period ∼20% longer, on average, than their young counterparts (**Figure 5A**). Similarly, tibialis anterior was active for a longer (∼30%) period in aged than in young subjects (**Figure 5A**). The median duration of tibialis anterior activity observed here, both for young (∼2%) and elderlies (∼30%), is well in agreement with the duration of activity periods reported by Laughton et al. (2003) for this muscle. From a first inspection of results presented in **Figure 5A**, we feel inclined to consider the co-activation mechanism as responsible for the age differences in the timing of plantar and dorsal flexors' activation during standing. More specifically, while young subjects predominantly activated their plantar flexors, elderlies activated both plantar and dorsal flexor muscles during standing (**Figures 3**, **4A**, **5A**). In spite of controversies on whether co-activation may be detrimental or may compensate for poor control of posture, co-activation is often associated with increased postural sways (Nagai et al., 2011; Baudry et al., 2012; Warnica et al., 2014). Corroborating this common view, in the elderlies, we observed the CoP was confined within an elliptic area almost twice as large as that confining the CoP of young subjects. Regardless of the mechanisms underpinning age-differences in posture control, current results here suggest elderlies activate their ankle muscles for longer durations during standing than young subjects.

Do Elderly and Young Recruit Their Calf Muscles to a Similar Extent during Standing?

Two notes on our estimates of the degree of activity are necessary before interpreting results. Young subjects activated tibialis anterior and lateral gastrocnemius somewhat rarely (**Figures 3**, **5A**). We therefore disregarded both muscles from age comparisons. A second observation concerns how we conceived muscle activity. While the amplitude of EMGs is traditionally considered to assess the degree of muscle activity, here we considered both the amplitude and the size of skin region where EMGs with relatively high amplitude were sampled (**Figures 2**, **4**). As argued below, the extent to which elderly and young activate their calf muscles depends both on the amplitude and on the amplitude distribution of surface EMGs.

The proximo-distal distribution of the amplitude of medial gastrocnemius EMGs distinguished aged from young individuals during standing. While young subjects presented EMGs with relatively high amplitude in the gastrocnemius distal region, corroborating previous findings (Hodson-Tole et al., 2013), EMGs with similarly high amplitude were sampled from a larger, proximo-distal muscle region in aged individuals (c.f. gray circles in **Figures 4B**, **5C**). Different sources could have accounted for a somewhat extensive distribution of EMG amplitude in the elderlies. A first issue to consider is the potential difference in muscle architecture between groups. Both subcutaneous thickness and pennation angle have shown to affect dramatically the amplitude distribution of surface EMGs; thicker subcutaneous tissue and smaller pennation angle result both in more spatially diffused surface EMGs (Farina et al., 2002; Mesin et al., 2011). Current results however did not indicate significant, age differences in gastrocnemius architecture. The lack of anatomical differences between groups leads us to consider the possibility that elderlies activated a larger gastrocnemius volume than young subjects during standing. In spite of recent controversies (Blouin et al., 2016; Vieira et al., 2016), it seems well-accepted that, for the gastrocnemius muscle, EMGs sampled in different proximo-distal regions reflect the activity of different muscle fibers (Vieira et al., 2011). The amplitude of EMGs detected distally and proximally, for example, is associated with

the number of active fibers in the muscle distal and proximal regions respectively (Mesin et al., 2011). Given the mean amplitude of EMGs sampled from medial gastrocnemius was similar between groups (**Figure 5B**), the wider skin region from where EMGs with high amplitude were detected (**Figure 5C**) suggests a relatively greater proportion of muscle fibers may have been recruited in the elderlies.

Age differences in the distribution of activity for soleus were not as clear as for gastrocnemius. Since soleus is largely covered by the gastrocnemius muscles, spatial differences in soleus activation were assessed by comparing the amplitude of EMGs detected laterally and medially (**Figure 1C**). Our decision to assess both regions was based on previous evidence showing medio-lateral differences in soleus activation (Staudenmann et al., 2009; Reffad et al., 2014). Given we were here interested in assessing the degree of muscle activity during standing, sampling EMGs unilaterally could provide a biased view on the actual degree of soleus, postural activity. Indeed, even though results in **Figure 5B** indicate EMGs with equal amplitude were detected medio-laterally for both age groups, stating young and aged subjects activate a similar proportion of their soleus muscle in standing is potentially fairly speculative. Considerations on the relevance of spatial differences in soleus activation with age are therefore conditioned to the possibility of sampling EMGs from a greater soleus region (with e.g., intramuscular electrodes) in future investigations.

Future Perspectives and Limitations

Spatial differences in the amplitude of EMGs collected from elderlies and young during standing have methodological and physiological implications. A first crucial point to consider is the localized representation of surface EMG during standing. Here we show that, depending on where a single bipolar EMG is collected from the gastrocnemius muscle, different conclusions maybe drawn on age differences during standing. The local sampling of muscle activity provided by bipolar surface EMGs may indeed contribute to explaining current disparities observed in the literature. While some studies did not report age differences in the degree of plantar flexors' activity during standing at ease (Amiridis et al., 2003; Laughton et al., 2003), others have however documented a significantly higher degree of plantar flexor activation with aging (Nagai et al., 2011; Baudry et al., 2012). Anticipating the differences between studies were due to inappropriate EMG sampling is a statement we strongly discourage. On the other hand, though, our current results suggest that different interpretations may emerge from EMGs detected locally during standing. Of more physiological, applied interest, is the suggestion that elderlies tend to stand with a greater degree of muscle effort than young subjects (**Figures 5A,C**). According to recent evidence, standing with minimal muscular effort while affording some degree of bodily sways may be advantageous; it may reduce the metabolic cost of standing (Bottaro et al., 2008), eliminate motor noise (Loram et al., 2011) and compensate for delays in the feedback loop (Cabrera and Milton, 2002). While acknowledging the value of different protocols so far devised for the balance training (Li et al., 2005; Sayenko et al., 2010), here we suggest that learning to efficiently activate dorsal and plantar flexors during standing could be beneficial for the control of standing posture in aged individuals.

Some additional considerations on the results presented here are necessary. Both young and aged subjects showed a somewhat large variability in the duration of ankle muscles activity (**Figure 5A**). A first possible explanation to such inter-individual variability is the difference in ankle stiffness between subjects (Loram and Lakie, 2002a). Additionally, the inter-individual variability in muscle activation during standing, in particular the duration of tibialis anterior activation in the elderly, may be due to different neural sources. With aging, an assortment of impairments arising at the peripheral and central levels of the nervous system may develop, each impacting detrimentally and differently on the control of the standing posture (Horak et al., 1997). By testing subjects without a sedentary lifestyle we expect to have limited the repertoire of posture-related impairments affecting present results. A final consideration regards whether crosstalk could have affected our results. We believe this possibility is unlikely. First because action potentials were represented locally in the surface EMGs. For example, the fact that action potentials detected from a given gastrocnemius region did not appear in neighbor channels (cf. **Figure 2** and expanded view of EMGs in **Figure 4**) suggest any crosstalk from muscles other than gastrocnemius was relatively marginal. Moreover, the duration of activity of both muscles would be the same if crosstalk from soleus had contributed substantially to EMGs collected from gastrocnemius. In spite of these considerations, our results show the duration and the region of muscle activity, as quantified from surface EMGs, discriminate well-aged from young individuals during standing.

AUTHOR CONTRIBUTIONS

FD and TV were involved with all aspects of the study. TP contributed to acquire, analyse and interpret the data. MG contributed to analyse and interpret the data. All authors contributed to draft the work and revise it critically.

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frontiers in Human Neuroscience

ORIGINAL RESEARCH
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Effects of Age-Related Macular Degeneration on Postural Sway

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Purpose: To compare the impact of unilateral vs. bilateral age-related macular degeneration (AMD) on postural sway, and the influence of different visual conditions. The hypothesis of our study was that the impact of AMD will be different between unilateral and bilateral AMD subjects compared to age-matched healthy elderly.

Methods: Postural stability was measured with a platform (TechnoConcept®) in 10 elderly unilateral AMD subjects (mean age: 71.1 ± 4.6 years), 10 elderly bilateral AMD subjects (mean age: 70.8 ± 6.1 years), and 10 healthy age-matched control subjects (mean age: 69.8 ± 6.3 years). Four visual conditions were tested: both eyes viewing condition (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), and eyes closed (EC). We analyzed the surface area, the length, the mean speed, the anteroposterior (AP), and mediolateral (ML) displacement of the center of pressure (CoP).

Results: Bilateral AMD subjects had a surface area ($p < 0.05$) and AP displacement of the CoP ($p < 0.01$) higher than healthy elderly. Unilateral AMD subjects had more AP displacement of the CoP ($p < 0.05$) than healthy elderly.

Conclusions: We suggest that ADM subjects could have poor postural adaptive mechanisms leading to increase their postural instability. Further studies will aim to improve knowledge on such issue and to develop reeducation techniques in these patients.

Keywords: age-related macular degeneration, postural sway, elderly, visual condition, balance

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INTRODUCTION

Age-Related Macular Degeneration (AMD) is the first cause of blindness after fifty years old in developed countries (Kocur and Resnikoff, 2002; Augood et al., 2006). This pathology is characterized by uni- or bi-lateral photoreceptor degeneration, which generates a large scotoma including central vision (Leveziel et al., 2009). Peripheral vision is conserved. AMD is a multifactorial and polygenic pathology with three main risk factors: age, environment and genetics (Chakravarthy et al., 2007; Wang et al., 2008, 2009). AMD represents a true public health issue because of the prevalence (1.6% before 64 years old and 27.9% after 85 years old; Ferris, 1983; Hyman and Neborsky, 2002; Friedman et al., 2004), the cost of care (which increases with disease severity; Bandello et al., 2008), psychological impact and functional disability (difficulty reading,

driving restriction, difficulty of stereoscopic vision, difficulty recognizing faces, etc.; Augustin et al., 2007; Christoforidis et al., 2011; Hochberg et al., 2012; Sengupta et al., 2014; McCloud and Lake, 2015). This pathology affects more than one million people in France.

According to HAS (*Haute Autorité de Santé)* and other authors, 33% of subjects older than 65 years have experienced at least one fall per year (Tinetti et al., 1988; Campbell et al., 1989; Wood et al., 2011). It is a real public health problem because of autonomy loss and of the medical cost ($6–8 billion by year in the United States alone; Carroll et al., 2005).

Postural control is an elaborated process which allows a coordinated relationship of body segments (static and dynamic positions; Paillard, 1971; Gurfinkel and Shik, 1973). It is controlled by vestibular, proprioceptive, and visual information (Nashner, 1979; Horak and Shupert, 1994; Fetter and Dichgans, 1996). The vestibular system contributes to postural stability with eyes open (Fitzpatrick and McCloskey, 1994). Vision and proprioception participate to the detection of slow movements in the visual environment. When the visual or the vestibular system is affected, subjects need to compensate with other sensorial inputs (Brandt, 2003).

Some studies examined the impact of AMD on postural control (Elliott et al., 1995; Wood et al., 2009; Kotecha et al., 2013). Elliott et al. (1995) explored balance control (anterior-posterior sways of CoP) in AMD subjects compared to age-matched control subjects on a stable/unstable platform. They showed that postural stability in AMD subjects was poor when the inputs of kinesthetic sensory system were disrupted. The authors suggested that in normal standing condition, the vestibular and kinesthetic systems compensated for the lack of visual information in AMD subjects. Wood et al. (2009) studied postural stability in older adults with age-related maculopathy in order to identify the visual factors associated with postural control and falls. They proved that diminution of contrast sensitivity and visual field loss lead to postural instability and mobility difficulties. Kotecha et al. (2013) examined the effect of a secondary task on standing balance in elderly subjects with central visual field loss (AMD) or peripheral visual field loss (glaucoma) compared with age-matched healthy subjects. They compared two standing conditions: eyes open on a firm or a foam surface. These authors found that during the secondary task, AMD subjects were more unstable than healthy elderly on a firm and foam surface, while glaucoma subjects were more unstable on the foam surface only. Authors suggested that when subjects have visual impairment, they have to increase somatosensory contribution to obtain a good postural stability, and that peripheral vision is important when somatosensory inputs are disturbed.

The role of central vs. peripheral vision information in control of movements and posture was examined in numerous studies (i.e., Berencsi et al., 2005; Marigold and Patla, 2007). These authors suggested that peripheral vision is used for postural control and most particularly for stabilization of fore-aft sways; central vision is more used for foot trajectory planning, targeting, obstacle avoidance, and for stabilization of lateral sways.

Taken together all these findings showed poor postural stability in patients with AMD, particularly under eyes open condition; the novelty of the present study was to explore further AMD pathology (i) unilateral vs. bilateral AMD (ii) and the effect of different visual condition (both eyes open, and one eye alternatively open, dominant and non-dominant).

The hypothesis of our study was that the impact of AMD could be different between unilateral and bilateral AMD subjects compared with age-matched healthy elderly, and that postural sways could be different for different eye viewing conditions.

MATERIALS AND METHODS

Subjects

A total of 10 unilateral AMD patients between 62.8 and 76.7 years old (mean age: 71.1 ± 4.6 years) and 10 bilateral AMD patients between 57.1 and 78.5 years old (mean age: 70.8 ± 6.1 years) participated in the study. We also tested 10 age-matched healthy controls (mean age: 69.8 ± 6.3 years). All participants were recruited from the Department of Ophthalmology, Hôtel-Dieu Hospital in Paris and from the *Centre Ophtalmologique du Val-d'Oise* (France). Their participation was voluntary.

All participants had to fulfill criteria: ametropia inferior to five dioptries (spherical equivalent), no ocular surgery background, no retina laser treatment, no other ophthalmology pathologies, no diabetes, no known cognitive loss, no known vestibular abnormality, and no known orthopedic surgeries and abnormalities.

The investigation adhered to the principles of the Declaration of Helsinki and was approved by our Institutional Human Experimentation Committee (*Comité de Protection des Personnes CPP, Ile de France V*). Written informed consent was obtained from each participant after an explanation of the experimental procedure.

Ophthalmologic and Orthoptic Evaluation

All AMD subjects underwent ophthalmologic and orthoptic examination to evaluate their visual function. Clinical data of each AMD patients are shown in **Tables 1, 2**. Clinical data of healthy elderly subjects are shown in **Table 3**.

Visual acuity was measured separately for each eye at far distance (5 m) with the Monoyer chart. Next we have translated to ETDRS with an adapted scale. Stereoscopic acuity was measured by TNO test (Test of Netherlands Organization for Applied Scientific Research; Walraven, 1975). Unilateral AMD patients have a corrected monocular visual acuity between 20/125 and 20/20, and bilateral AMD patients a corrected monocular acuity between 20/800 and 20/25. Only eight of the ten AMD participants have a stereoscopic acuity <480 s of arc. Visual functions are also evaluated for control subjects. They have a monocular corrected visual acuity of 20/20 and stereoscopic acuity for 120 s of arc.

Age-related macular degeneration severity scale of AREDS was used for each eye (AREDS, 2001). SD-OCT (Spectralis®, Heidelberg Engineering) for each eye allows identifying AMD level by locating geographic atrophies (deterioration of the photoreceptors) and choroidal neovascularization (growth of

TABLE 1 | Clinical characteristics of unilateral AMD subjects.

Patient (Age, years)	ETDRS		Glasses correction		AMD level		Type of AMD	Scotoma		Stereoacuity (TNO)	Eye dominant
S1 (62.8)	RE:	20/40	RE:	+1.75 (−0.75) 100°	RE:	3	CNV	RE:	Perimacular	200″	LE
	LE:	20/20	LE:	+1.5 (−1.75) 85°	LE:	1	/	LE:	/		
S2 (63.8)	RE:	20/125	RE:	+2.25 (−0.25) 130°	RE:	4	GA	RE:	Perimacular	/	LE
	LE:	20/20	LE:	+2 (−0.5) 60°	LE:	1	/	LE:	/		
S3 (63.5)	RE:	20/20	RE:	+1.25 (−0.25) 80°	RE:	2	/	RE:	/	/	RE
	LE:	20/32	LE:	+1.5 (−0.25) 85°	LE:	4	CNV	LE:	/		
S4 (70.5)	RE:	20/40	RE:	+0.75 (−0.75) 40°	RE:	4	CNV	RE:	Perimacular	/	LE
	LE:	20/25	LE:	+2.5 (−0.75) 160°	LE:	2	/	LE:	/		
S5 (72.4)	RE:	20/20	RE:	−0.5 (−0.5) 105°	RE:	1	/	RE:	/	/	RE
	LE:	20/32	LE:	+0.5 (−0.75) 80°	LE:	4	CNV	LE:	Paramacular		
S6 (72.5)	RE:	20/25	RE:	+4.75	RE:	3	GA	RE:	/	480″	LE
	LE:	20/20	LE:	+4.75 (−0.75) 130°	LE:	2	/	LE:	/		
S7 (72.7)	RE:	20/20	RE:	+2.5 (−1) 90°	RE:	1	/	RE:	/	/	RE
	LE:	20/50	LE:	+2.75 (−1.5) 100°	LE:	4	CNV	LE:	Perimacular		
S8 (73.4)	RE:	20/40	RE:	+1.75 (−0.75) 80°	RE:	4	CNV	RE:	Perimacular	480″	LE
	LE:	20/40	LE:	+2 (−1)110°	LE:	3	/	LE:	/		
S9 (76.3)	RE:	20/32	RE:	+3 (−0.75) 95°	RE:	3	CNV	RE:	/	480″	LE
	LE:	20/20	LE:	+3.25 (−0.75) 125°	LE:	1	/	LE:	/		
S10 (76.7)	RE:	20/20	RE:	+0.75 (−0.75) 115°	RE:	1	/	RE:	/	480″	RE
	LE:	20/40	LE:	+0.75 (−0.75) 60°	LE:	4	CNV	LE:	Paramacular		

Data are reported for each participant with unilateral AMD. Their corrected visual acuity (ETDRS), glasses correction, AMD level, type of AMD (GA, geographic atrophy; CNV, choroidal neovascularization), stereoscopic acuity (seconds of arc, TNO test) and dominant eye are reported (LE, left eye; RE, right eye).

pathologic blood vessels from the choroid into the subretinal space).

Among participants, 60% of bilateral AMD and 80% of unilateral AMD are choroidal neovascularization. Other studies have reported that there is two AMD with choroidal neovascularization for one AMD with geographic atrophy (Chakravarthy et al., 2007).

The eye with the better corrected visual acuity is considered as the dominant eye.

Posturography

A force platform (AFP40/16 Stabilotest, principle of strain gauge) consisting of two dynamometric clogs was used to measure and quantify postural stability (Standards by *Association Française de Posturologie*, produced by TechnoConcept®, Céreste, France; **Figure 1**). Foot position is standardized with footprints. This platform included a 16-bit analog-digital and acquisition frequency was 40 Hz. The excursion of center of pressure was measured during 25.6 s. Postural parameters were calculated following Gagey's standards (Gagey et al., 1993; Gagey and Weber, 1999).

Postural Recording Procedure

In a dark room, participants stood on the platform and fixed a target (3 × 3 cm; identically for all subjects) in front of their eye level (150 cm). Four visual conditions were tested: binocular eye viewing (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), and eyes closed (EC). We choose to test postural control separately for each eye in order to compare the impact of level of AMD on postural stability in order to develop training techniques for these subjects, even if these conditions are not physiological. Subjects were instructed to stay as still as possible with their arms along their body, to fix the target and stand quietly on the platform. Three randomized trials were performed for each visual condition successively. A short break was done between each condition. The total duration of the trial was 10 min.

Data Processing

To quantify the effect of AMD and visual conditions on postural control we analyzed the surface area (mm^2), the length (mm), the mean speed (mm/s), and the anteroposterior (AP) and mediolateral (ML) displacements (mm) of the CoP that are the standard deviation of the displacement. Surface area is an

TABLE 2 | Clinical characteristics of bilateral AMD subjects.

Patient (Age, years)	ETDRS		Glasses correction		AMD level		Type of AMD		Scotoma	Stereoacuity (TNO)	Dominant eye
S11 (57.1)	RE:	20/40	RE:	+5 (−0.5) 80°	RE:	4	CNV	RE:	Perimacular	/	LE
	LE:	20/20	LE:	+3.5 (−0.5) 105°	LE:	3	CNV	LE:	Paramacular		
S12 (65.9)	RE:	20/800	RE:	+1.75 (−0.5) 110°	RE:	4	CNV	RE:	Perimacular	/	LE
	LE:	20/100	LE:	+1 (−0.75) 150°	LE:	4	CNV	LE:	Perimacular		
S13 (69.6)	RE:	20/20	RE:	+2 (−0.5) 130°	RE:	3	GA	RE:	Perimacular	480″	RE
	LE:	20/25	LE:	+2 (−0.5) 50°	LE:	3	GA	LE:	Perimacular		
S14 (69.8)	RE:	20/800	RE:	/	RE:	4	CNV	RE:	Paramacular	/	LE
	LE:	20/50	LE:	/	LE:	3	CNV	LE:	Perimacular		
S15 (69.9)	RE:	20/25	RE:	+0.5 (−0.75) 95°	RE:	3	CNV	RE:	/	480″	RE
	LE:	20/63	LE:	+0.75 (−0.5) 90°	LE:	4	CNV	LE:	/		
S16 (71.7)	RE:	20/800	RE:	/	RE:	4	GA	RE:	Para- and perimacular	/	RE
	LE:	20/320	LE:	/	LE:	4	GA	LE:	Paramacular		
S17 (74.1)	RE:	20/125	RE:	/	RE:	3	GA	RE:	Perimacular	/	RE
	LE:	20/20	LE:	+0.5 (−0.25) 145°	LE:	3	CNV	LE:	Paramacular		
S18 (74.8)	RE:	20/25	RE:	+1.25 (−0.75) 100°	RE:	3	GA	RE:	/	480″	RE
	LE:	20/32	LE:	+1.25 (-0.75) 70°	LE:	3	GA	LE:	Paramacular		
S19 (76.4)	RE:	20/800	RE:	/	RE:	4	CNV	RE:	Perimacular	/	LE
	LE:	20/32	LE:	/	LE:	3	GA	LE:	Paramacular		
S20 (78.5)	RE:	20/63	RE:	/	RE:	3	CNV	RE:	Perimacular	/	RE
	LE:	20/63	LE:	/	LE:	4	CNV	LE:	/		

Data are reported for each participant with bilateral AMD. Their corrected visual acuity (ETDRS), glasses correction, AMD level, type of AMD (GA, geographic atrophy; CNV, choroidal neovascularization), stereoscopic acuity (seconds of arc, TNO test) and dominant eye are reported (LE, left eye; RE, right eye).

effective measurement of CoP variability and corresponds to an ellipse with 90% of CoP (Chiari et al., 2002; Gagey and Weber, 2004; Vuillerme et al., 2008). Length is a path of CoP. Mean speed is an efficient indicator to quantity the neuro-muscular activity required to regulate postural control (Geurts et al., 1993).

Statistical Analysis

Data were analyzed with ANOVA/MANOVA using the three groups of subjects (unilateral, bilateral AMD subjects, and control subjects) as inter- subject factor, and the four visual conditions (both eyes opens, dominant and non-dominant eye open, and both eyes closed) as within-subject factor.

In the case of significant effects *post-hoc* Bonferroni test was performed. The effect of a factor was considered as significant when the *p*-value was below 0.05.

RESULTS

ANOVA test failed to show significant age differences between the three groups [$F_{(2,27)} = 0.66$, $p = 0.54$].

Figure 1 shows the surface area of the CoP (mm^2) for each visual condition tested (BEV, DEV, NDEV, EC) for the three groups of subjects (control, unilateral AMD, bilateral AMD). The analysis of variance (ANOVA) indicated a group effect [$F_{(2,\ 27)} = 3.28$, $p < 0.05$]. *Post-hoc* comparison showed a significant difference between "Control" and "Bilateral AMD" ($p < 0.05$): bilateral AMD subjects had a larger surface area than control subjects. There was a significant effect of visual condition [$F_{(3.81)} = 3.04$, $p < 0.03$]. *Post-hoc* comparison showed that surface area of CoP was significantly smaller under DEV with respect to EC ($p < 0.02$). ANOVA did not show any significant interaction between group and visual condition [$F_{(6.81)} = 0.69$, $p = 0.65$].

Figure 2 shows the length of the CoP (mm) for each visual condition tested (BEV, DEV, NDEV, EC) for the three groups of subjects (control, unilateral AMD, bilateral AMD). ANOVA did not show a significant group effect [$F_{(3.81)} = 2.29$, $p = 0.1$] but indicated a significant effect of visual condition [$F_{(3.81)} = 18.69$, $p < 10^{-6}$]. *Post-hoc* comparison showed that the length of the CoP was significantly smaller under BEV than under NDEV ($p < 0.03$) and under EC ($p < 10^{-6}$). The length of the CoP was also significantly larger under EC than under DEV ($p < 10^{-6}$) and NDEV ($p < 10^{-4}$). ANOVA did not show a significant interaction between group and visual condition [$F_{(6.81)} = 0.64$, $p = 0.67$].

TABLE 3 | Clinical characteristics of age-matched healthy subjects.

Patient (Age, years)	ETDRS		Glasses correction		AMD level		Scotoma		Stereoacuity (TNO)	Dominant eye
S21 (60.1)	RE:	20/20	RE:	(−0.75) 88°	RE:	1	RE:	/	480″	LE
	LE:	20/20	LE:	(−0.75) 100°	LE:	1	LE:	/		
S22 (63.2)	RE:	20/20	RE:	+1.50 (−0.25) 65°	RE:	1	RE:	/	480″	LE
	LE:	20/20	LE:	+2.50 (−1.5) 160°	LE:	1	LE:	/		
S23 (64.9)	RE:	20/20	RE:	+3.25 (−0.5) 105°	RE:	1	RE:	/	480″	RE
	LE:	20/20	LE:	+3.25 (−0.5) 80°	LE:	1	LE:	/		
S24 (66.5)	RE:	20/20	RE:	+0.50 (−0.5) 80°	RE:	1	RE:	/	480″	LE
	LE:	20/20	LE:	+0.25	LE:	1	LE:	/		
S25 (67.8)	RE:	20/20	RE:	+2.50 (−0.5) 60°	RE:	1	RE:	/	480″	RE
	LE:	20/20	LE:	+3 (−0.75) 105°	LE:	1	LE:	/		
S26 (69.8)	RE:	20/20	RE:	+0.25 (−0.5) 10°	RE:	1	RE:	/	480″	LE
	LE:	20/20	LE:	(−0.25) 150°	LE:	1	LE:	/		
S27 (69.9)	RE:	20/20	RE:	+1.25	RE:	1	RE:	/	480″	LE
	LE:	20/20	LE:	+1.25	LE:	1	LE:	/		
S28 (77.2)	RE:	20/20	RE:	+3	RE:	1	RE:	/	480″	RE
	LE:	20/20	LE:	+3	LE:	1	LE:	/		
S29 (79.2)	RE:	20/20	RE:	−1.5	RE:	1	RE:	/	480″	LE
	LE:	20/20	LE:	−1.75	LE:	1	LE:	/		
S30 (79.5)	RE:	20/20	RE:	+2.75 (−2) 5°	RE:	1	RE:	/	480″	RE
	LE:	20/20	LE:	+0.5 (−1.5) 20°	LE:	1	LE:	/		

Data are reported for each healthy age-matched participant. Their corrected visual acuity (ETDRS), glasses correction, AMD level, stereoscopic acuity (seconds of arc, TNO test) and dominant eye are reported (LE, left eye; RE, right eye).

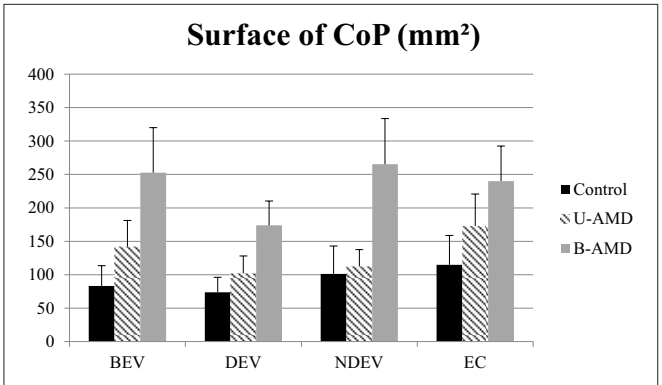

FIGURE 1 | Surface of CoP. Mean value of the surface of CoP (mm^2) for each group of subject tested (control age-matched elderly, unilateral AMD and bilateral AMD), for each visual conditions, binocular eye viewing (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), eyes closed (EC). Vertical bars indicate the standard error.

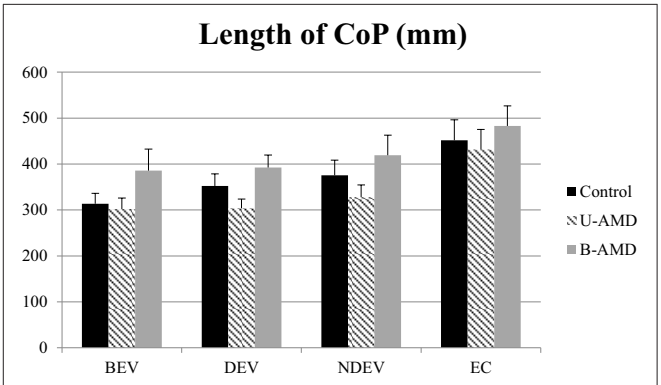

FIGURE 2 | Length of CoP. Mean of the Length of CoP (mm^2) for each group of subject tested (control age-matched elderly, unilateral AMD and bilateral AMD), for each visual conditions, binocular eye viewing (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), eyes closed (EC). Vertical bars indicate the standard error.

Figure 3 shows the mean speed of the CoP (mm/s) for each visual condition tested (BEV, DEV, NDEV, EC) in the three groups of subjects (control, unilateral AMD, bilateral AMD). The analysis of variance (ANOVA) did not show a significant group effect [$F_{(2,\ 27)} = 2.88$, $p = 0.07$] but indicated an effect of visual condition [$F_{(3,\ 81)} = 9.68$, $p < 10^{-4}$]. *Post-hoc* comparison showed that the mean speed of the CoP was higher under EC than

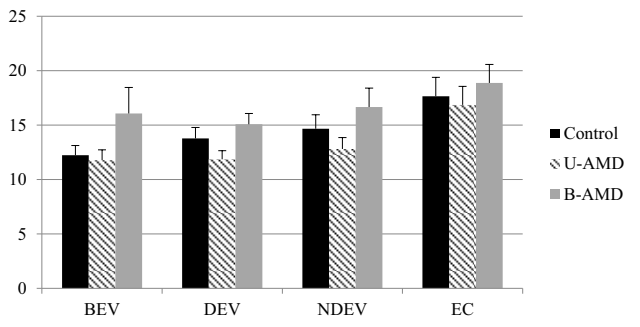

FIGURE 3 | Mean speed of CoP. Mean of the mean speed of CoP (mm^2) for each group of subject tested (control age-matched elderly, unilateral AMD and bilateral AMD), for each visual conditions, binocular eye viewing (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), eyes closed (EC). Vertical bars indicate the standard error.

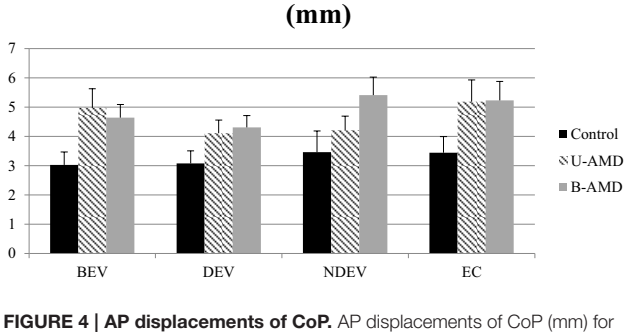

FIGURE 4 | AP displacements of CoP. AP displacements of CoP (mm) for each group of subject tested (control age-matched elderly, unilateral AMD and bilateral AMD), for each visual conditions, binocular eye viewing (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), eyes closed (EC). Vertical bars indicate the standard error.

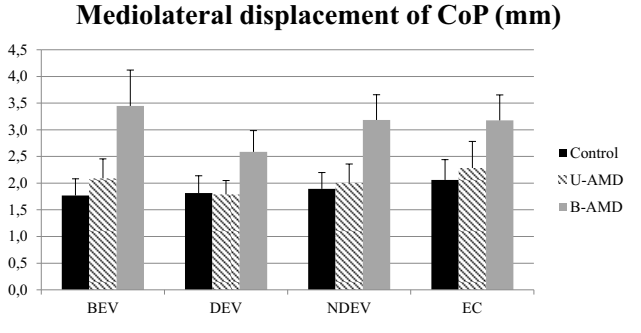

FIGURE 5 | ML displacements of CoP. ML displacements of CoP (mm) for each group of subject tested (control age-matched elderly, unilateral AMD and bilateral AMD), for each visual conditions, binocular eye viewing (BEV), dominant eye viewing (DEV), non-dominant eye viewing (NDEV), eyes closed (EC). Vertical bars indicate the standard error.

under BEV ($p < 10^{-4}$), under DEV ($p < 10^{-4}$), and under NDEV ($p < 10^{-2}$). There was no significant interaction between group and visual condition [$F_{(6, 81)} = 0.42$, $p = 0.85$].

Figure 4 shows the AP displacements of the CoP (mm) for each visual condition tested (BEV, DEV, NDEV, EC) in the three groups of subjects (control, unilateral AMD, bilateral AMD). The analysis of variance (ANOVA) indicated a significant group effect [$F_{(2, 27)} = 3.43$, $p < 0.04$]. The AP displacement was larger in AMD subjects than in healthy control age-matched subjects: *post-hoc* comparison showed that AP displacement of the CoP was shorter in control subjects than in bilateral AMD subjects ($p < 0.01$) and unilateral AMD subjects ($p < 0.05$). There was no significant effect of visual condition [$F_{(2, 27)} = 2.51$, $p = 0.06$] or interaction between group and visual condition [$F_{(6, 81)} = 1.4$, $p = 0.22$].

Figure 5 shows the ML displacements of the CoP (mm) for each visual condition tested (BEV, DEV, NDEV, EC) in the three groups of subjects (control, unilateral AMD, bilateral AMD). The analysis of variance (ANOVA) did not show any significant group effect [$F_{(2, 27)} = 2.64$, $p = 0.08$], or any effect of visual condition [$F_{(3, 81)} = 1.94$, $p = 0.1$], or any interaction between group and visual condition [$F_{(6, 81)} = 0.50$, $p = 0.8$].

DISCUSSION

The main findings of this study are as follows: (i) the surface area and the AP displacement of the CoP are larger in bilateral AMD subjects than in unilateral AMD subjects; (ii) postural stability in elderly subjects depends on visual conditions. These findings are discussed individually below.

Bilateral AMD Subjects Are More Unstable than Unilateral AMD Subjects

In this study we found that AMD subjects had poor postural stability with respect to controls. This finding is in agreement with others studies (Elliott et al., 1995; Kotecha et al., 2013). Moreover, two postural parameters (surface area and AP displacement of CoP) were significantly different in bilateral AMD subjects compared with healthy elderly, and the AP displacement of CoP was significantly affected in unilateral AMD only.

Based on this finding we could assume that a postural evaluation, particularly of the surface area of the CoP, at the beginning of the AMD diagnosis may be predictive of future postural difficulties in these patients. An early postural rehabilitation care would prevent the risk of falling and in the future, studies leading with postural, and/or visual training will be necessary to improve the everyday life.

Postural balance changes throughout life. Qiu et al. (2012) studied the somatosensory system during aging and the impact of age on postural stability. Elderly patients (mean age: 72 years) have an augmentation of surface area and length of the CoP, and an augmentation of AP and ML sways, in comparison with young adults (mean age: 27 years). These authors suggested that mechanoreceptors sensibility decreases with aging as well as the capacity of treatment of sensorial information by the central nervous system. According to Faraldo-García et al. (2016), older subjects could have poor ability of adapt their body to disturbed

sensory situations. Note that in younger subjects with loss of central vision (Stargardt disease) Agostini et al. (2016) found that compensatory strategies are used to control their postural stability. Such adaptive mechanisms are working well also in children with strabismus (see works of our groups, i.e., Lions et al., 2014; Bucci et al., 2016); we could make the hypothesis that in older subjects with AMD pathologies such compensations are not well developed, most likely because at this age plasticity occurs less frequently.

Postural Stability in Elderly Subjects Depends on Visual Conditions

Our results proved that AP displacements of CoP was higher in AMD subjects than controls in closed eyes condition, most likely because AMD subjects have low mobility and degraded physical performance. Such hypothesis is confirmed by previous studies (Rovner et al., 2009; Chomistek et al., 2013; Loprinzi et al., 2015). These authors suggested that physical inactivity facilitated the progression of vision loss (Chomistek et al., 2013) and cognitive loss like depressive disorders (Rovner et al., 2009). Moreover, (Loprinzi et al., 2015) showed that AMD subjects, and more generally subjects with low visual acuity increased sedentary behavior, leading to increase of risk of developing metabolic, cardiovascular, and cerebrovascular diseases.

Few studies examined postural stability under monocular viewing. (Moraes et al., 2009), studied the impact of binocular vs. monocular viewing in controlling posture in quiet stance in young adults without visual abnormalities (mean age: 22.7 years). They suggested that binocular viewing allowed a greater postural control.

Note that even if our results failed to show any interaction effect between subjects and visual condition data on monocular viewing, they suggested that AMD subjects are more stable under dominant eye viewing than under both eyes viewing condition. Studies with more patients are needed to confirm this result. We made the hypothesis that monocular visual field of the dominant eye is less disturbed than binocular visual field in AMD subjects. The confirmation of this result would open perspectives of developing of training techniques without replacing the standard follow-up of the AMD subjects by clinical ophthalmological examination. In fact, in theory, neutralization process is expected to erase some of the scotoma (no view area) in the binocular visual field. But this process is difficult for elderly people due to the age-related decrease of brain plasticity.

The role of central vs. peripheral vision information in control balance was examined in several studies. Marigold and Patla (2007) examined the role of central or peripheral vision to avoid an obstacle. These authors reported that peripheral vision was sufficient for successful obstacle avoidance during locomotion. Moreover, more recently, Timmis et al. (2016) proved, in young adults, the impact of visual field loss (to 10° compared 20°) on risk of falls. They showed that only visual field loss to 20° increased risk of falls. We could hypothesis that the size of scotoma in AMD subjects may be predictive of postural instability. According to Berencsi et al. (2005), in young adults, central, and peripheral vision contributes to maintaining a stable standing posture. They suggested that peripheral vision control more the AP than ML displacements of CoP. Actually our result contrast this one, AP displacement of CoP is larger in AMD subjects with central field loss could be due to the different age of subjects tested in the two studies. Indeed, it is well-known that older subjects used more hip strategies to maintain postural control whereas young adults used ankle strategies (Daubney and Culham, 1999). Further studies comparing young and old subjects with poor vision are needed to explore postural strategies.

LIMITATIONS

It is important to note that in this study we used a platform with a frequency of 40 Hz and this could explain the small displacement and mean speed values reported here comparing to others studies. Secondly, a larger number of subjects with AMD will be necessary to explore further their postural instability in relationship with their scotoma measures.

CONCLUSION

The present study showed that AMD subjects, suffering from visual impairment in the central but not in the peripheral field, had worse postural performance than healthy age-matched control subjects, especially in the surface area (unilateral and bilateral AMD subjects) and AP displacements of the CoP (bilateral AMD subjects only). Because of aging, AMD subjects could have poor postural adaptive mechanisms which increase instability and risk of falls. Further studies will aim to improve knowledge and to develop reeducation techniques in these patients.

AUTHOR CONTRIBUTIONS

HC, LT, OL, AnA, AlA, TB, SS, MB: substantial contributions to the conception of the word, logistic support for the recruitment of participants, acquisition, analysis and interpretation of data for the work, drafting the work and revising critically for important intellectual content, final approval of the version to be published, Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Head Stability and Head-Trunk Coordination in Horseback Riders: The Contribution of Visual Information According to Expertise

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Maintaining equilibrium while riding a horse is a challenging task that involves complex sensorimotor processes. We evaluated the relative contribution of visual information (static or dynamic) to horseback riders' postural stability (measured from the variability of segment position in space) and the coordination modes they adopted to regulate balance according to their level of expertise. Riders' perceptual typologies and their possible relation to postural stability were also assessed. Our main assumption was that the contribution of visual information to postural control would be reduced among expert riders in favor of vestibular and somesthetic reliance. Twelve Professional riders and 13 Club riders rode an equestrian simulator at a gallop under four visual conditions: (1) with the projection of a simulated scene reproducing what a rider sees in the real context of a ride in an outdoor arena, (2) under stroboscopic illumination, preventing access to dynamic visual cues, (3) in normal lighting but without the projected scene (i.e., without the visual consequences of displacement) and (4) with no visual cues. The variability of the position of the head, upper trunk and lower trunk was measured along the anteroposterior (AP), mediolateral (ML), and vertical (V) axes. We computed discrete relative phase to assess the coordination between pairs of segments in the anteroposterior axis. *Visual field dependence-independence* was evaluated using the Rod and Frame Test (RFT). The results showed that the Professional riders exhibited greater overall postural stability than the Club riders, revealed mainly in the AP axis. In particular, head variability was lower in the Professional riders than in the Club riders in visually altered conditions, suggesting a greater ability to use vestibular and somesthetic information according to task constraints with expertise. In accordance with this result, RFT perceptual scores revealed that the Professional riders were less dependent on the visual field than were the Club riders. Finally, the Professional riders exhibited specific coordination modes that, unlike the Club riders, departed from pure in-phase and anti-phase patterns and depended on visual conditions. The present findings provide evidence of major differences in the sensorimotor processes contributing to postural control with expertise in horseback riding.

Keywords: head stability, postural stability, head-trunk coordination, visual information, field dependence-independence, horseback rider, expertise, riding simulator

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INTRODUCTION

Horseback riding is a challenging task that requires regulating postural balance while sitting on a moving base of support. To control their balance, riders need to adapt their movements to those of the horse while picking up information in the environment to direct the horse toward the intended goal. Stabilizing the head in this context is very challenging and yet crucial for motor performance. Because the head contains the visual and vestibular systems that play a decisive role in balance control, its stabilization in space is important for optimal processing of visual and vestibular information (e.g., Gresty and Bronstein, 1992; Amblard et al., 2001) and therefore, to provide a stable base for action (e.g., Ripoll et al., 1986; Clément et al., 1988; Pozzo et al., 1990). In the present study, we sought to assess whether (i) postural stability[1], and more specifically head stability, is a signature of expertise in horseback riders, (ii) the contribution of visual information to riders' postural stability is reduced among expert riders in favor of vestibular and somesthetic reliance, and (iii) expert riders adopt specific postural coordination modes to preserve head stability.

Balance control involves the visual, vestibular and somesthetic systems. The contribution of vision to balance has received the greatest attention in the literature and has been tested in numerous conditions including the suppression of visual afferences by eye closure (e.g., Perrin et al., 1998; Perrot et al., 1998; Callier et al., 2001; Rougier et al., 2003), the stimulation of the central or peripheral visual field (e.g., Berencsi et al., 2005), the deterioration of visual acuity or the reduction of the visual field (e.g., Laurent et al., 1989; Schmid et al., 2008), the inclination or displacement of the visual environment (Isableu et al., 1997, 2010, 2011; Gautier et al., 2008), the selective suppression of dynamic visual cues by stroboscopic illumination (e.g., Amblard et al., 1985) or their gain in a ground optical flow (e.g., Baumberger et al., 2004). The results of these studies highlighted the importance of vision in balance control, but these conclusions should be moderated in the context of sporting expertise. Indeed, sports activities involve complex sensorimotor skills and constrain the subjects to act and process multiple information sources (proprioceptive, tactile, auditory, etc.) with a particularly high level of accuracy and rapidity.

To be efficient, the expert develops, through years of training, optimal responses to both external and internal constraints (Ericsson et al., 1993; Ericsson and Lehmann, 1996). In particular, the contribution of sensory information to postural control evolves with training and differs according to the level of practice (Era et al., 1996; Perrot et al., 1998; Bringoux et al., 2000), the type of physical activity (Hosseinimehr et al., 2009), and the specificity of gesture, support, task, or position in the environment within the same sport or sport family (Robert et al., 2004; Bizid and Paillard, 2006; Stambolieva et al., 2011). Overall, these studies showed that the contribution of vision to the regulation of postural balance tends to decrease with expertise, while somesthetic and vestibular information become more critical. For example, experts in soccer, surfing, dance, and gymnastics can use the remaining sensory modalities to compensate for a lack of vision in unstable postures (e.g., Perrin et al., 1998; Vuillerme et al., 2001a,b; Paillard et al., 2006, 2011).

Studies on horseback riding have investigated various topics such as equine gait (e.g., Galloux et al., 1994; Peham et al., 2004), horse-rider interactions (e.g., Lagarde et al., 2005; Byström et al., 2009; Wolframm et al., 2013; Münz et al., 2014), rider muscle activity (e.g., Terada, 2000; Terada et al., 2004), rider joint position (e.g., Kang et al., 2010), and rider body movements (e.g., Münz et al., 2013; Byström et al., 2015; Eckardt and Witte, 2016; Engell et al., 2016). However, very little research has been devoted to the use of sensory information in horseback riding and none has been devoted to the contribution of sensory information to rider postural stability. Some authors have suggested that expert riders use mainly proprioceptive information rather than visual information to control the horse's pace (Laurent and Pailhous, 1982; Laurent et al., 1989). Others have emphasized the importance of haptic information for coordination between the rider's movements and those of the horse (e.g., Lagarde et al., 2005). Indeed, various contacts (e.g., with the saddle, rein, stirrup) and pressures (between the rider's pelvis and the horse's saddle, primarily) are produced during the horse/rider interaction in riding. They provide rich and patterned somesthetic information (proprioceptive and tactile) that are of utmost importance to the rider in regulating and coordinating his/her movements with those of the horse. Thus, an interesting question is whether the contribution of somesthetic information to postural stability increases with expertise in horseback riding at the expense of vision, as was observed in other sports activities.

A related question concerns interindividual differences in the use of sensory information for spatial orientation, and more specifically the visual field dependence-independence (e.g., Witkin, 1950; Oltman, 1968; Paillard, 1971; Isableu et al., 1997, 2010). It has been proposed that Field Dependence (FD) or Independence (FI) reflects the weight each individual assigns to visual or non-visual information (Isableu et al., 1997, 2003, 2010, 2011; Bringoux et al., 2016). At one extreme, field-dependent subjects are affected by the surrounding visual field and are thus assumed to rely predominantly on visual information, while, at the opposite end of the continuum, field-independent subjects are less affected by the visual surroundings and so are assumed to rely more on somesthetic and vestibular cues. The influence of this perceptual typology has been observed regularly in both perceptual orientation and postural tasks (e.g., Witkin, 1950; Crémieux and Mesure, 1994; Collins and De Luca, 1995; Luyat et al., 1997; Golomer et al., 1999; Kluzik et al., 2005; Rousseu and Crémieux, 2005; Slaboda et al., 2011).

Visual field dependence-independence is of particular interest for the present study as it has been shown both to be related to expertise in sport (e.g., Liu, 2003; Guillot and Collet, 2004; Rousseu and Crémieux, 2005) and to induce interindividual differences in postural control (e.g., Golomer et al., 1999; Isableu

[1]In the dynamical systems perspective, stability has a precise definition related to a system's response to a change in initial conditions or to a perturbation (e.g., Strogatz, 1994). In this view, the term postural stability refers to the stability of the underlying movement dynamics (e.g., Newell et al., 1993). In the present paper, we use the term "postural stability" in its most widespread sense in the literature on postural control, which supposes a reduced amount of variability of the segments in space.

et al., 2003, 2010). Several studies have shown that experts tend to be more field-independent in a number of physical activities such as acrobatic sports (e.g., Liu, 2003; Guillot and Collet, 2004; Rousseu and Crémieux, 2005). Moreover, some studies have highlighted a relationship between perceptual typologies and postural performance (e.g., Isableu et al., 1997; Golomer et al., 1999; Isableu et al., 2003, 2010) showing that field-dependent subjects were less stable than field-independent subjects in postural tasks, in particular when visual conditions were altered (through the inclination of the visual frame, the suppression of dynamic visual information using stroboscopic illumination or the suppression of visual information).

To date, no study has investigated interindividual differences or the relationship between perceptual typologies and sensorimotor performance in horseback riders (Olivier et al., 2012). Addressing these questions could help understand the differences between expert and non-expert riders in the weight they assign to visual information and in their ability to use non-visual information to regulate balance. Based on the results of previous studies, it can be expected that expert riders would be less dependent on the visual field, leading them to better stabilize their head compared to novice riders.

Beyond perceptual aspects, addressing the question of postural stability in riders also raises the question of the coordination modes used to regulate balance. Postural coordination during upright stance has been studied intensively in various contexts and according to different theoretical approaches (e.g., Nashner and McCollum, 1985; Assaiante and Amblard, 1993, 1995; Bardy et al., 1999; Faugloire et al., 2005). Overall, these studies have shown that head stability—and more generally postural stability—can be achieved through different coordination modes which were found to evolve with development (Assaiante and Amblard, 1995), motor learning (e.g., Zanone and Kelso, 1992; Vereijken et al., 1997; Faugloire et al., 2006, 2009), and expertise in sports activities (Marin et al., 1999; Gautier et al., 2009). In particular, Marin et al. (1999) compared the postural coordination modes adopted by novices and experts in gymnastics in terms of hip-ankle relative phase. Their results showed that increasing the difficulty of the postural task produced a change from an in-phase pattern between the ankle and the hips (almost synchronized flexion-extension of the joints) to an anti-phase pattern (joints moving in opposite directions) occurring earlier in non-gymnasts than in gymnasts. The fact that expert gymnasts were able to maintain the in-phase pattern at greater task difficulties than non-gymnasts demonstrates that expertise in gymnastics leads to a functional modification of existing postural coordination modes.

In horseback riding, riders have to anticipate and compensate for the horse's movements in a sitting posture. While the maintenance of stance in an upright posture, either on a stable or an unstable base of support, involves mainly the ankle, hip and knee joints (e.g., Nashner and McCollum, 1985; Bardy et al., 1999), riders primarily regulate balance through movements of the pelvis, trunk and neck (Vitte et al., 1995; Silva e Borges et al., 2011; Janura et al., 2015). Thus, the results obtained in studies on postural coordination in an upright stance do not apply to horseback riding situations. Interesting insights are provided by studies on postural regulation in a sitting position (e.g., Forssberg and Hirschfeld, 1994; Vibert et al., 2001; Keshner, 2003, 2004). In these studies, participants sat on a sled that was translated in anteroposterior directions (Forssberg and Hirschfeld, 1994; Vibert et al., 2001; Keshner, 2003, 2004), sideways (Vibert et al., 2001), or rotated in the sagittal plane (Forssberg and Hirschfeld, 1994). In most studies, the participants' legs and shins were resting horizontally in front of them (Forssberg and Hirschfeld, 1994; Keshner, 2003, 2004) and visual information was suppressed (Vibert et al., 2001; Keshner, 2003, 2004). Overall, the results showed that the head lagged behind the trunk in response to the perturbation (e.g., Forssberg and Hirschfeld, 1994; Vibert et al., 2001; Keshner, 2003, 2004) and that somatosensory information generated at the pelvis level, and not vestibular information from the head, appears to trigger postural responses during sitting (e.g., Forssberg and Hirschfeld, 1994; Keshner, 2003, 2004). These interesting results do not help to understand the contribution of vision because the availability of visual information was not manipulated: vision was either suppressed by eye closure (Vibert et al., 2001) or darkness (Keshner, 2003, 2004), or was available in all conditions (Forssberg and Hirschfeld, 1994). Also, the important differences between these studies and horseback riding situations in terms of the sitting position (closed vs. open coxo-femoral angle), the nature of the movements of the base of support (linear translation in the horizontal plane vs. pitch and vertical movements) and their rhythmicity (discrete vs. cyclic) do not allow to generalize these results to riders' postural coordination modes.

The purpose of the present study was to evaluate the relative contribution of visual information to head and trunk stability in Club and Professional horseback riders and the coordination modes adopted to regulate balance depending on expertise. With this aim, the participants were asked to ride a riding simulator while facing a dynamic virtual scene under four visual conditions: in normal lighting allowing the participants to access dynamic visual cues (*continuous simulated scene condition*), under stroboscopic illumination, preventing access to dynamic visual cues (*stroboscopic simulated scene condition*), in normal lighting with full visual access to the fixed surroundings but without the projected scene and thus without the visual consequences of the displacements corresponding to the context of a ride (*no simulated scene condition*) and with no visual cues (*no vision condition*).

(i) Our first hypothesis was that expert riders produce lower postural displacements and deploy more efficient postural control from the top of the head to the lower trunk leading them to better stabilize their head.

(ii) Our second hypothesis was that the contribution of visual information to riders' postural stability is reduced among expert riders in favor of vestibular and somesthetic reliance, leading experts to maintain head stability better in visually altered conditions than less experienced riders. This differential reliance is also expected to be revealed by specific perceptual typologies according to expertise, with Professional riders being less dependent on the visual field than Club riders.

(iii) Our third hypothesis was that expert horseback riders exhibit specific coordination modes to maintain a high level of postural stability, as has been observed in studies on postural coordination and expertise in other sports (Marin et al., 1999; Gautier et al., 2009).

METHODS

Participants

Twenty-five participants were divided into two groups based on their level of horseback riding expertise. The characteristics of the two groups of participants are presented in **Table 1**. One group was composed of 12 elite Professional riders who specialized in show jumping and cross country riding. These members of the French National Horseback Riding School had a minimum of 20 years of practice and had participated in international competitions. The other group was composed of 13 Club riders who were ranked "Galop 5" by the French Riding Federation and had no particular specialty in any of the equestrian sports. Some of them had participated in competitions at a regional level. All of the participants were novices in the use of a riding simulator.

All of the participants had normal or corrected-to-normal vision, and reported no balance disorder, injury or pathology that might affect their ability to perform tests on a riding simulator. Local ethical approval from the Université Paris-Sud EA 4532 ethics committee was granted for this study. Each participant signed an informed consent statement after receiving oral and written descriptions of the procedure.

TABLE 1 | Mean characteristics of the Professional and Club riders (standard deviation in parentheses).

	Professional riders	Club riders
Number of participants	12 [2 women]	13 [7 women]
Age	38.33 years (7.05)	29.85 years (6.07)
Height	179.58 cm (8.47)	171.23 cm (10.43)
Weight	70.75 kg (8.62)	64.54 kg (9.65)
Years of practice	29.67 years (5.48)	10.23 years (6.02)
Years of practice in competition	16.67 years (6.14)	1.54 years (2.18)
Amount of practice per week	36.17 h/week (6.56)	1.31 h/week (1.75)

Apparatus

Figure 1 illustrates the set-up used in this experiment. The participants rode the riding simulator Persival (Persival Industrie, Saumur, France) from the French National Horseback Riding School at a simulated gallop (stride cycle frequency of 1.4 Hz, vertical displacement amplitude of 17 cm). The use of a riding simulator ensured that the same motion of the base of support was applied to every participant. Displacements of the participants' head and trunk were measured with an electromagnetic tracking system (Fastrack, Polhemus Inc., Colchester, VT, USA), sampled at 40 Hz. Three receivers were placed on the participants: on the top of the head, on the seventh cervical vertebra (C7), corresponding to the base of the neck, and on the third lumbar vertebra (L3), which corresponds to the center of the lordotic curve of the lower back. The receiver on the top of the head was attached to the rider's helmet and the other two were attached directly to the skin using double-sided adhesive and medical cloth tape. The transmitter was located 90 cm above and 35 cm behind the back of the simulator saddle, on a shelf attached to the ceiling. The receivers attached to the head, C7, and L3 were within 52, 72, and 112 cm of the transmitter, respectively, leading to a positional resolution of 0.0025, 0.0163, and 0.095 cm, respectively (the resolution of electromagnetic tracking system measurement is affected by the distance between the transmitter and the receiver).

The participants sat on the saddle of the Persival simulator at a distance of 3.20 m from the projection screen (1.92 × 1.36 m), creating a visual angle of about 33.40° horizontally and 23.99° vertically. In order to minimize peripheral visual information, opaque black curtains were placed parallel to the rider's line of vision on either side of the experimental set-up from the edges of the projection screen to the back of the simulator. SimPiste software (Persival Industrie, Saumur, France) was used to create a computer-generated movie projected on the screen. The resulting 3D animated scene represented a classic situation of a ride in a show jumping arena from the rider's viewpoint and was synchronized with the simulator's movements. The visual environment included several fences around which the horse-rider pair moved at a gallop. Thus, the visual scene simulated displacement around the fences and the mechanical movements of the simulator maintained a gallop pace with no jumps.

Procedure and Experimental Design

The experimental session began with the assessment of the participants' visual field dependence using a portable Rod and Frame Test (RFT; Oltman, 1968). In this test, participants are required to adjust a rod enclosed within a square frame on the physical vertical. The frame and the rod were tilted 18° clockwise or counterclockwise from the vertical, where the frame effect has been found to be maximal (Zoccolotti et al., 1993). Each of the four resulting conditions was presented five times, resulting in 20 randomized trials. Clear and stable differences have been found among subjects' scores on the RFT and have led to the establishment of the well-known dimension of "field dependence–independence" (Oltman, 1968; Gueguen et al., 2012): Field Dependent participants (FD) align the rod on the framework, whereas Field Independent participants (FI) align the rod on the gravitational vertical.

Next, the participants were invited to mount the riding simulator and were equipped with the Fastrack receivers. After a short period of familiarization (30 s) with the simulator, four visual conditions were presented in a randomized order as separate 50-s trials. The mechanical horse's movements were similar in every visual condition and reproduced a gallop gait. The participants were instructed to "look straight ahead and to stabilize their posture as in real practice" for each of these conditions.

– In the *no simulated scene condition* (No scene), the virtual scene was not projected and the participants faced the white projection screen under normal lighting. In this condition, continuous visual information was available from the fixed

FIGURE 1 | Experimental set-up.

surroundings, constituting a stable reference frame for postural control.

– In the *continuous simulated scene condition* (Cont scene), the animated virtual scene from SimPiste was projected on the screen with normal lighting. In this condition, the visual scene reproduced what a rider sees in the real context of a ride in a show jumping arena, with forward displacements and turns in the virtual environment.

– In the *stroboscopic simulated scene condition* (Strob scene), the animated virtual scene was projected on the screen but its dynamic visual cues were eliminated by stroboscopic illumination (2.8 flash/s). In this condition, visual information was reduced to static visual cues in order to evaluate the various contributions of static visual cues vs. dynamic visual cues, available in normal lighting, to postural stability (Amblard and Crémieux, 1976; Amblard et al., 1985).

– In the *No vision condition* (No vision), the participants wore opaque glasses (swimming goggles covered with opaque adhesive tape) that prevented access to environmental information. This condition assessed the general contribution of vision to the riders' postural stability.

The Strob scene and No vision conditions corresponded to visually altered conditions in which the availability of dynamic visual cues (Strob scene) or the totality of the visual scene (No vision) was suppressed. The No scene condition was used as a reference condition in which postural control was expected to be facilitated by the presence of fixed surroundings (e.g., Lee and Lishman, 1975; Guerraz et al., 2001).

The participants were given a few minutes' break between conditions. The experiment took about 40 min to complete from the RFT to the last vision condition on the simulator.

Data Analysis

The raw position data collected by the magnetic tracking system were processed and analyzed using Matlab software (R2009b, The MathWorks Inc., Natick, MA, USA). In order to eliminate the initiation of the simulator's motion and participants' adaptation phase to it, we considered position data from the fifth second to the end of each trial. Two types of dependent variables were computed from the position data. First, the variability of the displacement of each segment (head, C7, L3) was quantified by computing the standard deviation of the position along the anteroposterior (SD_{AP}), mediolateral (SD_{ML}), and vertical (SD_{V}) axes. These measurements were used to quantify the degree of stability of the head, the cervical segment (upper trunk) and the lumbar segment (lower trunk) in space (the lower the standard deviation of position, the more stable the segment is in space).

Second, we evaluated the coordination modes the riders used to stabilize their posture. Because the control of the hips, trunk and neck impacts mainly the displacements of the upper body in the AP axis, we analyzed postural coordination along this axis. Coordination modes were computed from position data in the AP axis using the mean relative phases ϕ_{L-C}, ϕ_{L-H}, and ϕ_{C-H} between the lumbar and the cervical segments, the lumbar segment and the head, and the cervical segment and the head, respectively (**Figure 2A**). The standard deviations of the mean relative phases ($SD\phi_{L-C}$, $SD\phi_{L-H}$, $SD\phi_{C-H}$) were computed as measurements of the within-participants dispersion around the mean relative phase.

Prior to relative phase computation, position data were filtered with a recursive second-order Butterworth filter with a cutoff frequency of 2 Hz. For each pair of segments, we computed the point estimate of relative phase (e.g., Zanone and Kelso, 1992) using the maximum position of each segment in the AP axis for every movement cycle:

$$\phi_{rel} = \frac{(t_1 - t_2)}{(t_1 - t_0)} \times 360^{\circ} \quad (1)$$

where t_0 and t_1 are the time of occurrence of two successive maximum positions along the AP axis for the reference segment, and t_2 is the time of occurrence of maximum position of the

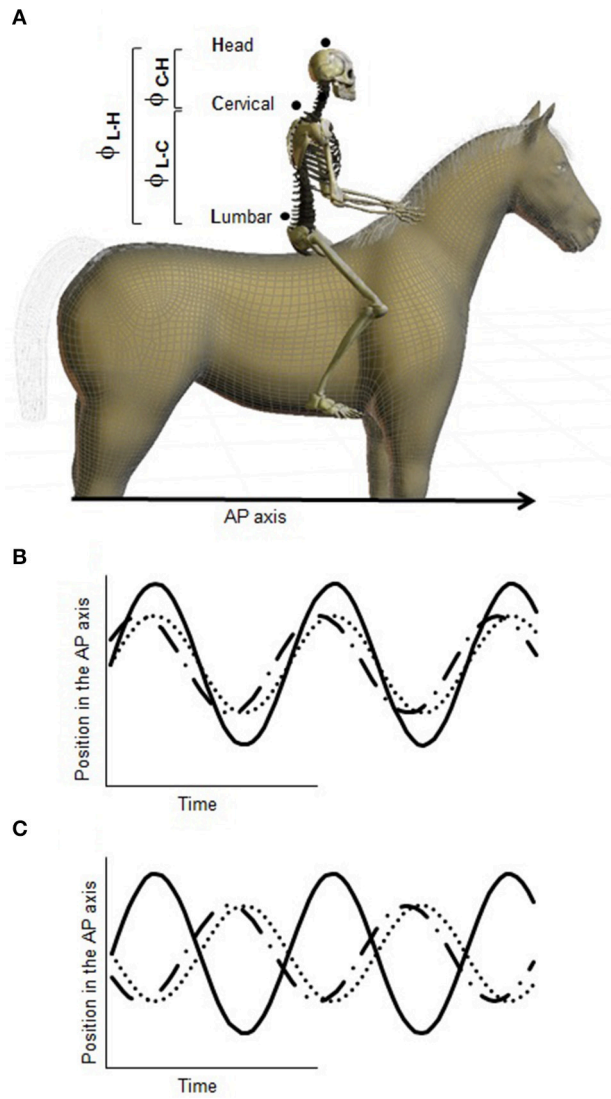

FIGURE 2 | Illustration of the coordination modes with different relative phase values. (A) Illustration of the relative phases computed (ϕ_{L-C}, ϕ_{L-H}, ϕ_{C-H}). **(B)** In-phase coordination between the referent segment (bold line) and the segment represented by the dotted line (the segments move synchronously in the same direction resulting in a relative phase of 0°); relative phase of −30° (=330°) between the referent segment (bold line) and the segment represented by the dash-dotted line. **(C)** Anti-phase coordination (the segments move synchronously in opposite directions, resulting in a relative phase of 180°) between the referent segment (bold line) and the segment represented by the dotted line; relative phase of 150° between the referent segment (bold line) and the segment represented by the dash-dotted line.

second segment. In other words, the time difference between the position peaks of the two segments is expressed in degrees relative to the period of the reference segment.

Each trial (corresponding to one visual condition) comprised about 65 movement cycles. Mean relative phases and their standard deviations were computed in a circular fashion (Batschelet, 1981) over the 65 resulting discrete relative phase values. **Figures 2B,C** illustrates different relative phase values in the temporal domain. A mean relative phase of 0° (corresponding to an in-phase coordination mode) indicates that the two segments were moving synchronously forward and backward. A relative phase of 180° (corresponding to an anti-phase coordination mode) indicates that the two segments were moving in opposite directions. Other relative phase values indicate a lead or a lag of one segment with respect to the other: for ϕ_{L-C} and ϕ_{L-H}, values between 0 and 180° indicate that the movement peak of the lumbar segment preceded the movement peak of the cervical segment and the movement peak of the head, respectively; for ϕ_{C-H}, values between 0 and 180° indicate that the movement peak of the cervical segment preceded the movement peak of the head.

Finally, RFT perceptual scores revealing errors in the gravitational vertical estimation due to the tilted frame were computed using Nyborg and Isaksen's method 1974.

Statistical Analysis

Levene's tests were conducted on SD_{AP}, SD_{ML}, and SD_V to assess the homogeneity of variance between the Professional and Club riders for each vision condition (No scene, Cont scene, Strob scene, No vision) and each segment (head, C7, L3). Of the 36 resulting comparisons, only two were significant (at an uncorrected significance level of 0.05) with the standard deviation of the head being higher for the Club riders than for the Professional riders in the AP axis in the No Vision condition (uncorrected $p = 0.028$) and in the ML axis in the Cont scene condition (uncorrected $p = 0.034$). Since the variances of the groups were homogenous overall, we conducted separate Expertise (Professional riders, Club riders) × Segment (Head, Cervical, Lumbar) × Vision (No scene, Cont scene, Strob scene, No vision) ANOVAs with repeated measures on the two last factors on SD_{AP}, SD_{ML}, and SD_V. In order to address our second hypothesis, planned comparisons of least-squares means were used to compare specifically head variability between the Professional and Club riders in the different conditions of vision.

Rayleigh Uniformity Tests conducted on ϕ_{L-C}, ϕ_{L-H}, and ϕ_{C-H} for each trial and each participant revealed that relative phase distributions were significantly directional (i.e., not uniform), $ps < 0.05$. One of the Club riders presented a distribution that did not differ from a uniform distribution in several trials ($ps > 0.05$) and was thus removed from the analyses on coordination modes. Levene's tests conducted on ϕ_{L-C}, ϕ_{L-H}, and ϕ_{C-H} for each vision condition revealed no significant difference between the variance of the Professional and Club riders (uncorrected $ps \geq 0.063$). These results, plus the fact that the range of mean relative phase values over participants did not exceed 180° in every experimental condition, allowed us to conduct analyses of variance[2] on ϕ_{L-C}, ϕ_{L-H}, ϕ_{C-H}, and on their standard deviations. For each variable, we conducted an Expertise (Professional riders, Club riders) × Vision (No scene, Cont scene, Strob scene,

[2]When the range of distribution does not exceed 180°, circular statistics (Batschelet, 1981; Mardia and Jupp, 2000) and regular linear statistics result in virtually identical outcomes.

No vision) ANOVA with repeated measures on the second factor.

For each significant effect, we conducted *post-hoc* comparisons with corrected *p*-values according to the Holm-Bonferroni procedure. The results were considered significant at the level of 5% and the effect size was estimated using partial eta squared (η_p^2).

RESULTS

Postural Stability

In order to address our main hypotheses with conciseness, we describe the results of the three separate ANOVAs conducted on SD_{AP}, SD_{ML}, and SD_V together for each main effect and each interaction in the following paragraphs (**Table 2**).

The ANOVAs revealed a significant main effect of Expertise on SD_{AP} [$F_{(1, 23)} = 5.64$, $p = 0.026$] showing that anteroposterior motion was greater for the Club riders (mean ± SE: 2.58 cm ± 0.09) than for the Professional riders (mean ± SE: 2.27 cm ± 0.10). The main effect of Expertise was not significant for SD_{ML} [$F_{(1, 23)} = 3.76$, $p = 0.065$] and SD_V [$F_{(1, 23)} = 1.37$, $p = 0.254$].

The main effect of Segment did not reach significance for SD_{AP} [$F_{(2, 46)} = 2.89$, $p = 0.066$] but was significant for SD_{ML} [$F_{(2, 46)} = 23.56$, $p < 0.001$] and SD_V [$F_{(2, 46)} = 18.68$, $p < 0.001$]. Holm-Bonferroni *post-hoc* tests showed that for both axes, head variability (mean ± SE: $SD_{ML} = 1.37$ cm, ± 0.11; $SD_Z = 5.17$ cm, ± 0.09) was greater, $ps < 0.001$, than the variability of the cervical segment (mean ± SE: $SD_{ML} = 0.86$ cm, ± 0.04; $SD_V = 4.76$ cm, ± 0.05) and the lumbar segment (mean ± SE: $SD_{ML} = 0.73$ cm, ± 0.04; $SD_Z = 4.71$ cm, ± 0.06), which did not differ from each other, $ps > 0.20$.

The Expertise × Segment interaction was significant for SD_V [$F_{(2, 46)} = 3.95$, $p = 0.026$], revealing that the head was more stable along the vertical axis for the Professional riders (mean ± SE: 4.97 cm ± 0.13) than for the Club riders (mean ± SE: 5.34 cm ± 0.12), $p = 0.047$. No influence of expertise was found for the cervical segment and the lumbar segment, $ps > 0.95$ (**Figure 3**). The Expertise × Segment interactions were not significant for SD_{AP} [$F_{(2, 46)} = 0.14$, $p = 0.867$] and SD_{ML} [$F_{(2, 46)} = 2.76$, $p = 0.074$].

The ANOVAs also revealed main effects of Vision on SD_{AP} [$F_{(3, 69)} = 5.07$, $p = 0.003$] and SD_{ML} [$F_{(3, 69)} = 7.75$, $p < 0.001$], but not on SD_V [$F_{(3, 69)} = 0.76$, $p = 0.522$]. Holm-Bonferroni *post-hoc* tests showed that SD_{AP} was significantly lower in the No scene condition than in the No vision condition, $p = 0.010$, and that SD_{ML} was significantly greater in the Cont Scene condition than in the No scene and the No vision conditions, $ps \leq 0.007$.

The main effects of Vision can be further specified by the significant Segment × Vision interactions observed on SD_{AP} and SD_{ML} (**Figure 4**). For SD_{AP}, the Segment × Vision interaction [$F_{(6, 138)} = 4.86$, $p < 0.001$] indicated that the vision condition influenced the anteroposterior variability of the head and cervical segment, but had no effect on the lumbar segment (**Figure 4A**). More precisely, Holm-Bonferroni *post-hoc* tests showed that the No scene condition led to lower anteroposterior variability of head movements than the No vision condition ($p < 0.001$) and that the variability of C7 in the anteroposterior axis was significantly lower in the No scene condition than in all other vision conditions ($ps \leq 0.002$). There was no other significant difference in segment variability between vision conditions for the AP axis.

For SD_{ML}, the Segment × Vision interaction [$F_{(6, 138)} = 2.73$, $p = 0.015$] also indicated that lumbar segment variability was not influenced by the vision condition unlike variability of the head and cervical segment (**Figure 4B**). Holm-Bonferroni *post-hoc* tests conducted on SD_{ML} showed that both the Cont scene condition and the Strob scene condition led to greater mediolateral variability of head movements than the No vision and No scene conditions ($ps \leq 0.012$). Mediolateral variability of the cervical segment was significantly greater in the Cont scene condition than in the No scene condition ($p = 0.001$). There was no other significant difference in segment variability between vision conditions for the ML axis.

Finally, the ANOVA conducted on SD_{ML} indicated that the Expertise × Segment × Vision interaction was close to significance [$F_{(6, 138)} = 2.16$, $p = 0.051$]. The Expertise × Segment × Vision interactions were not significant for SD_{AP} and SD_V [$Fs_{(6, 138)} \leq 1.21$, $ps \geq 0.302$], and there were no significant Vision × Expertise interactions in any axis of movement [$Fs_{(3, 69)} \leq 2.00$, $ps \geq 0.122$].

TABLE 2 | Results of the Expertise × Segment × Vision ANOVAs conducted on SD_{AP}, SD_{ML}, and SD_V.

	SD_{AP}			SD_{ML}			SD_V		
	F	***p***	η_p^2	***F***	***p***	η_p^2	***F***	***p***	η_p^2
Expertise	**5.64**	**0.026**	**0.197**	3.77	0.065	0.141	1.37	0.254	0.056
Segment	2.89	0.066	0.112	**23.56**	**0.000**	**0.506**	**18.68**	**0.000**	**0.448**
Vision	**5.07**	**0.003**	**0.181**	**7.75**	**0.000**	**0.252**	0.76	0.522	0.032
Segment × Expertise	0.14	0.867	0.006	2.76	0.074	0.107	**3.95**	**0.026**	**0.147**
Vision × Expertise	1.76	0.163	0.071	2.00	0.122	0.080	0.91	0.438	0.038
Segment × Vision	**4.86**	**0.000**	**0.175**	**2.73**	**0.015**	**0.106**	0.96	0.453	0.040
Segment × Vision × Expertise	0.46	0.837	0.020	2.16	0.051	0.086	1.21	0.302	0.050

Significant differences are indicated in bold. η_p^2 = Partial Eta Squared.

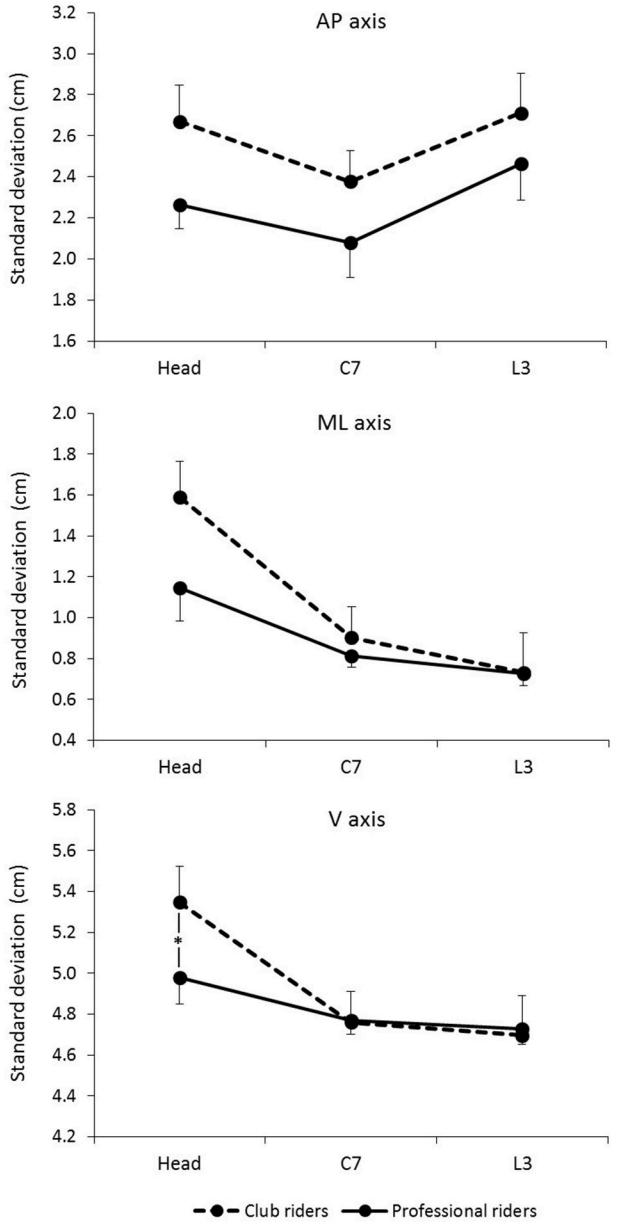

FIGURE 3 | Mean standard deviation of segment position for the Club riders and the Professional riders in the three axes of movement. The Expertise × Segment interaction was significant for SD_V and not significant for SD_{AP} and SD_{ML}. See the text for details. *$p < 0.05$. The error bars represent standard error.

Contribution of Visual Information to Head Stability Depending on Expertise

Effect of Expertise on Head Stability

The ANOVAs presented in the previous section revealed a main effect of Expertise on SD_{AP} and some interactions involving Expertise for SD_{ML} and SD_V. In order to specifically address our second hypothesis that head variability would be lower for the Professional riders compared to the Club riders under visually altered conditions, we conducted planned comparisons of least-squares means on SD_{AP}, SD_{ML}, and SD_V for the head only for each vision condition (**Figure 5**).

We found that the position of the head was significantly less variable for the Professional riders than for the Club riders in the anteroposterior axis (SD_{AP}) in the Strob scene [$F_{(23)} = 7.37$, $p = 0.012$] and in the No Vision [$F_{(23)} = 4.93$, $p = 0.036$] conditions. In the mediolateral axis, the position of the head was significantly less variable for the Professional riders than for the Club riders in the Cont scene [$F_{(23)} = 5.09$, $p = 0.033$] and in the Strob scene [$F_{(23)} = 5.60$, $p = 0.026$] conditions. In the vertical axis, the difference between Professional and Club riders was close to significance in the Strob scene condition [$F_{(23)} = 3.93$, $p = 0.059$], in the No Vision condition [$F_{(23)} = 3.62$, $p = 0.070$] and in the Cont scene condition [$F_{(23)} = 3.57$, $p = 0.072$]. Other differences were not significant, $ps \geq 0.186$.

Visual Field Dependence-Independence and Head Stability

A *t*-test comparing the RFT perceptual scores of the Professional and Club riders revealed a significant difference between the two groups [$t_{(23)} = 4.53$, $p = 0.044$]. The 13 Club riders achieved a mean error of 7.30° (SE ± 1.35°) and the 12 Professional riders a mean error of 4.13° (SE ± 0.49°). These results indicated that the Professional riders were less dependent on the visual field than were the Club riders.

To evaluate the relation between perceptual style and postural stability, we performed Pearson's correlation analyses between RFT scores and head variability. We found significant positive correlations between the standard deviations of the head in the ML axis and the RFT scores in all conditions of vision: Cont scene [$r_{(24)} = 0.54$, $p < 0.001$], Strob scene [$r_{(24)} = 0.55$, $p < 0.001$], No scene [$r_{(24)} = 0.39$, $p < 0.001$], and No vision [$r_{(24)} = 0.23$, $p = 0.014$]. We also found a significant positive correlation between head stability along the V axis and RFT scores in the Cont scene [$r_{(24)} = 0.15$, $p = 0.048$] and No vision [$r_{(24)} = 0.23$, $p = 0.013$] conditions. Finally, no significant correlation was found between head displacements along the AP axis and RFT scores.

Coordination Modes

Analyses of the variability of segment position revealed significant differences between the Professional and Club riders. In particular, the Professional riders were found to stabilize their head better in the anteroposterior axis than the Club riders. The following analyses were conducted to assess whether this better stabilization was associated with specific postural coordination modes in the anteroposterior axis. For each variable, we conducted an Expertise × Vision ANOVA with repeated measures on the second factor. The results of these analyses are reported in **Table 3**. **Figure 6** presents the mean relative phases for the Club and Professional riders in the four vision conditions.

Coordination between the Lumbar and Cervical Segments (ϕ_{L-C} and $SD\phi_{L-C}$)

The ANOVA conducted on ϕ_{L-C} revealed a main effect of Expertise [$F_{(1, 22)} = 8.20$, $p = 0.009$] with a mean relative phase

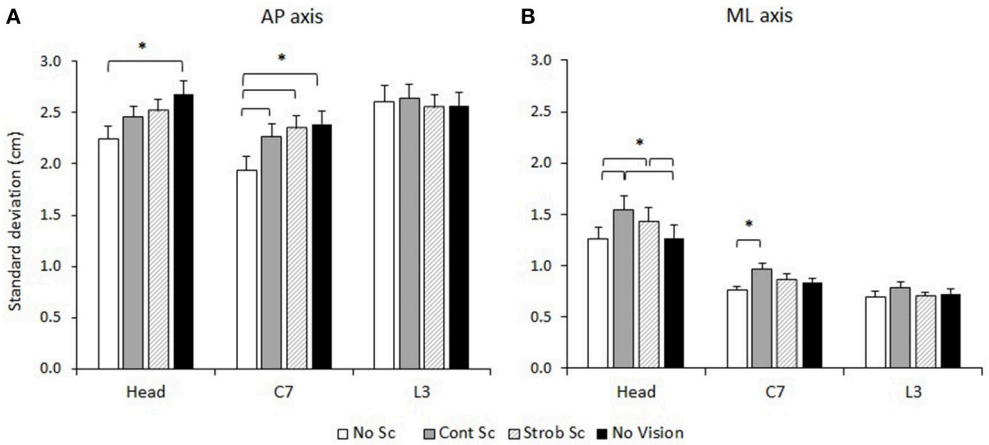

FIGURE 4 | Segment × Vision interactions on SD_{AP} (A) and SD_{ML} (B). No Sc, no simulated scene condition; Cont Sc, continuous simulated scene condition; Strob Sc, stroboscopic simulated scene condition; No vision, No vision condition. *$p < 0.05$. See the text for details. The error bars represent standard error.

of 188.27° ($SD\phi_{L-C} = 24.24°$) for the Club riders and of 153.99° ($SD\phi_{L-C} = 22.67°$) for the Professional riders. This result shows that unlike the Club riders who exhibited an anti-phase pattern between the lower and the upper trunk, the movement cycle of the upper trunk appeared sooner after the movement cycle of the lower trunk in the Professional riders. The main effect of Vision [$F_{(3, 66)} = 1.77$, $p = 0.161$] and the Expertise × Vision interaction [$F_{(3, 66)} < 0.99$, $p = 0.043$] were not significant.

The ANOVA conducted on $SD\phi_{L-C}$ revealed a main effect of Vision on the within-participants dispersion around the mean relative phase [$F_{(1, 66)} = 3.26$, $p = 0.027$]. However, Holm-Bonferroni *post-hoc* tests revealed no significant difference between vision conditions from pairwise comparisons, $p \geq 0.18$. The main effect of Expertise [$F_{(1, 22)} < 0.15$, $p = 0.694$] and the Expertise × Vision interaction were not significant [$F_{(3, 66)} < 0.19$, $p = 0.898$].

Coordination between the Lumbar Segment and the Head (ϕ_{L-H} and $SD\phi_{L-H}$)

The ANOVA conducted on ϕ_{L-H} revealed a main effect of Vision [$F_{(3, 66)} = 4.59$, $p = 0.006$]. Holm-Bonferroni *post-hoc* tests showed a significant difference between the coordination modes in the No vision condition ($\phi_{L-H} = 152.4 \pm 47.16°$) and the Strob scene and No scene conditions, $ps \leq 0.050$, with mean relative phases of 172.16° (± 42.59°) and 168.01° (± 44.36°) for the Strob scene and the No scene conditions, respectively. No other difference between vision conditions was significant. The main effect of Expertise [$F_{(1, 22)} = 2.66$, $p = 0.117$] and the Expertise × Vision interaction were not significant [$F_{(3, 66)} = 2.24$, $p = 0.092$].

The ANOVA conducted on $SD\phi_{L-H}$ showed no main effect of Expertise [$F_{(1, 22)} < 1$, $p = 0.77$] and Vision [$F_{(3, 66)} = 1.33$, $p = 0.27$], but revealed a significant Expertise × Vision interaction [$F_{(3, 66)} = 4.95$, $p = 0.004$]. However, Holm-Bonferroni *post-hoc* tests revealed no significant difference from pairwise comparisons ($ps \geq 0.156$).

Coordination between the Cervical Segment and the Head (ϕ_{C-H} and $SD\phi_{C-H}$)

The ANOVA conducted on ϕ_{C-H} revealed a main effect of Vision [$F_{(3, 66)} = 3.09$, $p = 0.033$] and a significant Vision × Expertise interaction [$F_{(3, 66)} = 3.18$, $p = 0.030$]. Holm-Bonferroni *post-hoc* tests showed that ϕ_{C-H} differed between the No vision (mean $\phi_{C-H} = -10.30°$, $SD \pm 24.66°$) and the Cont scene (mean $\phi_{C-H} = 14.74°$, $SD \pm 34.13°$) conditions for the Professional riders only ($p = 0.037$), and that no other difference between vision conditions was significant for either group of participants. The main effect of Expertise was not significant [$F_{(1, 22)} < 0.66$, $p = 0.427$].

The ANOVA conducted on $SD\phi_{C-H}$ showed no main effect of Expertise [$F_{(1, 22)} < 1$, $p = 0.52$] or Vision [$F_{(3, 66)} = 2.53$, $p = 0.064$]. However, the Vision × Expertise interaction was significant [$F_{(3, 66)} = 7.08$, $p < 0.001$]. Holm-Bonferroni *post-hoc* tests specified that the within-participants dispersion around the mean relative phase was lower in the No vision condition than in the Cont scene condition ($p = 0.033$) and in the No scene condition ($p = 0.036$) for the Professional riders only.

DISCUSSION

The purpose of this study was to evaluate the relative contribution of visual information to head and trunk stability in Club and Professional horseback riders and the coordination modes adopted to regulate balance according to expertise. Modes of spatial referencing were taken into account to determine the riders' perceptual typology and its possible relation to postural stability.

Before addressing our main hypotheses, it should be noted that overall expertise levels and vision conditions, the head exhibited larger displacements than the upper trunk and the lower trunk in the mediolateral and vertical axes. We did not find such an effect of body segment along the anteroposterior axis: the displacements of the head, the upper trunk and the lower

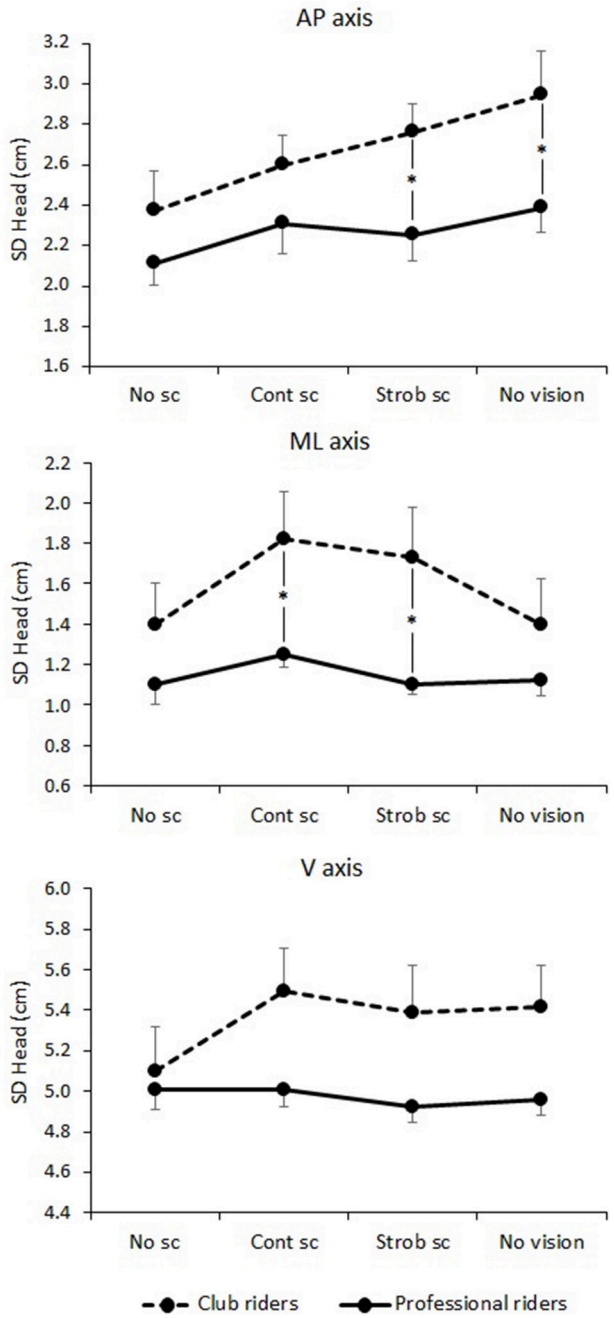

FIGURE 5 | Head variability depending on vision condition and expertise for the three axes of movement. No sc, no simulated scene condition; Cont sc, continuous simulated scene condition; Strob sc, stroboscopic simulated scene condition; No vision, No vision condition. *$p < 0.05$. See the text for details. The error bars represent standard error.

trunk remained in the same range of motion in the AP axis. This suggests that the inverted pendulum model of balance often used to describe quiet standing (e.g., Winter et al., 1997; Peterka, 2002) does not apply to postural regulation in horseback riding. This is a first indication that more complex coordination patterns take place to maintain balance in response to the perturbations induced by the simulator's movements.

We can also note several general results independent of expertise regarding the influence of vision condition on the stability of the different levels of the spine. First, we observed no influence of the vision condition on the variability of the lumbar segment. This result suggests, unsurprisingly, that the stability of the lower trunk is influenced mainly by the mechanical perturbations of the support surface and not by the visual information available. Second, the head and the cervical segments were significantly more stable in the AP axis when the riders faced the white projection screen (No scene condition) than in the other vision conditions. This result is in accordance with previous research that showed the stabilizing effect of fixed surroundings (e.g., Lee and Lishman, 1975; Guerraz et al., 2001). Third, we found no influence of the vision condition on postural stability along the V axis. A likely explanation is that the magnitude of the mechanical perturbations induced by the movements of the riding simulator along the vertical axis has much more influence on postural stability than the visual information available.

Postural Stability and Horseback Riding Expertise

Our first hypothesis was that Professional riders would produce lower postural displacements and deploy more efficient postural control from the top of the head to the lower trunk, leading them to better stabilize their head. Our findings support this hypothesis. First, riding expertise appears to be characterized by the ability to minimize postural displacements in the anteroposterior axis. Overall body segments (i.e., head, upper trunk, and lower trunk) and vision conditions, the Professional riders exhibited greater postural stability in the anteroposterior axis than the Club riders. Overall vision conditions, the Professional riders also exhibited greater head stability in the V axis than the Club riders, while there was no significant difference in the stability of the upper trunk and the lower trunk based on the level of expertise. These findings suggest that postural stability of the overall upper body in the AP axis and more specifically of the head in the V axis is a signature of expertise in horseback riding. However, a closer look at the results according to vision conditions is needed to specify the influence of expertise on postural stability.

Relative Contribution of Sensory Information to Riders' Postural Stability Depending on Expertise

Our second hypothesis was that the contribution of visual information to riders' postural stability is reduced among expert riders in favor of vestibular and somesthetic reliance, leading the experts to maintain head stability better in visually altered conditions. Based on our hypothesis, we expected the selective or total suppression of static and dynamic visual cues to induce greater displacements of the head in the Club riders than in the Professionals.

We found no difference in head stability between the Professional and the Club riders in the two unrestricted visual

TABLE 3 | Results of the Expertise × Vision ANOVAs conducted on the mean relative phases and their standard deviations.

	Lumbar-Cervical (ϕ_{L-C})			Lumbar-Head (ϕ_{L-H})			Cervical-Head (ϕ_{C-H})		
Mean (ϕ)	***F***	***p***	η_p^2	***F***	***p***	η_p^2	***F***	***p***	η_p^2
Expertise	**8.20**	**0.009**	**0.271**	2.66	0.117	0.108	0.66	0.427	0.029
Vision	1.77	0.161	0.074	**4.59**	**0.006**	**0.173**	**3.09**	**0.033**	**0.123**
Expertise x Vision	0.99	0.401	0.043	2.24	0.092	0.092	**3.18**	**0.030**	**0.126**
Standard deviation (*SD*ϕ)									
Expertise	0.15	0.694	0.007	0.08	0.775	0.004	0.42	0.522	0.019
Vision	**3.26**	**0.027**	**0.129**	1.33	0.271	0.057	2.53	0.064	0.103
Expertise x Vision	0.19	0.898	0.009	**4.95**	**0.004**	**0.184**	**7.08**	**0.000**	**0.243**

Significant differences are indicated in bold. η_p^2 *= Partial Eta Squared.*

conditions (Cont scene and No scene) for the different axes of movement (AP, ML, V). The only exception was head variability in the ML axis in the Cont scene condition, with the Club riders exhibiting greater head displacements than the Professional riders. One possible explanation for this result might be that Club and Professional riders use different strategies during the turns simulated by the visual scene. Indeed, the riding simulator reproduces the perturbation of the chosen pace (gallop in our case) with a fixed orientation of the mechanical horse. Thus, unlike a real ride, the back of the mechanical horse does not turn in the horizontal plane when the visual scene indicates a curved trajectory of the route. The riders might have dealt with this discrepancy differently depending on their level of expertise. It is also possible that the Club riders did not use the visual information provided by the simulated scene with sufficient efficiency to stabilize their head in the ML axis as well as the Professional riders. Solving this question would necessitate a coupling between movement measures and data from the simulated visual scene that is not currently available with the Persival simulator. This coupling would represent a major evolution of the apparatus for research purposes.

The results obtained under stroboscopic illumination were in accordance with our hypothesis. In this condition, the Club riders exhibited greater head displacements compared to the Professionals. The difference was significant in the AP and ML axes, and close to significance in the vertical axis. Dynamic visual cues have been shown to play a major role in postural stabilization during upright stance (e.g., Amblard and Crémieux, 1976; Amblard and Carblanc, 1980; Amblard et al., 1985). In particular, postural stability was found to be severely impaired under stroboscopic illumination (Amblard and Crémieux, 1976; Paulus et al., 1984; Amblard et al., 1985; Assländer et al., 2015), though with some interindividual differences (Crémieux and Mesure, 1994; Isableu et al., 2010, 2011). The present findings highlight these interindividual differences in relation to sports expertise. Suppressing dynamic visual cues differently affected head stability depending on the level of expertise in horseback riding: the Club riders appear to rely more on dynamic visual cues than the Professionals in order to control head stability.

The results obtained in the absence of visual information also agreed with our hypothesis. The position of the head along the AP axis was less variable for the Professional riders than for the Club riders in the No vision condition. However, we found no significant difference along the ML and V axes. These findings reveal that experts handle the absence of visual information better than less experienced riders to maintain head stability in the AP axis.

In order to complete our analysis on the relative contribution of sensory information to postural stability, we examined the relations between perceptual typologies, postural stability and expertise in horseback riding. The perceptual scores obtained with the RFT revealed that the Professional riders were less dependent on the visual field than the Club riders. This predominant perceptual typology in experts agrees with previous findings in other physical activities (e.g., Golomer et al., 1999; Liu, 2003; Guillot and Collet, 2004; Rousseu and Crémieux, 2005) and, in line with our second hypothesis, suggests that expert horseback riders rely more on vestibular and somesthetic information than less experienced riders. This enhanced reliance on non-visual information likely explains the greater head stabilization observed in the Professional riders in visually altered conditions (i.e., No vision and Strob scene conditions) compared to the Club riders (Isableu et al., 2003, 2010; Brady et al., 2012). Correlation analyses showed that field dependence–independence scores measured with the RFT were positively correlated with the variability of the head along the ML and V axes. This result provides an additional demonstration of the effect of perceptual typology on postural control (e.g., Isableu et al., 2010, 2011).

The joint analysis of postural stability and perceptual typology highlights a major result of the present study. Except for the mediolateral variability of the head in the Cont scene condition discussed above, the Club riders managed to maintain a level of head stability similar to the Professional riders when visual information was available, whether the visual environment was fixed (No scene condition) or simulated displacements corresponding to a ride (Cont scene condition). In fact, in these unrestricted visual conditions, the Club riders could rely on visual information to stabilize their head in space. Given that the Club riders tended to be field-dependent, the postural task was considerably harder in visually altered conditions. The Club riders appeared unable to reweight the sensory information to respond to the lack of visual cues. In contrast,

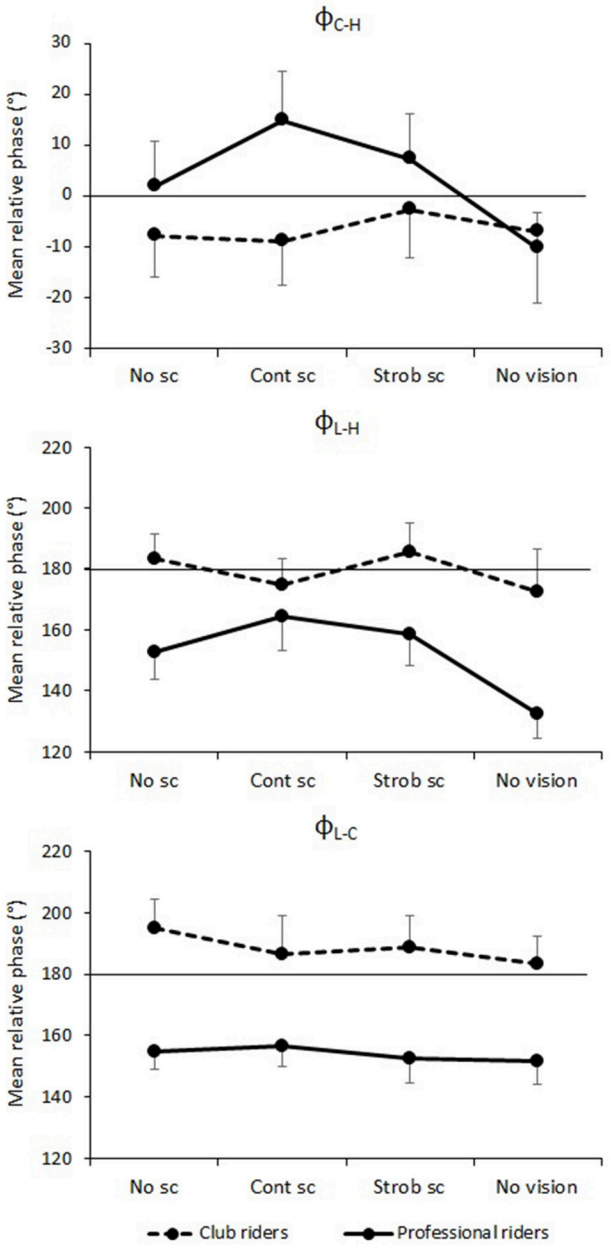

FIGURE 6 | Mean relative phases in degrees between the cervical segment and the head (ϕ_{C-H}), between the lumbar segment and the head (ϕ_{L-H}), and between the lumbar and the cervical segments (ϕ_{L-C}) according to visual condition and expertise. No sc, no simulated scene condition; Cont sc, continuous simulated scene condition; Strob sc, stroboscopic simulated scene condition; No vision, No vision condition. See the text for statistical significance. The error bars represent standard error.

the Professional riders, who were more field-independent, were able to maintain a high level of head stability regardless of the availability of visual information. These results strongly suggest that the capacity to reweight the relative contribution of different sensory information depending on environmental conditions is a more prominent indicator of expertise in horseback riding than the rider's postural stability in unrestricted visual conditions. However, this conclusion does not tell us if there are different sensorimotor processes involved in expert and non-expert riders to reach the same level of head stability in unrestricted conditions of vision. The experts' ability to use vestibular and somesthetic information in altered visual conditions does not necessarily mean that they do not use visual information when it is available. Also, the fact that head stability was equivalent in experts and non-experts does not necessarily mean that they adopted similar motor behaviors to achieve this level of stability. Fully addressing these questions would necessitate a complete specific design (e.g., Oie et al., 2001; Peterka, 2002). Nevertheless, the present results on postural coordination modes do provide initial insights.

Postural Coordination Modes

Our third hypothesis was that horseback riding experts would exhibit specific coordination modes to maintain a high level of postural stability. Research has shown that when two joints oscillate together, they are strongly attracted toward in-phase (relative phase close to 0°) or anti-phase (relative phase close to 180°) patterns. These two attractive states have been identified in numerous joint pairings, including bimanual (e.g., Yamanishi et al., 1980; Kelso, 1984), arm-leg (e.g., Kelso and Jeka, 1992), elbow-wrist (e.g., Kelso et al., 1991), ankle-wrist (e.g., Carson et al., 1995), and ankle-hip (e.g., Bardy et al., 1999; Faugloire et al., 2005). The execution of patterns differing from in-phase and anti-phase often requires intensive practice (e.g., Zanone and Kelso, 1992; Faugloire et al., 2006, 2009). The results of the present study demonstrate that these spontaneous modes found in many effector systems are also found in the postural coordination of horseback riders in the anteroposterior axis: The Club riders exhibited an anti-phase coordination mode (segments moving synchronously in opposite directions) both between the lower trunk and the upper trunk and between the lower trunk and the head, and an in-phase coordination mode (segments moving synchronously forward and backward) between the upper trunk and the head.

Interestingly, the Professional riders adopted coordination modes that departed from pure in-phase and anti-phase patterns. In particular, they exhibited a mean relative phase of 154° between the lower and the upper trunk (ϕ_{L-C}) in every vision condition, while the Club riders adopted an anti-phase pattern (mean $\phi_{L-C} = 188°$). In other words, the Professional riders anticipated the anteroposterior movements of the upper trunk compared to the Club riders: the maximal position of the cervical segment occurred sooner in the Professional riders than in the Club riders, for whom the maximal position of the cervical segment (forward) was almost perfectly synchronized with the minimal position of the lumbar segment (backward).

Another interesting result is that, unlike the Club riders, the Professional riders exhibited changes in coordination modes between the cervical segment and the head depending on available visual information. The Club riders exhibited a close to in-phase coordination mode with a slight lag of the cervical segment with respect to the movement of the head (indicated by the negative values of the relative phases) in every vision condition (mean ϕ_{C-H} ranging from −8.83° in the Cont

scene condition to −2.75° in the Strob scene condition). By contrast, the Professional riders adopted coordination patterns ranging from +14.74° in the Cont scene condition to −10.30° in the No vision condition (**Figure 6**). When the simulated scene was projected on the screen, the Professional riders anticipated the cervical segment's movements with respect to the head's movements (positive ϕ_{C-H} of +14.74° in the Cont scene condition). When no visual information was available, the Professional riders adopted a coordination pattern similar to the Club riders with the movement of the cervical segment following the head movement with a slight delay (negative ϕ_{C-H} of −10.30° in the No vision condition). Again, it is interesting to note that this cervical-head coordination mode observed when no visual information was available was also adopted by the Club riders in every other vision condition. This result reveals that, although the Professional riders were able to stabilize their head better than the Club riders in visually altered conditions, they did not rely only on vestibular and somesthetic information in unrestricted visual conditions. The specific relative phase between the cervical segment and the head exhibited by the Professional riders in the Cont scene conditions suggests that the experts did use visual information in this condition to adapt their postural coordination modes to environmental conditions. This interesting result is difficult to discuss further and would have to be connected to other dependent variables such as the flexion-extension of the neck and the visual search behavior of the participants.

Finally, we found that the coordination between the lumbar segment and the head (ϕ_{L-H}) depended on the vision condition over the two levels of expertise, with a significant difference between the No vision condition ($\phi_{L-H} = 152.42°$) and every other vision condition (ϕ_{L-H} ranging from 168.01° in the No scene condition to 172.16° in the Strob scene condition). **Figure 6** (middle panel) strongly suggests that this effect of vision is due mainly to a change in the coordination mode of the Professional riders who exhibited relative phases between the lumbar segment and the head ranging from 164.33° in the Cont scene condition to 132.42° in the No vision condition, while the Club riders maintained an anti-phase coordination mode in every vision condition. This result is likely to be the direct consequence of the behavior observed on the two underlying levels of lumbar-head coordination, namely lumbar-cervical and cervical-head coordination.

Limitations and Perspectives

The present study is the first to investigate the contribution of visual information to postural stability and the postural coordination modes in horseback riding depending on expertise. As such, several experimental features can potentially be enhanced in future work. Using an equestrian simulator enabled us to overcome difficulties encountered in studies on horseback riding such as controlling and reproducing the horses' movements, facilitating data collection, and manipulating vision conditions. However, while the projected visual scene simulated the horizontal displacements corresponding to a ride, including turns, the mechanical horse's orientation was fixed. Therefore, while the riding simulator faithfully reproduced the vertical and pitch perturbations of the chosen pace, it did not produce any horizontal movements, either in yaw or in translation. Consequently, the mechanical perturbations were only partially similar to a real ride. In addition, there was a discrepancy between the visual information provided by the projected visual scene and the mechanical horse's motion. Given the current technical constraints of riding simulators, it seems that only a study in the field could overcome these limitations, though with all the other difficulties that this method would entail. A related issue concerns the possibility to match precisely the data from the projected visual scene and movement measures. This coupling would help understand more finely how riders react to the different events simulated in the visual scene, such as the aforementioned turns. This might have helped interpret the difference in head stability in the mediolateral axis between the Professional and Club riders that we observed only when the simulated visual scene was projected.

Another limitation concerns the size of the visual field occupied by the projected scene. The simulated scene used in the present study was limited to the participants' central visual field, thereby reducing the possibility of using peripheral vision which is known to play an important role in postural control (e.g., Pavard et al., 1976; Amblard et al., 1985). A multi-sided immersive environment would make it possible to strengthen and extend the conclusions of the present study. Another, non-exclusive, perspective would be to collect and combine additional data about pelvis orientation, angular displacements (of the hips, neck and knees), and/or horse-rider interactions, for example. Indeed, the new insights we have gained through the study of horseback riders' postural control encourage further investigations to better understand the highly complex task that is horseback riding.

CONCLUSIONS

The present study demonstrates a differential contribution of visual information to postural stability in horseback riding depending on expertise. First, compared to the Club riders, the Professional riders exhibited greater head stability in the anteroposterior axis when vision conditions were altered. Second, RFT perceptual scores revealed that the Professional riders were less dependent on the visual field than the Club riders. Third, we found that the more dependent the riders were on the visual field, the greater their head variability. These results suggest that expert horseback riders rely more on vestibular and somesthetic information to stabilize their head in space than less experienced riders. Our assessment of the coordination modes between the different levels of the spine completes and specifies this conclusion. Unlike the Club riders, who exhibited similar in-phase or anti-phase patterns in the different vision conditions, the Professional riders exhibited changes in coordination modes depending on the visual information available. Thus, even though the expert riders proved to be less dependent on visual information to stabilize their head than the non-expert riders, they appeared to make use of visual information when it was available to adapt their postural coordination modes. The combination of stability, perceptual

typology and postural coordination measures therefore strongly suggests that expert riders are better able to reweight sensory information in order to control their posture according to task constraints.

AUTHOR CONTRIBUTIONS

AO, LL, and EF designed the study. AO and SB performed the experiments. AO and EF analyzed the data and AO, EF, LL, and BI wrote the manuscript.

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Plantar Sole Unweighting Alters the Sensory Transmission to the Cortical Areas

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It is well established that somatosensory inputs to the cortex undergo an early and a later stage of processing. The later has been shown to be enhanced when the earlier transmission decreased. In this framework, mechanical factors such as the mechanical stress to which sensors are subjected when wearing a loaded vest are associated with a decrease in sensory transmission. This decrease is in turn associated with an increase in the late sensory processes originating from cortical areas. We hypothesized that unweighting the plantar sole should lead to a facilitation of the sensory transmission. To test this hypothesis, we recorded cortical somatosensory evoked potentials (SEPs) of individuals following cutaneous stimulation (by mean of an electrical stimulation of the foot sole) in different conditions of unweighting when standing still with eyes closed. To this end, the effective bodyweight (BW) was reduced from 100% BW to 40% BW. Contrary to what was expected, we found an attenuation of sensory information when the BW was unweighted to 41% which was not compensated by an increase of the late SEP component. Overall these results suggested that the attenuation of sensory transmission observed in 40 BW condition was not solely due to the absence of forces acting on the sole of the feet but rather to the current relevance of the afferent signals related to the balance constraints of the task.

Keywords: plantar sole afferents, unweighting, EEG, standing balance

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INTRODUCTION

Somatosensory processes have been accorded an important role in triggering and shaping rapid postural responses to unexpected perturbation of the support surface while standing. Indeed, when removing somatosensory inputs in cats with Pirydoxine, Stapley et al. (2002) showed delayed postural responses. The importance of cutaneous inputs in the setting of forces exerted on the ground is supported by a deficit in weight-bearing during locomotion in cats after cutaneous nerve section (Bouyer and Rossignol, 2003). Equally in humans, the significance of cutaneous inputs for controlling postural adjustments has been evidenced by studies of anesthetized foot plantar soles (Do et al., 1990). In addition, in vestibular-loss animals after bilateral labyrinthectomy (Inglis and Macpherson, 1995), the latencies of the postural responses were normal (∼375 ms) or even earlier (∼325 ms) suggesting a critical role of somatosensory inputs in balance control during perturbation rather than a vestibular-based control. However, when balance control is not challenged (i.e., due to a perturbation or voluntary movements) during the maintenance of normal standing, Meyer et al. (2004) showed that the reduced plantar sensitivity after anesthesia did not alter the postural sway.

These studies and others (Ruget et al., 2008; Mouchnino and Blouin, 2013) have highlighted the role of cutaneous afferents when relevant for the task (i.e., challenged balance control). Remarkedly, modulation of the excitability of somatosensory areas can be observed in tasks requiring high somatosensory control (Staines et al., 1997; McIlroy et al., 2003). Indeed, cortical responsiveness to sensory stimuli can be increased in challenging balance situations while standing still (Bolton et al., 2011). For instance, using the somatosensory-evoked potential (SEP) technique, Bolton et al. (2011) found an increased sensitivity to somatosensory inputs of the hand when participants, who were standing with one foot in front of the other (i.e., Romberg's challenging balance task), lightly touched a fixed support surface with their hand. Importantly, this sensory facilitation was associated with improved balance control (i.e., less postural oscillations) compared to a condition with the same light touch on a support attached to the participant's wrist (i.e., not referenced to the external environment). Bolton et al. (2011) concluded that the external-referenced touch enhanced the perception of self-generated postural oscillations relative to the external world. Therefore, enhancing the transmission of relevant somatosensory input from the foot sole during challenging balance control, would allow participants to control body sway relative to the external gravity and balance constraints.

However, compensatory postural regulations and functional consequences are load-dependent changes. Carrying extra weight on the body translates into a decreased of the SEP likely indicating a depressed transmission of cutaneous input (Lhomond et al., 2016). Indeed, such variations were observed by Desmedt and Robertson (1977) as early as 55 ms after a tactile electrical stimulation. This early component was interpreted as reflecting the activity of the primary somatosensory cortex (SI; Hari et al., 1984; Hämäläinen et al., 1990). For example, Salinas et al. (2000) showed that the majority of SI neurons in monkeys were phase-locked with the vibratory stimulus. These neurons encoded the stimulus frequency, suggesting a high relationship of SI activity with the incoming sensory inputs. The decrease in the transmission of the afferent cutaneous inflow arising from the periphery to SI could originate from foot deformation resulting from the extra loading. Indeed, it has been reported that obese individuals (Hills et al., 2001) showed higher pressures under the heel, mid-foot and metatarsal regions of the foot compared to normal-weight individuals. Subsequently other studies have observed a greater total plantar force and a greater total contact area (Gravante et al., 2003; Birtane and Tuna, 2004) in obese individuals. A related study by Vela et al. (1998) showed similar observations when normal-weight individuals were loaded with external weights to simulate obesity. Therefore, skin compression where the tactile receptors were embedded could be at the origin of sensory transmission attenuation. For example, under foot loading, the height of the arch of the foot decreases (Bandholm et al., 2008; McPoil et al., 2009) and almost 50% of this change could be accounted for by skin compression (Wright et al., 2012). These behavioral studies together with Lhomond et al.'s (2016) electrophysiological study suggest that the attenuation of the sensory transmission of cutaneous inputs comes from a mechanical origin due to foot sole loading. This phenomenon may be explained by refractoriness in the peripheral nerves themselves (skin receptors firing is already saturated due to load), by depression of synaptic transmission (slowly adapting receptors reduce their input due to adaptation from the foot sole loading), or by alteration of the transmission anywhere along the ascending sensory pathway and within the cortex itself. Therefore if the mechanoreceptors are even partly silenced by the additional weight compressing the skin of the foot sole, the transmission to S1 should be altered.

On the basis of the behavioral and electrophysiological findings reported above, we hypothesized that unweighting the plantar sole should lead to a facilitation of the sensory transmission. To this end, we recorded cortical SEPs following cutaneous stimulation (by mean of an electrical stimulation of the foot sole) in different conditions of unweighting.

MATERIALS AND METHODS

Ten participants (6 males and 4 females) performed a bipedal balance task (mean age: 32 ± 13 years; mean height: 173 ± 9 cm; mean weight: 65 ± 4 kg). All participants were free of neurological and musculoskeletal disorders that could influence postural control and had a good fitness base (for review see Paillard, 2017). Informed consent was obtained from all participants, and all procedures were in accord with the ethical standards set out in the Declaration of Helsinki and ethic committee Sud Méditerranée (ID RCB:2010-A00074-35). A Lower Body Positive Pressure (LBPP) treadmill (M310 Anti-gravity Treadmill®, AlterG Inc., Fremont, CA, USA) enables an individual's bodyweight (BW) to be varied. LBPP technology applies a consistent and substantial lifting force opposite to BW. The AlterG® treadmill includes an airtight flexible chamber applied distally to the subject's iliac crest. This creates local unweighing of the lower limbs while the upper body and all gravity-receptors still experience earth gravity (Sainton et al., 2015; **Figure 1A**). The electrical signal of the differential pressure (Patmospheric − Pchamber) was recorded with the vertical ground reaction force obtained from four dynamical load cells (XA-shear beam load cell, Sentran®, Ontario, CA, USA) located under the frame of the AlterG® treadmill. The ground reaction forces were summed to compute the real BW of the participants.

Participants wore neoprene shorts and stood barefoot on the AlterG® treadmill. Initially, they remained stationary, with their arms alongside their bodies (**Figure 1A**). The neoprene shorts were sealed to the inflatable chamber. The seal height was adjusted to be level with each participant's iliac crest, so that the seal itself exerted little or no vertical force. In addition, the compliance properties of the chamber were such that participants' body was free to move in all directions and participants were even able to walk and run comfortably as shown by Cutuk et al. (2006).

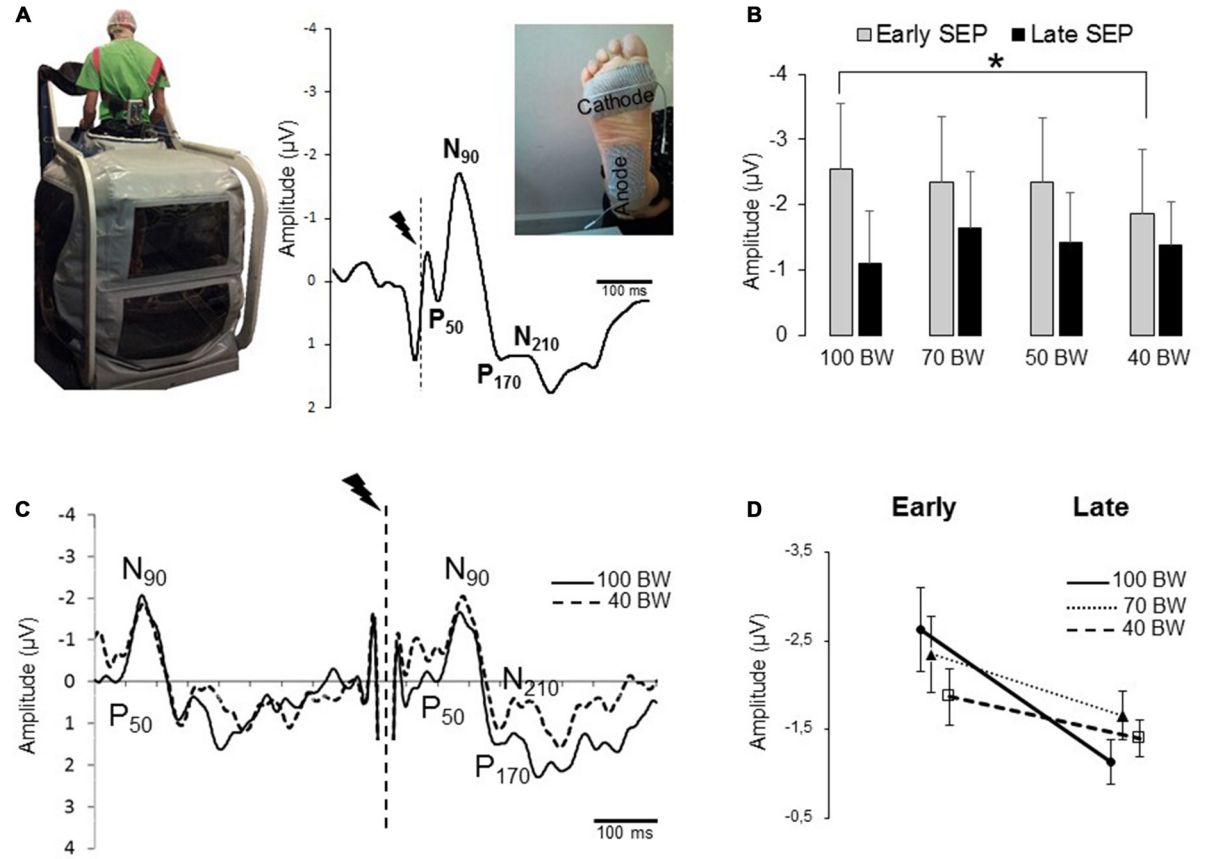

FIGURE 1 | (A) Image displaying the position of participants in the Anti-gravity Treadmill®. Grand-average EPs for 10 participants recorded over Cz electrode during quiet standing which exhibits an early somatosensory evoked potential (SEP; P_{50}-N_{90}) followed by a later component (P_{170}-N_{210}). The vertical dotted lines indicate the stimulation onset. **(B)** Mean for the 80 stimulations of the Early P_{50}-N_{90} and late P_{170}-N_{210} SEPs amplitudes for all participants (error bars are standard deviation across participants). (*$p < 0.05$). **(C)** The traces corresponds to the average SEP in 100 bodyweight (BW) and 40 BW conditions for one participant. The break in the curves corresponds to the electrical stimulation artifact. Note that the presence of a first P_{50}-N_{90} SEP is due to the time-window shown in the figure that encompasses two stimulations interspace of 500 ms. **(D)** Interaction between the early and late SEPs for 100 BW, 70 and 40 BW conditions. The error bars are standard error of the mean.

Participants were requested to self-select a side-by-side foot position (approximately feet shoulder-width apart, wide stance) and to keep their eyes closed. Here, particular attention was paid to maintaining the self-selected foot position (i.e., feet shoulder-width apart before each trial) because of the effect of stance width on both postural control and the use of sensory feedback. As shown by Jacobs et al. (2015), the corticomuscular coupling of the bêta frequency band known to represent both afferent and efferent coupling between sensorimotor regions of cerebral cortex and muscle, is sensitive to changes in biomechanical conditions (i.e., wide- or narrow-stance) but not to sensory conditions (foam surface or eyes closed).

The participants were then submitted to different unweighting conditions without changing this initial wide-stance. Four different weighting conditions were applied: 100% of BW, 70 BW, 50 BW and 30 BW. These target values set in the AlterG were held constant for a while (2–3 mn) during the recording session. The changes in BW were applied in a descending sequence (D) from 100D to 30D and then upwards from (U) 50U, 70U and 100U. The participants were blind to the weight conditions and to the sequence. Instead, they were instructed that the BW could be modulated randomly either by increasing or decreasing the weight.

At every stage of unweighting, the participants were asked to estimate the percentage of BW they were experiencing. In order to avoid any prediction of the percentage of the unweighting, the target weight was not reached directly but only after exploring other weighting. In a control task, participants adopted a semi-supine position (Supine, **Figures 1C**, **2A**) seated in a reclining chair with their plantar soles without a contact with a support surface. The order of the Supine and the Standing task on the treadmill were counterbalanced across participants.

Stimulation Procedure

While standing the plantar sole of the left foot was stimulated four times with a constant 500 ms interval between each electrical stimulus. This was designed to avoid the "interference phenomenon" (Burke and Gandevia, 1988; i.e., depressed

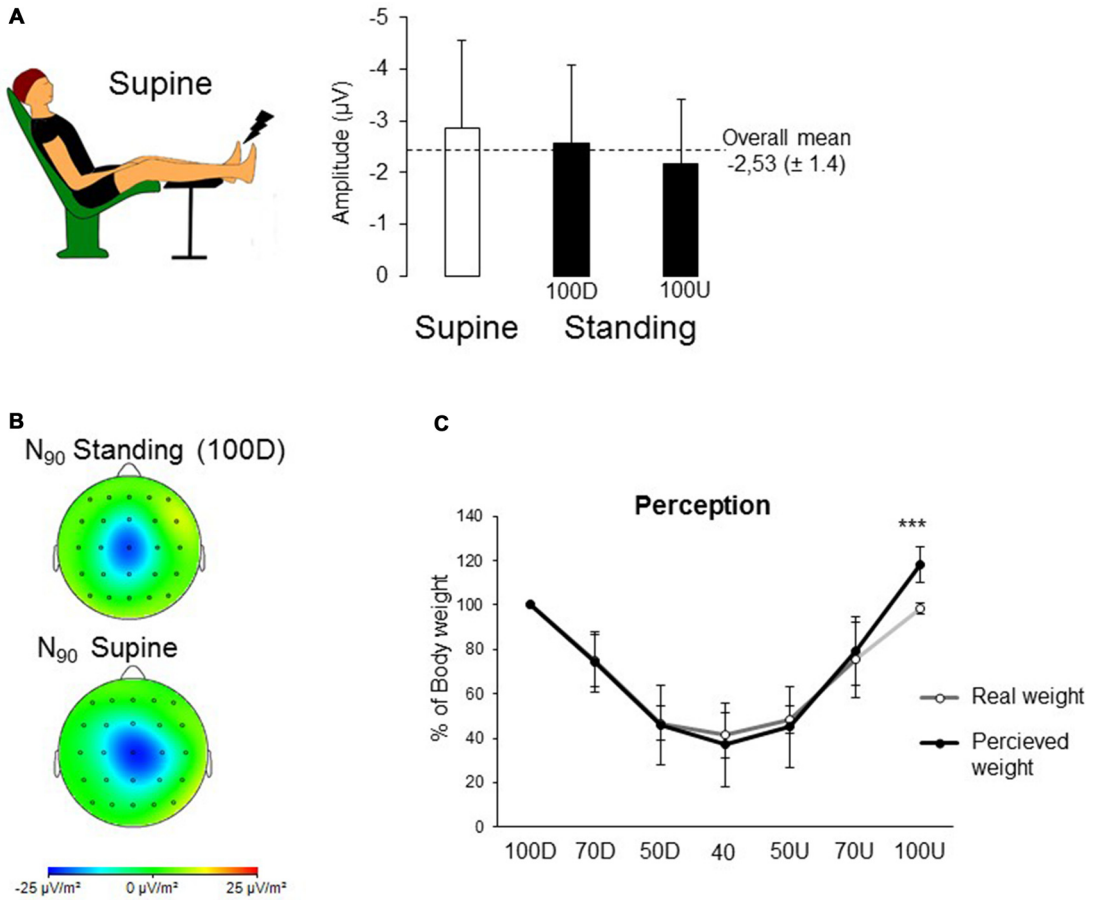

FIGURE 2 | (A) Image displaying the supine position. Mean SEPs for the supine position and both 100% of BW conditions. **(B)** To enhance the spatial resolution of the recordings, topographical current source density (CSD) maps were computed using Laplacian transformation with Brain Vision Analyzer. The signal was interpolated with a spherical spline interpolation procedure in order to compute the second order derivatives in two dimensions of space (order of splines: 3; maximal degree of Legendre polynomials: 15). CSDs are independent of the reference electrode site and are much less affected by far-field generators than monopolar recordings. The cortical maps are shown at the latency of the peak negativity (i.e., N90). **(C)** Comparison between the perception of BW given by the participants and the real weight computed by the vertical forces recorded by the treadmill. Each dot corresponds to the mean of 10 participants for all the weighting conditions (error bars are standard deviation across participants; ***$p < 0.001$).

SEPs when stimulations are too close in time, i.e., less than 300 ms according to Morita et al., 1998). The electrical stimulus was delivered by a DS5 isolated bipolar constant current stimulator (Digitimer, Welwyn Garden City, UK). The cathode was located under the metatarsal region and the anode was positioned underneath the heel of the supporting foot (**Figure 1A**, 5 × 9 cm electrodes, Platinum Foam Electrodes). The stimulation consisted of a single rectangular 10 ms pulse applied under the supporting foot. Taking into account the signature of the cutaneous reflexes reported in Sayenko et al.'s (2009) study, we carefully selected both the position of the electrodes to stimulate the plantar sole as a whole without targeting a specific portion of the foot, and the amplitude of the stimulation to avoid cutaneous reflexes. The stimulation intensity was set as in our previous studies (Mouchnino et al., 2015; Lhomond et al., 2016). For each participant, and while standing, we first found the minimum intensity which gave a constant perception of the stimulations (mean amplitude 6.2 ± 0.1 mA). This stimulation was determined as the baseline value. The stimulation intensity for each participant was set at 25% higher than the baseline value (i.e., well below the motor threshold). Each condition of weighting was divided into 20 standing trials of 5 s. During each trial 4 electrical stimuli were triggered (80 stimulations per condition).

Electroencephalography and Behavioral Recordings and Analyses

Electroencephalographic (EEG) activity was recorded continuously from 64 Ag/AgCl surface electrodes embedded on an elastic cap (ActiveTwo system, BioSemi, Netherlands). According to the specification of the BioSemi system, "ground" electrodes were replaced by Common Mode Sense active and Driven Right Leg passive electrodes. These two electrodes, located near Pz and POz electrodes, form a feedback loop, which drives the average potential of the participant (the Common

Mode voltage) as close as possible to the anolog-digital converter (ADC) reference voltage in the AD-box. The signals were pre-amplified at the electrode sites and post-amplified with DC amplifiers and digitized at a sampling rate of 1024 Hz (24-bit resolution). Signals from each channel were referenced using the average of the 64 scalp electrodes. The signals were further filtered off-line with 35 Hz (high cut-off) filters (digital filters, 48 dB/octave) and 0.1 Hz (low cut-off) filters (digital filters, 12 dB/octave; BrainVision Analyzer 2, Brain Products, Germany).

SEPs, (**Figure 1A**) were obtained by averaging, for each participant and condition, all synchronized epochs (i.e., 80) relative to the electrical stimulus. The average amplitude of the (−100; −50 ms) pre-stimulus epoch served as baseline. The −50 ms relative to the stimulation was chosen to avoid any artifact related to the stimulation procedure. We examined the SEPs over the Cz electrode as this electrode overlays the sensorimotor cortices on the homunculus, the feet are located on the inner surface of the longitudinal fissure. The earliest discernible positive (P_{50}) and negative (N_{90}) peaks after each stimulus were identified. Such peaks latencies are comparable to latencies observed by Altenmüller et al. (1995) and Duysens et al. (1995) evoked by stimulating the sural nerve. The fact that the sural nerve is a primarily/exclusively cutaneous nerve (Burke et al., 1981) lends argument for the P_{50}-N_{90} originating from cutaneous input. The amplitude of the P_{50}-N_{90} waveform was measured peak-to-peak., a late SEP component (P_{170}-N_{210}) was observed at a latency similar to latencies observed in Lhomond et al.'s (2016) study.

Head acceleration was measured by using a triaxial accelerometer (Model 4630: Measurement Specialties, Virginia, VA, USA) placed on the chin. The rationale for using head acceleration as an index for whole body stability relative to space is that for balance and posture the whole body can be assumed to act as a rigid segment (inverted pendulum model) about the subtalar joint of the feet (MacKinnon and Winter, 1993). For example, Jeka et al. (1997) showed that during a light finger touch on a stationary bar, the lateral displacements of head and center of pressure were in phase and superimposable. For each trial, after applying a 4th order *Butterworth* filter with 3 Hz cut-off frequency on the raw data over time, de-biasing and rectifying the signal, we computed the integral of a 1600 ms time-window which encompassed the four stimulations periods including the $P_{50}N_{90}$ component following the last stimulation (**Figure 3A**).

We analyzed the ground reaction force from one gauge (located on the right non-stimulated side). After applying a 4th order *Butterworth* filter with 3 Hz cut-off frequency on the raw data over time, the data were rectified, integrated and normalized relative to the body mass index of each participant.

Bipolar surface electromyography (EMG; Bortec AMT-8 system; Bortec Biomedical, Calgary, Canada) was used to record bilaterally the activity of the tibialis anterior (TA) and gastrocnemius medialis (GM) muscle. EMG signals were preamplified at the skin site (×1000), analog filtered with a preset bandpass (20–250 Hz) and sampled at 1000 Hz, then rectified. These recordings were performed to evaluate the level of muscle activation during the standing task. To quantify these activations, we computed the integral of the EMG activity (iEMG) for each muscle during five 400 ms time-windows. The first time-window was computed before the stimulation (i.e., baseline [−450; −50]). The other time-windows were computed after each stimulation (i.e., [50; 450], [550; 950], [1050; 1450], [1550; 1950]). As no differences were observed between the four iEMG-windows during the stimulation period we computed the mean iEMG from the four time-windows. One of the participants had no available recordings for the 100D condition and was discarded from the analyses.

Statistical Analyses

The amplitudes and latencies of the SEPs were submitted to repeated-measures analysis of variance (ANOVA) designed with conditions of weighting (100D, 70D, 50D and 30). Significant effects were further analyzed with Newman-Keuls *post hoc* tests. For the size effect calculation we used the η^2 (Eta squared), and to work out effect size we used the Cohen's (1988) guidelines (Fritz et al., 2012). We also conducted paired *t*-tests when necessary. The level of significance was set at 5% for all analyses. All dependent variables (EEG and behavioral data) showed normal distributions (i.e., $p > 0.05$, Kolmogorov-Smirnov test).

RESULTS

The assessment of the precision of the BW level was performed a posteriori; 70 BW corresponded to 75 ± 10%, 50 BW was 47 ± 5% and 30 BW was 41 ± 10% for all participants. In order to determine if the real unweighting experienced by each participant corresponded to the target unweighting set in the AlterG, the real unweighting was compared to a standard value (i.e., target unweighting) for each condition. These analyses revealed that the real weight for the 70 and 50 BW conditions were not different from their standard values ($t_9 = 1.32$; $p = 0.21$ and $t_9 = -1.48$; $p = 0.17$, respectively). In the 30 BW condition the real weight is increased relative to the standard value set in the AlterG ($t_9 = 3.81$; $p = 0.004$). We therefore chose a new and more appropriate standard value of 40 ($t_9 = 0.72$; $p = 0.48$). For clarity of purpose, we replaced the 30 BW condition by 40 BW below in the results section to denote each unweighting levels.

Somatosensory Evoked Potentials

During quiet standing, the foot stimulation evoked typical EEG signals. **Figure 1A** shows the grand average at electrode Cz for all participants. Both an early and a late sensory processes were identified. The early SEP consisted in a small positive component (P_{50}) followed by a prominent negative deflection (N_{90}). First of all, to assess that decreasing and increasing the weight on the feet (i.e., order effect) did not change the amplitude of the SEP, we compared the 100, 70, 50 Down with the 50, 70, 100 Up. SEP amplitudes were submitted to 2 modes (decreasing, increasing) × 3 BW (100, 70, 50 BW) repeated measures ANOVAs. The results showed that the amplitude of the P_{50}-N_{90} SEP did not depend on the order (i.e., Down or

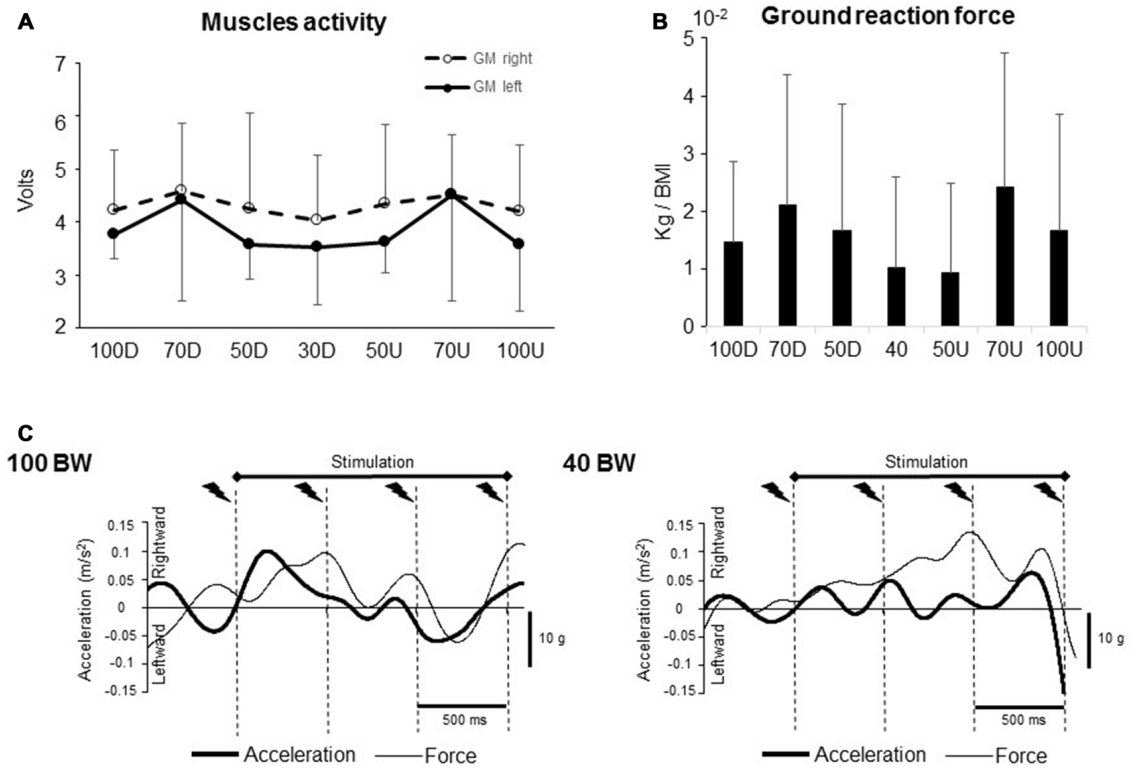

FIGURE 3 | (A) Integrals of both right and left gastrocnemius medialis (GM) muscles activity recorded during a 450 ms duration period. **(B)** Integrals of the vertical ground reaction force during a 2100 ms duration period that encompassed the whole stimulation procedure. **(C)** Mean head lateral acceleration and ground reaction force non-rectified traces for one participants (100 BW and 40 BW).

Up) of the unweighting ($F_{(1,9)}$ = 0.34; p = 0.57) nor on the BW ($F_{(2,18)}$ = 0.14; p = 0.86). Therefore we will use the descending order to compare the 100D, 70D, 50D and 40 BW conditions.

SEP data (amplitude and latencies) were submitted to repeated measures ANOVA with different condition of BW (100D, 70D, 50D and 40) as the main factor. The results showed a BW main effect on the P_{50}-N_{90} SEP amplitude ($F_{(3,27)}$ = 3.41; p = 0.031) with a large size effect of 0.27. As the decrease at 40% BW is relatively small with large standard deviation, we used the Tukey's HSD test (i.e., less liberal test than the Newman-Keul's *post hoc* test) and found that the SEP had a smaller amplitude in the 40 BW condition (−1.86 ± 1 μV) compared to the 100 BW conditions (−2.56 ± 1.5 μV; p = 0.02; **Figure 1B**). In addition, no BW effect was observed for the latencies of P_{50} ($F_{(3,27)}$ = 0.93; p = 0.43; overall mean of 64 ± 17 ms) and of N_{90} ($F_{(3,27)}$ = 0.59; p = 0.62; overall mean of 96 ± 19 ms). It was noticed that the ANOVA did not show a general BW effect (100, 70, 50 and 40 BW) on the late SEP component (**Figure 1B**, $F_{(2,27)}$ = 1.60; p = 0.21).

To assess whether the decreased SEP observed in 40 BW was due to an altered use of mechanoreceptors provoked by the unloading of BW, a supine position (i.e., weightless) was compared to both Standing conditions (i.e., 100D and 100U, **Figures 2A,B**). The results did not show a condition effect on the early SEP amplitude (overall mean: −2.53 ± 1.4; $F_{(2,18)}$ = 2.94; p = 0.07) or on the P_{50} and N_{90} latencies (P_{50} overall mean: 62 ms ± 13; $F_{(2,18)}$ = 0.60; p = 0.55 and N_{90} overall mean: 92 ms ± 15; $F_{(2,18)}$ = 0.42; p = 0.66).

To further test whether the attenuated transmission of sensory inputs (P_{50}-N_{90} SEP) in the 40 BW condition was associated with an altered late potential (P_{170}-N_{210} SEP), SEP data were submitted to repeated measures ANOVA with conditions (100 BW, 70 BW and 40 BW) and SEPs components (early P_{50}-N_{90} and late P_{170}-N_{210} components) as the main factor (**Figures 1C,D**). We have discarded the 50 BW condition from the analyses to lessen the variability. The results revealed a main component effect ($F_{(1,9)}$ = 7.17; p = 0.02 with an interaction SEP (early and late components) × BW ($F_{(2,18)}$ = 5.09; p = 0.17). Post hoc analyses showed that the early components were greater than the late components in 100 BW and 70 BW conditions ($p < 0.05$) and of approximately equal amplitudes in 40 BW condition (p = 0.12). In addition *post hoc* analyses confirmed that the early SEP recorded in the 100 BW condition was greater than the early SEP of the 40 BW condition (p = 0.016) but not different from the 70 BW condition (p = 0.35). What is informative (Hsu, 1996) is that the late SEP in the 70 BW condition was greater than in the 100 BW although this statistical value fell short of the conventional 0.05 cut-off value for statistical significance (p = 0.07). No difference was observed between the late SEP in 100 BW and in 40 BW (p = 0.23).

Perception and Behavior

Due to the difference between target value and real weight, it was considered more pertinent to compare the perception of the weight to the real weight. In addition, the 100D condition was excluded as it started the experiment in the AlterG and all participants were aware of the 100% BW condition. With regard to perception (**Figure 2C**), results showed a significant interaction between conscious perception of the BW and real conditions of weighting ($F_{(5,45)}$ = 2.58; p = 0.038) with a large size effect of 0.22; *post hoc* analyses confirmed that the participants' own BW was perceived heavier in the 100 Up (117 ± 8% of BW) than the real BW (i.e., 98 ± 2 of BW; $p < 0.001$).

The behavioral data (activity of ankle musculature, vertical ground reaction force, and head acceleration) were submitted to repeated measures ANOVA with different condition of BW (100D, 70D, 50D 40, 50U, 70U, 100U) as the main factor during the stimulation procedure (i.e., stimulation).

To verify if the difference in the SEPs amplitude was not due to a difference in the motor activity, we compared the iEMG of TA and GM muscles of both legs computed in the different conditions. The muscle activity did not change across the unweighting condition; however, the activity of the left GM showed a slight rise in activity for both 70D and 70U BW conditions without reaching the significant level (**Figure 3A**, $F_{(6,48)}$ = 2.09; p = 0.07). No condition effect was observed for the other ankle muscles ($F_{(6,48)}$ = 0.38; p = 0.88; $F_{(6,48)}$ = 1.36; p = 0.24; $F_{(6,48)}$ = 0.51; p = 0.79 for the right GM and right and left TA, respectively). Overall, these results suggest that the depression of the early SEP in 40 BW condition was not related to an increase in muscular activity which indeed could have induced a sensory suppression (Cohen and Starr, 1987; Seki and Fetz, 2012).

After normalization to the body mass index (including participant's weight and height), ground reaction force and head acceleration data were analyzed (**Figure 3C**). No difference was observed neither for the forces (**Figure 3B**, $F_{(6,54)}$ = 1.68; p = 0.14, for the main condition effect) or for the head acceleration ($F_{(6,54)}$ = 1.45; p = 0.21, $F_{(6,54)}$ = 1.63; p = 0.15, in the mediolateral and anteroposterior direction, respectively).

DISCUSSION

The aim of this study was to identify whether the sensory transmission from the plantar sole tactile receptors in a bipedal standing position is modulated relative to the force acting on the foot sole. A facilitation of the sensory transmission was expected in the unweighting condition.

Surprisingly our results did not show an increase in transmission as expected but rather a decreased early activity over SI in the unweighting 40 BW condition compared to full BW (i.e., 100 BW). One possible explanation for these findings is that the unweighting 40 BW condition with reduced loading of the feet could have induced a change in sensory noise (i.e., background sensory traffic). Indeed, mechanoreceptors adaptation to the static pressure due to normal BW could not take place under such unloading and may give raise to a sensorial "noise" (Weerakkody et al., 2007). This sensorial "noise" or interference phenomenon (Burke and Gandevia, 1988) could be at the origin of a low perception. For example Mildren and Bent (2016) have shown that cutaneous stimulation at different skin regions across the foot can influence proprioception at the ankle joint (i.e., perception of feet orientation). The authors concluded that inputs from cutaneous mechanoreceptors had an influence on ankle proprioception and this error of perception could be due to an inhibition of cutaneous or spindle proprioceptive feedback, causing the perception of smaller movement magnitudes. This sensorial "noise" could be also observed when wearing a loaded vest (i.e., low SEP, Lhomond et al., 2016) or when comparing standing to sitting (Mildren et al., 2016). However, the perception of participants' weight in the 40 BW condition was preserved (i.e., no difference between the real, 41% and the perceived weight, 37%) despite the decrease sensory transmission (i.e., lower early SEP). The accurate perception of BW in the 40 BW condition could not dismiss the sensory "noise" hypothesis. Indeed, Bays and Wolpert (2007) suggested that the noise in the sensory system could lead to a reweighting of the available sensory sources. Therefore, the integration of other modalities could compensate for the sensory "noise" and preserve an accurate perception of the BW.

While in most previous studies an increase in sensory transmission has been shown to be related to an increased perception of tactile stimuli when relevant to the motor task (Duysens et al., 1995; Cybulska-Klosowicz et al., 2011), our results suggest a less straightforward causal relationship between transmission and perception. In the current study, the perception was altered (i.e., overestimated, about 120%) with the presence of a full amplitude SEP (i.e., 100Up BW) and, conversely perception was preserved with a decreases SEP amplitude (i.e., in 40 BW). Therefore perception does not depend solely on early sensory transmission but rather relies predominantly on processing signals originating from sensorimotor-related neural mechanisms. Among these sensorimotor mechanisms were those involved in the prediction of the sensory consequence of our own action even if this action consists in preserving body equilibrium (Blakemore et al., 1998, 1999a,b; Voisin et al., 2011; Cullen and Brooks, 2015; Benazet et al., 2016).

Evidence for task-specific gating of the cortical transmission in the 40 BW condition observed in the current study parallels that seen in McIlroy et al.'s (2003) study. For instance, these authors showed that the SEPs evoked by tibial nerve stimuli in a seated task while the participants were to relax (i.e., Supine condition here, in our study) were similar to those of a task (termed "Threatened balance") in which the seated participants were maintaining the position of an inverted pendulum with threat of external perturbation by balancing a platform under their feet (i.e., Standing 100% BW here, in our study). In addition, in a third sitting task without a threat to the stability of the pendulum (i.e., No balance constraints) but with the same forces exerted on the foot sole (i.e., muscle contraction or ankle angle), the SEP was depressed by 28%. This study (McIlroy et al., 2003) together with the depressed SEP in the 40 BW condition (i.e., low balance constraints) may support the idea

that the central nervous system decreases sensory transmission according to the decrease in the balance constraints of the task. Indeed, the 40 BW condition did not endanger the equilibrium as it was reported by Ritzmann et al. (2015) in underloading situations during parabolic flight (i.e., 0.16 and 0.38 g). These authors showed that the center of gravity is suitably adjusted above the base of support and that was achieved by a slow body motion control resulting from the noticeably reduced ankle joint torque.

Our results suggest that the brain exerts a dynamic control over the transmission of the afferent signal (i.e., attenuation) according to their current relevance to the task. The idea that the attenuation probably occurs at a cortical level has been previously suggested by Applegate et al. (1988). This study suggests that the attenuation of short latency cerebral potentials during standing relative to voluntary isometric plantarflexion while sitting may not be explicable entirely by the change in background muscle activity and by non-specific effects exerted on relay nuclei by standing because the subcortical component (P_{32}-N_{38}) was not reduced by stance. Additional support suggesting that the altered transmission of afferent inputs is centrally-driven comes from the late SEP analyses. Remarkably, the decrease of the early SEP in 40 BW condition was not associated with an increase in the late sensory processes (i.e., same amplitude of late SEP in 40 BW and in 100 BW) contrary to what was observed in overloading condition (Lhomond et al., 2016). In this previous study, the enhancement of the late-stage sensory integration was interpreted as a mechanism aimed at compensating for decreased early sensory transmission in order to control whole body stability which was decreased with additional loading. Even though the transmission of cutaneous input is depressed and the late integrative process remained unchanged in the current study, both head acceleration and vertical force exerted onto the ground were similar to the normal weight condition. These results suggested that there was no need for further compensation (i.e., increase late sensory process) as body balance was not endangered by the unweighting 40 BW condition.

In addition, the late SEP was greater and associated with an increased lateral head acceleration during the first unweighting change experienced by the participants (i.e., 70D condition). This condition separates for the first time the gravitational somatosensory information (i.e., altered) provided by the contact forces of the feet with the supporting surface from the vestibular cues provided by the gravity acceleration (i.e., unchanged). The late sensory upregulation together with the decreased whole body stability observed here most likely reflects an enhancement of the integration of somatosensory and vestibular inputs from the head acceleration, to reset an internal model of gravity (Papaxanthis et al., 2003; Indovina et al., 2005; Herold et al., 2017). A similar increased activation has been reported by Miyai et al. (2006) in healthy participants during gait on a treadmill with unusual partial BW support (10%).

In conclusion, our study is the first to examine the unweighting effects on the transmission of afferent inputs from the periphery to the cortical areas during upright standing. We observed a suppression of sensory transmission in particular within a threshold range from 47% to 41% of BW (i.e., respectively, 50 BW and 40 BW conditions) experienced by the healthy participants. This is partly because the tactile information from the foot sole is less relevant in terms of balance constraints with underloading. In this context, as the AlterG® treadmill can be considered as a safety device for loading and unloading lower extremities in patients with lower limb injuries and disorders, the efficacy of the rehabilitation programs should consider the sensory mechanisms together with the motor aspects of standing, walking and running.

AUTHOR CONTRIBUTIONS

LM, OL and PC contributed to the conception and design of the work. LM, OL, CM and PC contributed to the acquisition, analysis, or interpretation of data for the work, contributed to the writting of the work or revising it critically.

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Imaging Posture Veils Neural Signals

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Whereas modern brain imaging often demands holding body positions incongruent with everyday life, posture governs both neural activity and cognitive performance. Humans commonly perform while upright; yet, many neuroimaging methodologies require participants to remain motionless and adhere to non-ecological comportments within a confined space. This inconsistency between ecological postures and imaging constraints undermines the transferability and generalizability of many a neuroimaging assay. Here we highlight the influence of posture on brain function and behavior. Specifically, we challenge the tacit assumption that brain processes and cognitive performance are comparable across a spectrum of positions. We provide an integrative synthesis regarding the increasingly prominent influence of imaging postures on autonomic function, mental capacity, sensory thresholds, and neural activity. Arguing that neuroimagers and cognitive scientists could benefit from considering the influence posture wields on both general functioning and brain activity, we examine existing imaging technologies and the potential of portable and versatile imaging devices (e.g., functional near infrared spectroscopy). Finally, we discuss ways that accounting for posture may help unveil the complex brain processes of everyday cognition.

Keywords: posture, neuroimaging, EEG, fMRI, upright, supine, cognition, perception

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INTRODUCTION

From psychiatry and cognitive science to education and marketing, many experts draw on discoveries from human brain imaging to inform their practice. However, few consumers of neuroimaging findings fully appreciate the methodological and environmental variables that these techniques often impose. For example, in a typical functional magnetic resonance imaging (fMRI) experiment, participants lie motionless in a body-sized bore while piercing screeches, thumps, and hums thunder around their head for up to an hour. In a customary electroencephalography (EEG) experiment, participants sit upright, alone, in a small, silent, and often dimly lit room, while staring at and responding to a computer screen for extended periods of time. Of the many glaring discrepancies between such imaging environments and everyday life, this review focuses on the role of body posture. We summarize important findings from research examining the relationship between posture and brain data, highlight the mechanisms underlying these postural influences, and discuss experimental techniques that can help overcome postural caveats in human brain research.

Neuroimagers seldom draw on research suggesting that environmental variables impact human cognition. Meanwhile, an entire field of research, entitled "embodied cognition," highlights the intricate relationship among our cognitive capacities, ongoing sensorimotor state, and surrounding environment (Thompson and Varela, 2001; Wilson, 2002; Thompson, 2005; Di Paolo and Thompson, 2014). Relevant postural findings highlight that slouching increases measures of

helplessness and stress (Riskind and Gotay, 1982) and expansive postures increase testosterone, decrease cortisol, and amplify feelings of power and risk-tolerance (Carney et al., 2010). Static imaging environments further diminish cognitive loads related to balance, moving visual fields, and social interaction (Hari and Kujala, 2009). Considering these factors, some scientists demand a new neuroscientific model—the "embodied brain"—to better account for the ongoing interactions between brain, body, and environment (Kiverstein and Miller, 2015).

IMAGING METHODS AND IMAGING POSTURES

Popular functional neuroimaging modalities collect electromagnetic or hemodynamic brain data (**Table 1**). EEG and magnetoencephalography (MEG) record electric and magnetic signals from pyramidal neurons; fMRI measures deoxygenated blood concentrations that correlate with neural activity; and functional near infrared spectroscopy (fNIRS) measures oxygenated and deoxygenated blood flow. EEG and MEG come with spatial precision of about 1 cm, yet millisecond temporal resolution; fMRI provides millimetric spatial resolution but temporal precision of ∼1 s; fNIRS excels in neither temporal nor spatial resolution and comes with a high signal-to-noise ratio compared to fMRI (Cui et al., 2011). MEG outperforms EEG in terms of signal-to-noise ratio when accessing deeper brain regions (Goldenholz et al., 2009). Each imaging modality, moreover, permits a subset of body positions. Participants can wear EEG and fNIRS caps throughout a wide range of postures (see **Table 1**) and, with proper equipment, can move and interact with their environment; MEG restricts participants to an adjustable seat that can adopt any position between an upright chair and a horizontal bench; and most fMRI options constrain participants to horizontal positions. Compared to portable technologies (i.e., EEG and fNIRS), the large and static imaging devices (i.e., fMRI and MEG) permit fewer posture, yet provide higher-quality data. These intrinsic differences lend certain imaging modalities more advantageous for specific applications and research questions but less so for others (e.g., the postural constraints of most MRI scanners would make fMRI a good way to explore the sleeping brain, but less ideal to study the driving brain).

Two canonical imaging postures dominate brain research even though more ecological alternatives exist (see **Table 1**). These established positions include sitting upright—common in EEG, MEG, fNIRS, and most of cognitive and psychological research; and lying supine—the standard for fMRI. Whereas, a limited number of imaging experiments stray from these standardized postures, humans perform many cognitive tasks while standing and moving, yet few while lying down. Experiments leveraging non-standard body positions often ask particular questions which demand these postures. For example, researchers have participants stand or walk to better understand balance, gait, and motor disorders such as Parkinson's disease (Bakker et al., 2007; Koenraadt et al., 2014; Mahoney et al., 2016), lie supine titled 6–12° head-down past horizontal to simulate a microgravity environment (e.g., Spironelli and Angrilli, 2011), or lie prone to investigate gravitational forces on cranial fluids (Rice et al., 2013). Whereas, the execution of these experiments fully depends on the use of non-standard imaging postures, the supine and sitting positions hardly impede researchers from conducting most neuroimaging experiments. This situation may encourage neuroimagers to continue employing standardized imaging postures even when ecological comportments could better unveil the neural mechanisms of everyday cognition.

POSTURE INFLUENCES COGNITION

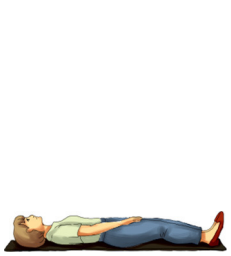
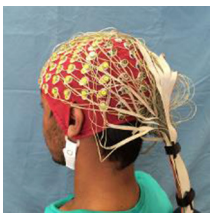
Posture alters sensory perception and behavior (**Figure 1**). For example, when upright compared to supine: Olfactory thresholds increase for select odorants (e.g., Lundström et al., 2008), pain ratings amplify (e.g., Spironelli and Angrilli, 2011; Fardo et al., 2013), visual awareness improves (e.g., Goodenough et al., 1981; Marendaz et al., 1993), anticipatory anxiety heightens (e.g., Lipnicki and Byrne, 2008), approach motivation increases (Price et al., 2012), and conflicting thoughts decrease (e.g., Harmon-Jones et al., 2015). Posture further influences cognitive performance. Compared to lying supine, sitting upright improves non-verbal intelligence (e.g., Raven's Progressive Matrices; Lundström et al., 2008) and aids in composing mental images, but impairs the ability to inspect them (Mast et al., 2003). Standing compromises performance on problems requiring a burst of insight (e.g., anagrams: Lipnicki and Byrne, 2005) and improves psychomotor performance (Caldwell et al., 2000, 2003). Memories, moreover, are easier to retrieve when assuming the posture associated with the remembered event (Dijkstra et al., 2007).

The fMRI environment may alter the very phenomena researchers aim to study. This concern has motivated diverse research groups to test how posture and cognition interact (e.g., Lundström et al., 2008; Harmon-Jones and Peterson, 2009). Replication experiments, however, remain sparse, likely because posture receives more attention as a procedural caveat than a research field in its own right. Beyond posture, neuroimagers must also address several other procedural and statistical concerns before obtaining meaningful results (e.g., Eklund et al., 2016). All in all, these studies highlight the importance of considering posture across all cognitive and imaging research.

POSTURE INFLUENCES PHYSIOLOGY

Heart rate, respiratory volume, oxygen consumption, core body temperature, cortisol secretion, and other indicators of physiological arousal stabilize at higher levels when upright compared to supine (**Figure 1**; Cole, 1989; Kräuchi et al., 1997; Hennig et al., 2000; Badr et al., 2002; Jones and Dean, 2004). These physiological differences may influence the fMRI derived blood-oxygen-level dependent (BOLD) signal, regardless of whether or not brain processes actually change (Kastrup et al., 1999; Di et al., 2013). fMRI measures neuronal activity indirectly (see Shmuel, 2015); the BOLD signal stems from the hemodynamic properties of neural populations and remains

TABLE 1 | Each body posture raises particular considerations in terms of brain imaging modalities and cognitive experiments.

		Canonical imaging postures		Other everyday postures	
		Lying supine	Sitting upright	Standing erect	Sitting reclined
					
EEG		✓	✓	✓	✓
MEG		✓	✓	✘	✓
fMRI		✓	✘	✘	✘
fNIRS		✓	✓	✓	✓
Vigilance		Low	Medium	High	Medium/low
Assumed in waking life		Rare	Common	Common	Occasional
Associated cognitive tasks		Few	Many	Many	Few
Actions possible		Few	Many	Most	Few

To conduct fMRI beyond a horizontal body posture requires specialized scanners, which are extremely uncommon. Researchers can conduct EEG and fNIRS in any posture, but must care for occipital sensors in the supine position. Humans execute most physical and cognitive actions when sitting or standing. To better depict the posture assumed in fMRI, this photo shows a participant before entering the bore. During scanning, the head and upper body remain inside the bore, which measures about 60 cm in diameter for standard scanners.

highly sensitive to cardiopulmonary variables (Chang and Glover, 2009; Chang et al., 2009; Di et al., 2013; Weinberger and Radulescu, 2016). Thus, demonstrating that posture affects the BOLD signal falls short of confirming a change in neural activity; cardiopulmonary variables remain yoked to body position and also weigh heavily on BOLD activity.

Beyond BOLD, posture governs blood flow around the brain (Gisolf et al., 2004). A few experiments employ a stance-adjustable positron emission tomography (PET) gantry and report greater blood flow to both visual and cerebellar cortices when standing erect compared to lying supine (Ouchi et al., 1999, 2001). Using fNIRS, researchers document decreases in both oxygenated and deoxygenated cortical hemoglobin volume when participants move from lying supine to sitting upright (Edlow et al., 2010; Ozgoren et al., 2012). Due to a paucity of upright MRI scanners capable of functional sequences, researchers have yet to replicate postural fNIRS experiments with fMRI. Because fNIRS and fMRI measure similar signals (Cui et al., 2011), we can only presume that postural discrepancies would also influence fMRI data.

Beyond cardiovascular measures, posture exerts a quantifiable and direct impact on neural activity. A few EEG experiments demonstrate that, compared to lying horizontally, lying head-up on an incline between 30–45° (Cole, 1989; Vaitl and Gruppe, 1992) and sitting upright (Chang et al., 2011; Spironelli et al., 2016) increase high-frequency neural activity, associated with alertness and sensory processing, and dampen down low-frequency oscillations associated with relaxed or drowsy states. More recent studies leverage high-density EEG systems and reveal greater high-frequency power across the cortex in more upright postures (Thibault et al., 2014) as well as an 80% increase in occipital gamma power when supine compared to prone (Rice et al., 2013). Posture further alters event related potentials (ERPs) in response to standard visual paradigms (Rice et al., 2013), painful stimuli (Spironelli and Angrilli, 2011; Fardo et al., 2013), and emotional processing (Price et al., 2012; Messerotti Benvenuti et al., 2013). In contrast to these findings, a recent sensor-level MEG study revealed greater high-frequency power over common language areas only, rather than the entire cortex, when sitting upright compared to when supine or reclined (Thibault et al., 2015). Sensor-level MEG results, however, may represent only the strongest postural effects and source-level analyses of such data may reveal more widespread changes reminiscent of previous EEG findings (Lifshitz et al., under review). Whereas, the majority of these studies employ healthy young adults, posture may exert a particularly strong influence on brain function in the elderly and specific patient groups (e.g., cardiovascular disease or tramautic brain injury: Ouchi et al., 2005; Thompson et al., 2005). In this regard, converging evidence from cognitive, medical, and neuroscientific research supports the "embodied brain" hypothesis and underscores the importance of postural variables in modern imaging experiments.

UNDERLYING MECHANISMS BY WHICH POSTURE OPERATES

At least two physiological and one cognitive mechanism contribute to the influence of posture on brain data: (1) changes in noradrenalin output, (2) altered CSF thickness, and (3) a preparatory cognitive state based on the subset of interactions possible with the environment.

(1) The supine position hampers cortical excitability (Lipnicki, 2009; Spironelli et al., 2016). When lying horizontally, compared to upright, gravitational loads redistribute and stimulate arterial and cardiopulmonary baroreceptors, and in turn, lead to a reduction in sympathetic nervous system activity (Mohrman and Heller, 2003). This process appears to impede noradrenergic release from neurons in the locus coeruleus (Murase et al., 1994; Berridge and Waterhouse, 2003) and drives downstream cortical inhibition (Rau and Elbert, 2001). A cleverly designed experiment supports this theory (Cole, 1989). The researcher applied leg pressure via anti-shock trousers (normally used to treat severe blood loss) to maintain levels of baroreceptor activity between lying horizontally and lying head-up on a 40° incline. They found less high-frequency EEG activity only in the condition with reduced baroreceptor firing (i.e., 40° incline without leg pressure). Further theoretical (Lipnicki, 2009) and experimental reports (Vaitl and Gruppe, 1992; Schneider et al., 2008) support the idea that gravity initiates a physiological cascade that leads to cortical inhibition.

(2) Slight shifts in CSF thickness can drastically alter EEG data (Ramon et al., 2004, 2006; Wendel et al., 2008) and, to a lesser extent, MEG data (Vorwerk et al., 2014). Strong evidence for this interaction comes from a unique two-part multi-posture MRI and EEG study (Rice et al., 2013). The researchers found that when supine compared to prone, gravity draws the brain downwards, thins out the highly conductive CSF in occipital regions by 30%, brings the brain slightly closer to posterior scalp electrodes, and in turn, amplifies high-frequency occipital EEG power by an average of 80% (Rice et al., 2013). While this study provides a wealth of information, the scarcity of erect MRI scanners likely precluded an upright condition. And yet, a complementary low-field (0.5 T) MRI study scanned participants in the seated and supine positions and found that gravity draws fluids downward into the spinal canal when upright, decreases intracranial CSF and cerebral blood flow, and amplifies intracranial compliance (Alperin et al., 2005). Measures of CSF thickness in circumscribed cortical regions, however, were not reported. Thus, the quantitative differences in CSF thickness between supine and upright postures remains largely elusive. The finding that CSF not only distorts electromagnetic brain signals, but also varies in thickness among postures, raises particular concern regarding the standard practice of using anatomical MRI data acquired in the supine posture to construct head models for EEG and MEG analyses. Whereas, postural CSF discrepancies may correlate well with brain imaging data, a clear story hardly emerges relating CSF thickness to behavioral observations. This insight suggests that factors beyond CSF likely contribute to the influence of posture on human functioning.

(3) A preparatory cognitive state, set to act on the subset of possible interactions between the current position of a participant and their surrounding environment, may partially account for the influence of posture on brain activity. For example, when lying down, the brain may be poorly prepared for locomotion (de Lange et al., 2006), to observe a moving

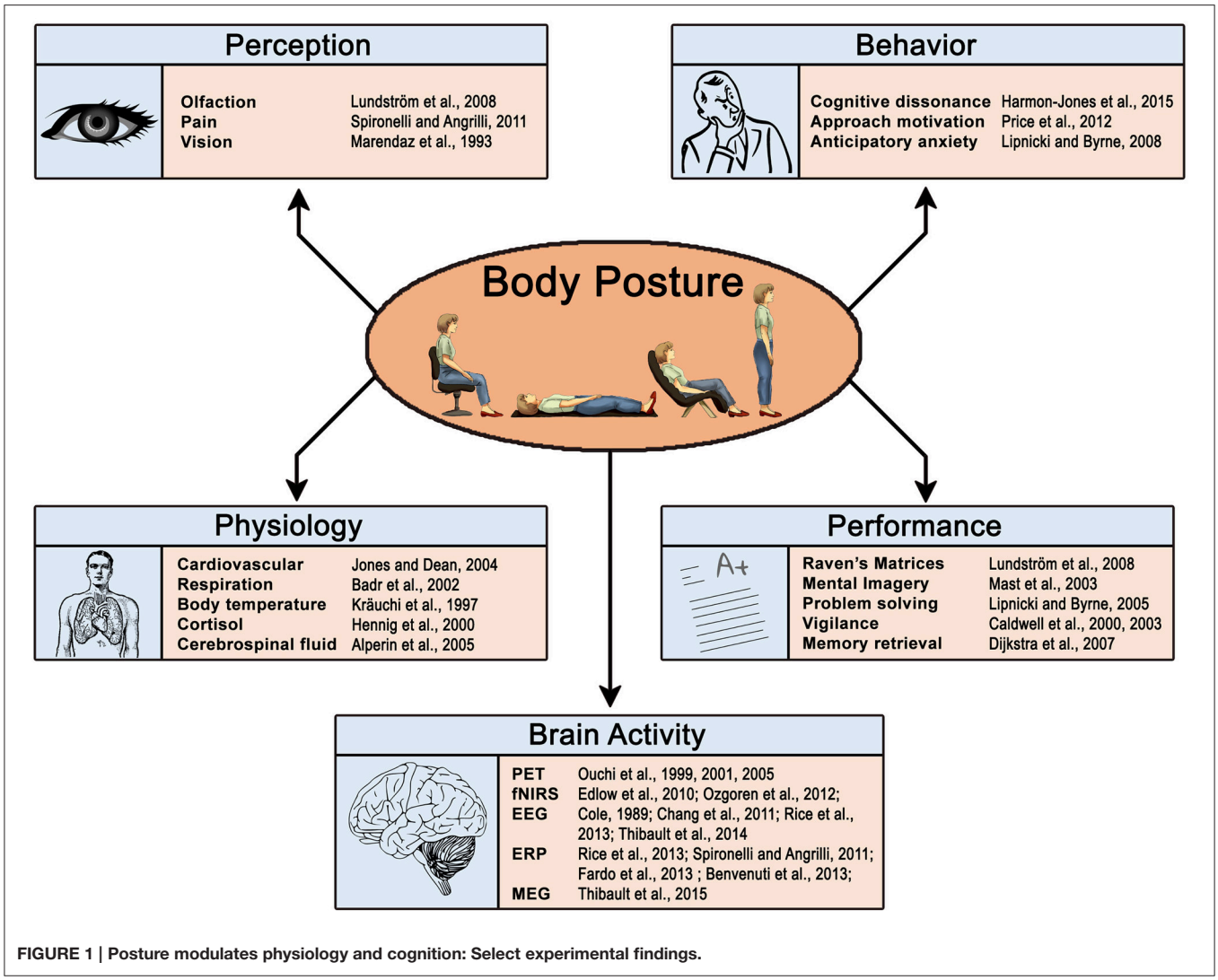


FIGURE 1 | Posture modulates physiology and cognition: Select experimental findings.

visual field (Kano, 1991), or to socially and physically interact with our environment (Hari and Kujala, 2009). Motor plans depend on ongoing limb configuration (de Lange et al., 2006), the excitability of motor cortex increases in free-standing compared to supported postures (Tokuno et al., 2009), and when sitting, compared to supine, people react more quickly to moving visual fields (Kano, 1991) and are more likely to perceive themselves as moving when exposed to a moving visual field (Guterman et al., 2012). Moreover, the supine posture decreases social behaviors (Harmon-Jones and Peterson, 2009; Price et al., 2012) and hardly invites typical social interactions known to modulate brain activity, such as eye contact (Ferri et al., 2014). These posture-dependent cognitive states may manifest in both resting-state brain oscillations (Chang et al., 2011; Thibault et al., 2014; Spironelli et al., 2016) and neural responses to stimuli (i.e., ERPs: Spironelli and Angrilli, 2011; Price et al., 2012; Fardo et al., 2013). The causality of interactions between cognition and brain activity may always remain elusive; cognitive states propel physiological change (i.e., top-down processes) and physiological parameters also weigh on cognitive states (i.e., bottom-up effects).

Taken together, physiological cascades, cranial fluids, and cognitive set all exert varying influences on brain imaging data across postures. Whereas, noradrenergic output and cognitive processing may directly influence cortical activity measured at the neuronal level, CSF shunts the transmission of electromagnetic activity from neurons to sensors and exerts little influence on neuronal activity itself. Adopting experimental designs that evaluate and integrate these three mechanisms can only help to better understand ecological human functioning.

CORRECTING AND ACCOUNTING FOR THE EFFECTS OF POSTURE

Two paths emerge to overcome postural caveats in neuroimaging. First, we can rework standard experimental designs to minimize

the influence of posture on brain activity; and second, we can embrace new imaging technologies conducive to everyday human behavior.

Accounting for the three aforementioned postural mechanisms would require a combination of innovative experimental designs, computational expertise, and a new body of research to draw upon. For example, to maintain cortical excitability in the supine posture, researchers could entertain the possibility of applying pressure to the body via anti-shock trousers to maintain baroreceptor firing (Cole, 1989), pharmacologically sustaining noradrenalin levels, or providing periodic stimulation via conversation or sensory input to sustain participant alertness. Overcoming variation in CSF thickness may require anatomical brain scans from each participant plus compensatory algorithms to calculate the standard redistribution of CSF as a function of posture. Such algorithms do not yet exist and would demand further head modeling research that taps into a database of posture-induced CSF perturbations across individuals (e.g., see Rice et al., 2013). Novel research on posture and cognition, moreover, could help future experimental designs minimize variations in cognitive state among postures. For example, research already demonstrates that poor sleep impedes working memory when supine compared to sitting (Muehlhan et al., 2014) and hampers psychomotor performance when sitting compared to standing (Caldwell et al., 2003). These findings suggest that weeding out sleep-deprived participants from supine imaging experiments could help researchers collect brain data that better reflect upright human functioning. Neuroimagers could further benefit from extending similar screening procedures to participants with mood and hormonal disturbances in response to MRI environments (Muehlhan et al., 2011) and mental performance problems in response to scanner noise (Pripfl et al., 2006). With diligence, neuroimagers can improve current research paradigms to account for a number of these postural discrepancies.

Imaging the human brain increasingly relies on smaller, lighter, and more mobile hardware. These devices hold the potential to thrust brain imaging toward investigating everyday interactive and social cognition. With the use of overhead gantries, participants undergoing EEG and fNIRS can now move and interact in a laboratory environment (Gramann et al., 2011; Mahoney et al., 2016). Recent developments, moreover, permit individuals to connect EEG electrodes to their smartphone and record brain activity in everyday contexts (Stopczynski et al., 2014). Moving while recording EEG, however, comes with caveats. Muscle activity, eye movement, and head motion all contaminate the EEG signal, especially in high-frequency bandwidths (Muthukumaraswamy, 2013). One potential concern is that researchers who are not careful may mistake these artifacts for brain oscillations themselves. The fNIRS signal also remains sensitive to motion artifacts, but responds less to muscle contamination. These portable devices sacrifice signal quality for ecological human functioning. The use of these technologies, however, is not an "either-or" dilemma. In a single experiment, we can combine data from the more precise and static imaging modalities with data from ecological yet coarser devices. Similar to how portable devices revolutionized the field of eye-tracking (Hayhoe and Ballard, 2005), wearable neuroimaging technologies hold promise to revolutionize how we study the living human brain.

CONCLUSION

Across numerous experiments, posture reliably influences brain data, core physiology, and cognitive performance. This reality rings alarm bells in a field that rarely considers postural constraints. Whereas, ecological comportments such as standing and moving recruit a host of additional brain processes and represent the base from which we perform our largest diversity of interactions, few brain imaging studies ask participants to stand or move. A pillar of neuroimaging, MRI, confines participants to a supine position seldom assumed during common wakefulness. This state of affairs brings into question the practice of using neuroimaging findings to inform our ecological behavior of everyday life. Bridging the lacuna between imaging context and ecological posture would further unveil the neural processes giving rise to the living human brain.

AUTHOR CONTRIBUTIONS

RT reviewed the literature, consulted with experts, and prepared the initial draft. RT and AR prepared the final draft together. AR provided comments throughout manuscript preparation.

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frontiers in Human Neuroscience

CORRECTION
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Corrigendum: Imaging Posture Veils Neural Signals

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Keywords: posture, neuroimaging, EEG, fMRI, upright, supine, cognition, perception

A corrigendum on

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Reason for Corrigendum:

In the original article, there was an error. A correction has been made to the Introduction, section 'Imaging Methods and Imaging Postures', first paragraph.

The sentence "MEG outperforms EEG in terms of signal-to-noise ratio when accessing deeper brain regions (Goldenholz et al., 2009)" should read "MEG outperforms EEG in terms of signal-to-noise ratio when accessing **superficial** brain regions (Goldenholz et al., 2009)."

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way.

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The Neuro-Mechanical Processes That Underlie Goal-Directed Medio-Lateral APA during Gait Initiation

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Gait initiation (GI) involves passing from bipedal to unipedal stance. It requires a rapid movement of the center of foot pressure (CoP) towards the future swing foot and of the center of mass (CoM) in the direction of the stance foot prior to the incoming step. This anticipatory postural adjustment (APA) allows disengaging the swing leg from the ground and establishing favorable conditions for stepping. This study aimed to describe the neuro-mechanical process that underlies the goal-directed medio-lateral (ML) APA. We hypothesized that controlled knee flexion of the stance leg contributes to the initial ML displacement of the CoP and to the calibration of the first step. Fourteen subjects initiated gait starting from three different initial stance widths of 15 cm (Small), 30 cm (Medium), and 45 cm (Large). Optoelectronic, force platform and electromyogram (EMG) measurements were performed. During APA, soleus activity diminished bilaterally, while tibialis anterior (TA) activity increased, more so in the stance leg than in the swing leg, and to a larger extent with increasing initial stance width. Knee flexion of the stance leg was observed during APA and correlated with the ML CoP displacement towards the swing leg. ML CoP and CoM displacements during APA increased with increasing stance width. The activity of stance-leg TA was correlated with the degree of knee flexion. Swing-leg tensor fasciae latae (TFL) was also active during APA. Across subjects, when stance-leg tibialis activity was low, TFL activity was large and vice versa. The modulation of the ML CoP position during APA allowed the gravity-driven torque to place the CoM just lateral to the stance foot during step execution. Accordingly, the gravity-driven torque, the ML CoM velocity during step execution, and the step width at foot contact (FC) were lower in the Small and greater in the Large condition. Consequently, the position of the stepping foot at FC remained close to the sagittal plane in all three conditions. Conclusively, coordinated activation of hip abductors and ankle dorsiflexors during APA displaces the CoP towards the swing leg, and sets the contact position for the swing foot.

Keywords: gait initiation, center of pressure, center of mass, frontal plane, knee flexion, ankle dorsiflexor muscles, hip abductor muscles

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INTRODUCTION

Gait initiation (GI) is a critical task because it involves transiting from stable bipedal stance to unstable unipedal stance. It requires anticipatory postural adjustments (APA) that reconfigure the position of the center of mass (CoM) with respect to the center of foot pressure (CoP) in order to take advantage of gravity and progress forward (Carlsöö, 1966; Brenière and Do, 1986, 1991; Brenière et al., 1987; Brenière, 2001).

It is well established that the displacement of CoM during APA is achieved by shifting the CoP backwards and in the direction of the swing leg (Jian et al., 1993; Elble et al., 1994; Lepers and Brenière, 1995). The backward shift of the CoP is caused by a reduction in soleus activity and activation of the tibialis anterior (TA; Crenna and Frigo, 1991). During APA, modulation of the antero-posterior distance between the vertical projections to the ground of the CoM and CoP positions generates a torque driven by gravity (henceforth termed disequilibrium torque) that propels the body forward (Lepers and Brenière, 1995; Michel and Do, 2002; Honeine et al., 2013, 2014). In the frontal plane, the initial CoP excursion in the direction of the future swing leg during APA causes gravity to move the CoM closer to the stance leg (Jian et al., 1993; Elble et al., 1994; Lepers and Brenière, 1995; McIlroy and Maki, 1999). By doing so, the nervous system disengages the swing leg from the ground. During the single-support phase of the first step, the distance between CoM and CoP in the frontal plane and the mediolateral (ML) fall of the CoM shape the positioning of the stepping foot at the moment of its contact with the ground (Lyon and Day, 1997, 2005; Caderby et al., 2014).

Carlsöö (1966) and later Winter (1995) stated that the initial displacement of the CoP in the direction of the swing leg is caused by unloading the stance leg and loading the swing leg, which they argued is produced by the hip abductor activity from the swing side. However, this may not be the sole mechanisms underpinning the disengagement of the future swing limb. When standing, the knee joint is extended due to the backward pull of the soleus on the tibia and to the action of gravity (Woodhull et al., 1985) connected with the anterior position of the CoM with respect to the knee. Therefore, the knee acts as a load-bearing joint (Walker and Erkman, 1975; Freeman et al., 1980). Notably, flexion of the knee of the stance leg during single-support is known to occur during gait (Segal et al., 2006; Shamaei et al., 2013). Hence, it may be appropriate to examine whether flexion of the knee also occurs during the APA in order to unload the stance leg during the preparation phase of GI. In this study, we tested the hypothesis that the central nervous system (CNS) employs stance-leg knee flexion as a complementary strategy to swing-leg hip abduction in order to unload the stance leg and displace the CoP in the direction of the swing leg during APA. Furthermore, we postulated that the modulation of the CoP displacement during APA also determines the disequilibrium torque and the lateral fall of the body towards the swing leg during step execution, with the purpose of positioning the stepping foot close to the sagittal plane at its foot contact (FC).

We asked volunteers to start walking from different initial stance widths at their spontaneous forward velocities. Increasing the stance widths prior to step execution has been shown to produce larger CoM and CoP displacements, in order to modulate the distance between CoM and CoP in the frontal plane and consequently the gravity-driven torque during step execution (Lyon and Day, 1997). If our hypothesis is correct, flexion of the knee of the stance leg should occur in the APA phase. The finding of a greater knee flexion of the stance leg accompanied by larger CoM and CoP displacement with a larger initial stance width would corroborate the proposition.

We also expected the ampler CoP displacement, which should occur the larger the initial stance width, to produce a greater gravity-driven torque during step execution. This would in turn increase the velocity of the CoM fall in the frontal plane prompting the stepping foot to land close to the subjects' sagittal plane.

MATERIALS AND METHODS

Participants

Fourteen (11 F) healthy young adults participated in the study. Their mean age, mass and height were 29 years (ranging from 21 to 41), 61 kg (47–80) and 1.68 m (1.58–1.80), respectively. As conformed to the Declaration of Helsinki, subjects provided written informed consent to the experiment, which was approved by the ethics committee of Fondazione Salvatore Maugeri (No. 2056CE).

Tasks and Procedures

Subjects stood with each foot on a distinct force platform (Kistler 9286BA, Winterthur, Switzerland). The position of each heel was equidistant to the border of each platform. Following the start of the acquisition, subjects were instructed to initiate walking in a self-paced mode. This was done to avoid the startle effect on GI, which occurs when subjects are asked to start walking following an acoustic command (Queralt et al., 2010). Subjects were not given any instruction about the speed at which to initiate walking and were left to execute GI at their preferred velocity. They performed three sets of conditions of GI, in which they started from predefined initial stance-widths of 15, 30 and 45 cm, termed Small, Medium and Large, respectively, in the text. There was no explicit instruction about the positioning of the first or successive footsteps. The order of the trials was randomized across subjects. Following GI, subjects were instructed to continue walking for at least six steps. Subjects were not specifically told to execute GI starting from a given leg (Hiraoka et al., 2014), even if in most of the trials subjects initiated gait with the same leg. Subjects performed as many trials as needed in order to achieve at least 12–15 trials per condition, all performed with the same leg. The distribution of the weight over each leg was checked during the experiment so that if the difference exceeded 1 kg before the CoP started moving, the trial was repeated in order to prevent the effects of anticipation on the GI features.

Data Acquisition

Twenty-three reflective markers were positioned on the subjects' body in the following anatomical locations: vertex, acromion, C7, L5 and bilaterally on lateral head, medial epicondyle of the elbow, head of the ulna, anterior superior iliac spine, greater trochanter, lateral epicondyle of the femur (knee), lateral malleolus, heel and 1st metatarsus-phalangeal joint. The Smart-D optoelectronic system (BTS Bioengineering, Italy) employed 12 infrared cameras that measured the position of the body markers with respect to the laboratory global reference. Anthropometric measurements of the segments of the body were made manually. This allowed for the computation of the three-dimensional position of the body's CoM (Winter, 1993). Bipolar electrodes (Freeemg, BTS Bioengineering, Italy) were employed to wirelessly record bilaterally the electromyogram (EMG) of TA, soleus, gastrocnemius medialis, biceps femoris (BF), semitendinosus (ST), semimembranosus (SM), tensor fasciae latae (TFL) and gluteus medius (nine subjects). Skin preparation and electrode placement were performed according to the SENIAM protocol (Merletti and Hermens, 2000). Optoelectronic, force platform and EMG data were recorded synchronously at acquisition frequencies of 140, 560, 1000 Hz, respectively. Data were stored in a computer for off-line analysis using a custom-made program written using Matlab (Mathworks, Natick, MA, USA).

Analysis of Biomechanical Variables

The global ML CoP position was calculated from the output of both force platforms according to Equation 1:

$$\mathrm{CoP}_{\mathrm{global}} = [(\mathrm{F}_1 * \mathrm{CoP}_1) + (\mathrm{F}_2 * \mathrm{CoP}_2)] / (\mathrm{F}_1 + \mathrm{F}_2) \quad (1)$$

where F_1 and F_2 are the vertical ground reaction forces under each leg, and CoP_1 is the ML position of CoP under one leg while CoP_2 is the ML position of the CoP under the other. The coordinates of CoP_1, CoP_2, CoP_{global} and the positions of each marker were referred to the same laboratory reference system.

The instant at which GI effectively started (t0) was set as the instant at which the ML CoP position exceeded the baseline by three standard deviations. The instant of the first heel-off (HO) was determined when the vertical position of the heel marker of the swing leg exceeded the value at baseline by 1 mm. The instant when the heel marker of the swing-leg reached its lowest vertical position signaled the instant of the successive FC (see **Figure 1**). Both instants were referred to t0. APA was defined as the time-period spanning from t0 to HO. The step execution phase extended from HO until swing foot landing (FC). The velocity of the CoM in the frontal plane was obtained by the derivation of the ML component of CoM position in time. Step length at FC was measured as the distance between the position of the heel of the stepping foot at t0 and at FC in the sagittal plane. Step width at FC was the distance in the frontal plane between the stance-foot heel marker at t0 and stepping-foot heel marker at its FC. The greater trochanter, knee and malleolus markers on both sides were used to calculate the knee angles in the sagittal plane.

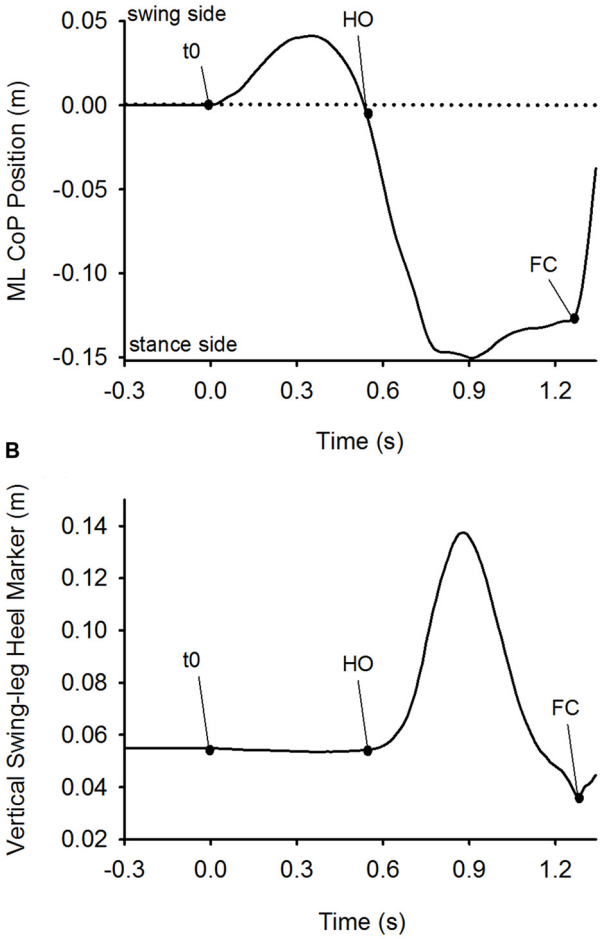

FIGURE 1 | Detection of t0, heel-off (HO) and foot-contact (FC). Panel **(A)** depicts the time-course of the mediolateral (ML) center of foot pressure (CoP) position. Panel **(B)** shows the time-course of the vertical position of the heel marker of the swing leg. Both plots were obtained from a single trial of one subject in the Medium stance-width condition. The dots on the curves indicate the time of initiation of CoP movement (t0), HO and FC. Anticipatory postural adjustment (APA) was defined as the time-period between t0 and HO, and step execution as the time-period between HO and FC.

The unloading of the stance leg was measured as the reduction of vertical ground reaction force at the instant of maximum CoP displacement during APA with respect to that measured at t0. The loading of the swing leg during APA was measured as the amount of increase in vertical ground reaction force at the instant of maximum CoP displacement during APA with respect to that measured prior to t0.

The instantaneous disequilibrium torque acting in the frontal plane was calculated as the product of the vertical ground reaction force and the distance between the ground vertical projection of CoM and CoP in the frontal plane (Equation 2). To calculate the torque, the CoP position and the vertical force were down-sampled to 140 Hz. Due to friction between the foot and the floor, the disequilibrium torque is converted to shear force.

In order to calculate the shear component of the ground reaction force generated by the torque, the latter was divided by the instantaneous height of CoM with respect to CoP (Equation 3):

$$\text{Torque} = \text{d}(\text{CoM} - \text{CoP}) * \text{F} \quad (2)$$

$$\text{Shear force} = \text{Torque}/\text{h} \quad (3)$$

where d(CoM−CoP) is the distance between CoM and CoP in the frontal plane, F is the vertical force acting on the CoM and h is the vertical position of CoM with respect to the ground. The impulse during APA and during step execution was measured as the product of the average shear force during APA or during step execution and the respective time periods in which the force was applied (Equation 4). The impulse was then normalized by dividing it by the corresponding subject's mass.

$$\text{Impulse} = \text{Shear force}_{\text{Avg}} * \Delta\text{t} \quad (4)$$

Analysis of EMG Activity

To calculate the start and end of EMG activities, the synchrosqueezed wavelet transforms of the raw EMG traces were calculated using the Morlet wavelet (Daubechies et al., 2011; Iatsenko et al., 2015). The final wavelet transform was composed of 125 frequency bins with a bandwidth of about 1.64 Hz ranging from 40 to 244.8 Hz for each time frame. A control-wavelet-coefficient matrix (154 × 1) was then created by averaging the coefficients that were found in the 25th percentile of the coefficient distribution. Multiple single-tailed Student's *t*-test was then used to compare each time-frame of the wavelet transform with the control-wavelet-coefficient matrix. Onset of muscle activation was considered the instant when *p*-value exceeded 0.05 for 50 consecutive time-frames. Offset was considered the instant when *p*-value was inferior to 0.05 for 50 consecutive time-frames (see **Figure 2**). The amplitude of EMG activity was calculated by rectifying the EMG raw traces, low-pass filtering the signal with a second order Butterworth no-lag filter with a cut-off frequency of 25 Hz, and calculating the area under the curve. Maximal EMG isometric activity of all muscles was measured by blocking the pertinent body segment against a rigid frame and asking the subject to exert a maximal isometric contraction against it for about 3–4 s. The peak activity of EMG was detected. The amplitude of the EMG activity during a time-window of 1 s centered around the peak activity was then calculated.

Statistics

We verified the distribution of each parameter by performing a Shapiro-Wilk test. Parameters that did not show a normal distribution were tested using non-parametric methods. Separate repeated-measures ANOVAs were used to test the effect of initial stance-width on the following variables: duration of APA; duration of step execution; anteroposterior (AP) instantaneous velocity of CoM at HO and at FC; maximum distance between CoP and CoM during APA and during step execution; EMG activities of stance-leg soleus, gastrocnemius, TFL and gluteus medius during step execution; position of the swing-leg heel marker at FC; position of the swing-leg hallux marker at FC. Separate 2 (swing − stance) × 3 (Small − Normal − Large) repeated-measures ANOVAs were used to test the statistical difference of the following variables: forward displacement of knee joints during APA; knees flexion during APA. Separate one-way Friedman repeated-measures analyses were used to test, during APA, differences in the amplitude of the swing- and stance leg TA EMG activity; effect of initial stance-width on the activity of the swing-leg TA activity; effect of initial stance-width on the activity of stance-leg tibialis activity; effect of initial stance-width on the activity of the swing-leg TFL. Pearson's method was used to test the linear relationship between the following variables: unloading and loading of the stance and swing legs, respectively, and the maximum displacement of CoP during APA; stance-leg knee forward displacement and stance-leg knee flexion; stance-leg knee flexion and maximum displacement of CoP during APA; amplitude of TA activity and knee flexion of the stance leg during APA; normalized impulse calculated during APA and normalized impulse during step execution; normalized impulse during step execution and ML CoM velocity at FC; normalized impulse during step execution and step width at FC. Hyperbolic fitting was used to determine the relationship between the TFL and TA activity in each

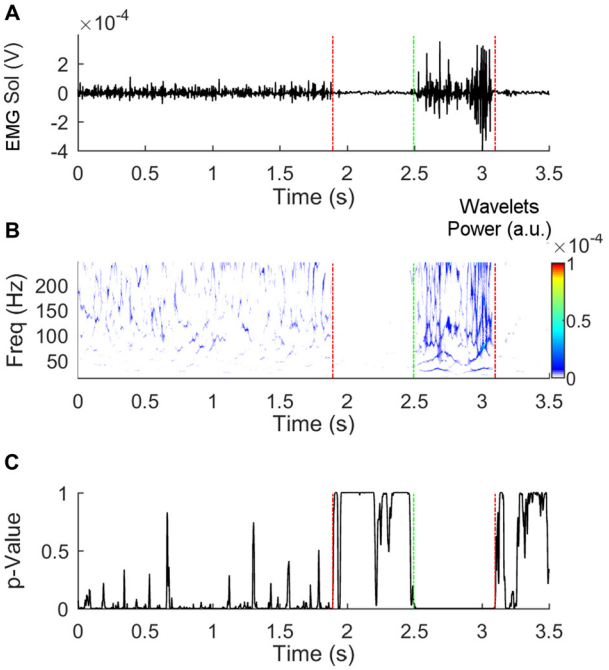

FIGURE 2 | Detection of the beginning and end of electromyogram (EMG) activity. Panel **(A)** shows a raw EMG trace obtained from the soleus muscle of the stance leg during Gait initiation (GI). Panel **(B)** represents the synchrosqueezed transform of the raw trace. The *p*-values of the *t*-test that compares the coefficients in each time-bin with the control-matrix-coefficients are shown in panel **(C)**. Fifty or more consecutive *p*-values inferior to 0.05 indicates that the muscle is active. The vertical dashed lines indicate the instants at which deactivation (red) and activation (green) were detected.

of the three conditions. Linear and hyperbolic relationship were done using Sigmaplot (Systat software Inc., San Jose, CA, USA). *Post hoc* analyses of variables following a normal distribution were made by the Fischer's LSD test. The Wilcoxon signed-rank test was used to test non-normally distributed variables. The level of significance in all tests was set at $p < 0.05$. The software Statistica (StatSoft, Tulsa, OK, USA) was used.

RESULTS

Global Kinematics

As expected, prior to stepping, CoP was initially displaced in the direction of the swing leg while CoM moved in the opposite direction. **Figure 3A** shows the time-course of the mean curves of the ML CoP and CoM positions in the three stance-width conditions of a single subject (mean curves were obtained by averaging 15 trials). The instant $t = 0$ s, which is referred to as t0 in the text, indicates the instant at which the ML CoP position starts moving towards the swing leg. As can be seen in the Figure, prior to HO, the CoP is displaced towards the swing leg and the CoM is moved, with a delay, in the direction of the stance leg. Then, the CoP starts moving towards the stance leg. Next, around mid-stance, the CoM lateral excursion peaks and starts moving towards the future stance leg in anticipation of the second step.

The distance between CoP and CoM in the frontal plane was measured at two distinct moments: the instant when CoP lateral excursion peaks during APA and the instant when CoM reaches its maximum displacement during step execution (as indicated by the arrows in **Figure 3A**). Their grand means and standard deviations are shown in **Figures 3B,C**. The ANOVA showed a significant effect of the initial stance-width on the maximal distance between CoP and CoM during APA ($F_{(2,26)} = 156.6$, $p < 0.001$), and on the maximal distance between CoP and CoM during step execution ($F_{(2,26)} = 153$, $p < 0.001$). *Post hoc* analyses showed that the maximal distance between CoP and CoM during APA and during step execution were the lowest in the Small and the greatest in the Large stance-width condition ($p < 0.001$ for all comparisons). The CoP displacement during APA was not significantly correlated with the subjects' height

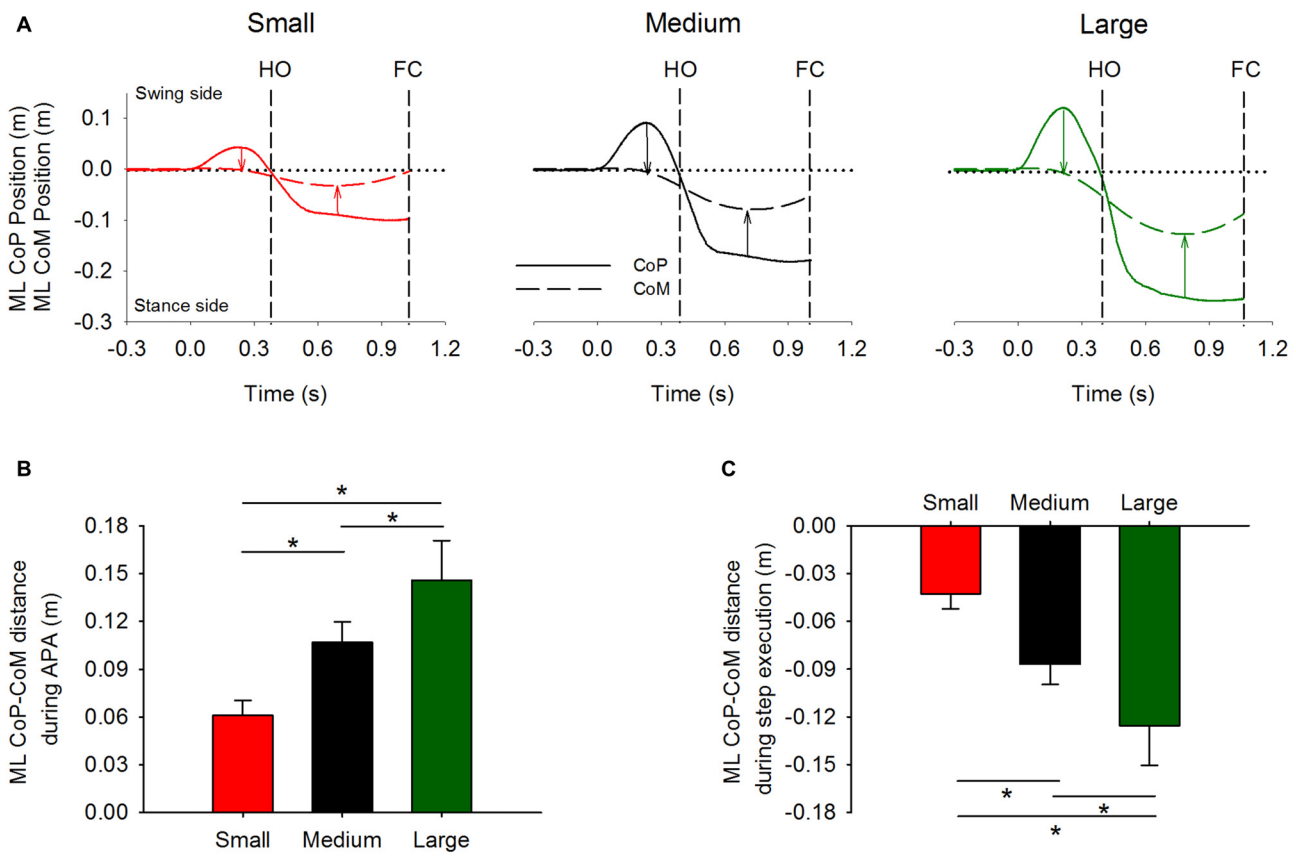

FIGURE 3 | Global kinematics variables in the frontal plane. The average time-course obtained from a single subject of the ML CoP (solid line) and center of mass (CoM) position (dashed line) are shown in panel **(A)**. The vertical dashed lines indicate HO and FC events. Panels **(B,C)** show the grand means and standard deviations of the distance between CoP and CoM at the instant at which CoP displacement peaked during APA (indicated by the leftmost arrows in panel **A**), and of the distance between CoP and CoM at the instant at which CoM displacement peaked during step execution (indicated by the rightmost arrows in panel **A**), respectively. *Indicates significant difference ($p < 0.05$).

TABLE 1 | Global gait initiation (GI) variables.

Condition	Duration of APA (s)	Duration of step execution (s)	CoM velocity at Heel-off (ms^{-1})	CoM velocity at foot-contact (ms^{-1})
Small	0.763 ± 0.06	0.635 ± 0.07	0.12 ± 0.03	0.81 ± 0.14
Medium	0.765 ± 0.05	0.629 ± 0.06	0.12 ± 0.04	0.80 ± 0.14
Large	0.784 ± 0.06	0.581 ± 0.07*	0.11 ± 0.05	0.74 ± 0.16*

*Indicates significant difference, $p < 0.05$.

(Small: $r^2 = 0.09$, $p = 0.31$; Medium: $r^2 = 0.04$, $p = 0.48$; Large: $r^2 = 0.06$, $p = 0.41$), or their pelvis width (Small: $r^2 = 0.13$, $p = 0.21$; Medium: $r^2 = 0.07$, $p = 0.36$; Large: $r^2 = 0.01$, $p = 0.7$).

Table 1 contains the grand mean and standard deviation of the duration of APA, the duration of step execution, the instantaneous forward velocity of the CoM at the time instant of HO, and the forward velocity of CoM at the time instant of FC. Repeated-measures ANOVA showed no effect of initial stance width on the duration of APA ($F_{(2,26)} = 2.5$, $p = 0.1$). The instantaneous forward velocity of CoM measured at the instant of HO was also comparable between the three conditions ($F_{(2,26)} = 1.1$, $p = 0.35$). The ANOVA showed an effect of initial stance width on the duration of step execution ($F_{(2,26)} = 11$, $p < 0.001$) and the instantaneous forward CoM velocity measured at the instant of FC ($F_{(2,26)} = 14.7$, $p < 0.001$). *Post hoc* analysis showed that both duration of step execution and forward velocity of CoM at FC were smaller in the Large stance-width condition with respect to the Small and Medium conditions ($p < 0.001$).

CoP ML Displacement and Flexion of the Knee of the Stance Leg

Figure 4 shows the time-course of the ML CoP position (panel **A**) and the vertical ground reaction force (Panel **B**) under each foot. The traces represent a single trial obtained in each of the three stance-width conditions (Small, Medium and Large). The dots on the curves represent the moment at which the CoP displacement peaked. The loading of the swing and the unloading of the stance leg were accompanied by the displacement of CoP in the direction of the swing leg. **Figure 4C** shows a scatter plot of the maximum displacement of CoP as a function of the sum of the unloading and loading of the stance and swing leg (measured peak to peak). Three distinct linear relationships were obtained between the unloading of the stance leg and the maximum displacement of CoP during APA (Small: $r^2 = 0.66$, Medium: $r^2 = 0.49$, and Large: $r^2 = 0.59$). The relationships diverge because the position of the CoP in the frontal plane is not only caused by the amplitude of the vertical ground reaction force under each leg, but is also dependent on the initial stance width (see Equation 1).

Figure 5A shows a stick diagram of the lower limbs taken at different time-intervals in the sagittal plane. The trial seen in this Figure is the same Medium stance-width trial used in **Figure 4**. **Figures 5B,C** show the time-course of the knee AP position of the stance and swing leg, respectively. **Figures 5D,E** show the time-course of the knee angle of the stance leg and swing leg, respectively. The dots on the curves represent the moment of maximal CoP displacement. As can be seen in the Figure, at t0, i.e., while still standing, both knees are positioned behind the vertical position of CoM, a circumstance that lets gravity extend the knees. Following t0, the stance-leg knee is displaced forward so that it moves anteriorly to the CoM, favoring gravity to flex the knee. Meanwhile, the swing-leg knee is more or less stationary. The stance-leg knee remains anterior to the CoM during APA. Following foot-off of the swing leg, the CoM advancement places the CoM in front of the stance-leg knee so that the action of gravity halts the knee flexion or in some cases extends it slightly.

The grand mean and standard deviation of the AP displacements and flexion angles of the knees at the moment of maximal CoP displacement, relative to the initial position (at t0), are provided in **Figures 5F,G**. The ANOVA showed a difference in the forward displacement between the knees of the stance leg and the swing leg ($F_{(1,13)} = 57$, $p < 0.001$). Knee forward displacement differed across the three conditions ($F_{(2,26)} = 66.2$, $p < 0.001$). A significant interaction between swing- and stance-leg knee forward displacement and initial stance width was also found ($F_{(2,26)} = 14.15$, $p < 0.001$). The knee angle of the swing leg was significantly different from that of the stance leg ($F_{(1,13)} = 210.4$, $p < 0.001$). There was a general effect of condition on knee angle ($F_{(2,26)} = 104.2$, $p < 0.001$). A significant interaction between swing and stance knee angle and initial stance width was also found ($F_{(2,26)} = 42.3$, $p < 0.001$).

Post hoc analysis showed that both forward displacement and the flexion angle of the stance-leg knee were significantly different across conditions ($p < 0.001$). Amplitudes of forward displacement and flexion of the stance-leg were lower for the Small condition and greater for the Large condition compared to Medium ($p < 0.001$). A linear relationship was found between the forward displacement and the flexion angle of the stance-leg knee ($r^2 = 0.52$, **Figure 5H**). Finally, a linear relationship was found between the maximum displacement of CoP and the knee flexion of the stance leg ($r^2 = 0.64$, **Figure 5I**).

EMG Activity During Gait Initiation

Figure 6A shows the time-course of the average traces of the TA, soleus, gastrocnemius medialis, BF, ST, semimenbranosus, TFL and gluteus medius from both legs obtained from one subject during the Medium stance-width condition. The grand mean and standard deviations of the onset and offset of the same muscles (across conditions) are shown by the horizontal bars in **Figure 6B**. When standing, both soleus and BF were

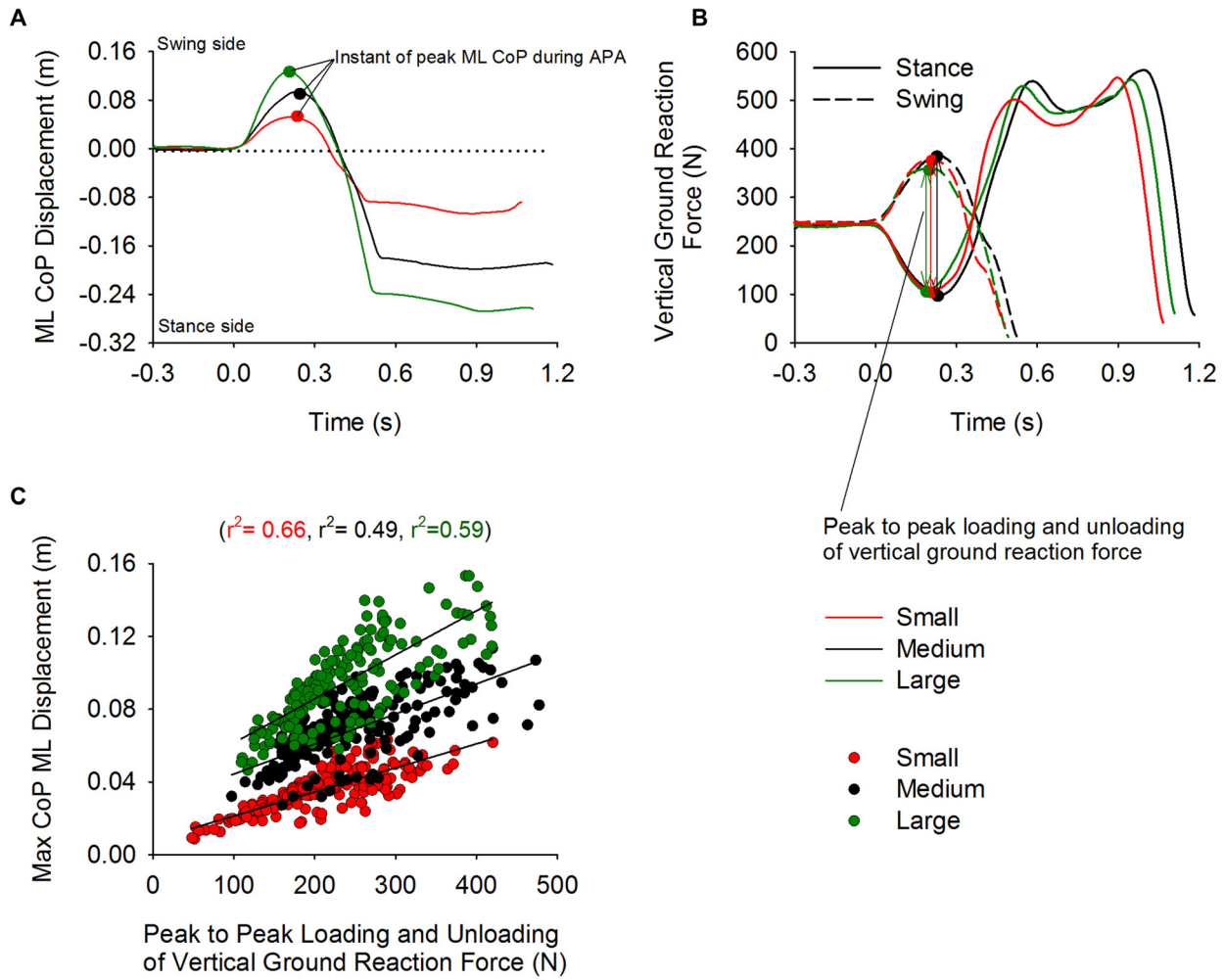

FIGURE 4 | Unloading and loading of the stance and swing leg and CoP displacement during APA. Panels **(A,B)** show the time-course of the CoP displacement and the vertical reaction force under the swing (dashed line) and stance foot (solid line), respectively. The curves were obtained from trials of a single subject from the Small, Medium and Large condition. The small circles on the plot indicate the instant at which the displacement of CoP in the direction of the swing leg peaked during APA. Panel **(C)** shows the three distinct linear relationships (one for each condition) that were found between maximal CoP displacement and the unloading and loading (measured peak to peak) of the stance and swing leg, respectively.

active. About 40 ms prior to t0 both soleus and BF were silenced in both legs while TA was activated bilaterally, concurrently with the swing-leg TFL. The offset of the EMG activity in the stance-leg TA and swing-leg TFL roughly coincided with the moment of HO. Triceps surae and hamstring muscles of the stance leg remained silent throughout the APA phase. The swing-leg TA showed two distinct bursts during the step execution phase that lasted until about 100 ms following FC. A brief increase in EMG activity of the triceps surae, hamstrings and TFL of the swing leg was detected about 100 ms prior to HO and ended around the same time as foot-off. During step execution, the beginning of triceps surae activity of the stance leg was recorded slightly prior to HO and ended about 100 ms following FC. The stance-leg TFL was activated about 150 ms prior to HO and was silenced slightly prior to FC. Finally, hamstrings of the stance leg showed a small burst about 100 ms long following HO that usually ended at about mid-single-stance.

Since hamstrings and gastrocnemius muscles are silent during APA, the only candidate responsible for bringing the stance knee forward and initiate knee flexion is the TA muscle that is active during APA. The time-course of the average traces of TA EMG activity of the swing and stance leg of a single subject is provided in the three upper panels of **Figure 7A**. **Figure 7B** shows the medians and the 25th and 75th percentiles of the amplitude of the EMG activity of the TA activity (with respect to maximum isometric contraction) of the swing leg and stance leg during APA. The Friedman repeated-measures test showed that the activity of TA was in general significantly lower in the swing- than stance-leg during APA ($\chi^2 = 24.4$, $p < 0.001$). The activity of the TA muscle of the swing leg did not differ across the three conditions ($\chi^2 = 1.28$, $p = 0.53$). However, starting to walk

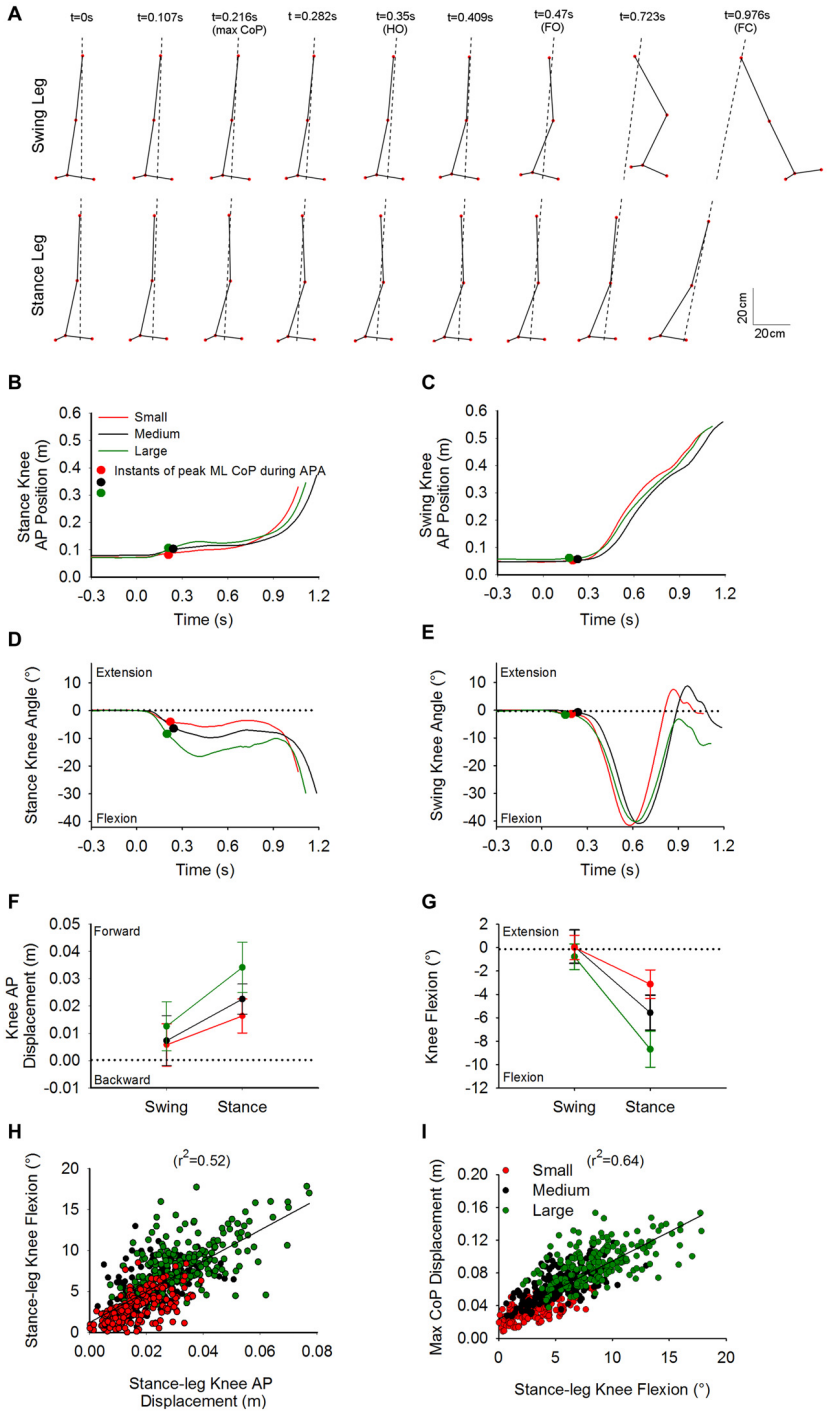

FIGURE 5 | Knee flexion and CoP displacement during APA. Panel **(A)** shows stick diagrams of the swing leg (top) and stance leg (bottom) taken at nine discrete instants in the sagittal plane. The stick diagrams represent the same Medium-condition trial as in **Figure 4**. The dashed lines represent the direction of the CoP-CoM vector. The instants comprise t0, instant of peak ML CoP during APA, HO, foot-off, FC and instants in between. As can be seen at t0, both knees are positioned behind the center of gravity. During APA, the swing-leg knee remains fixed while the ankle joint starts flexing and the stance-leg knee advances ahead of the center of gravity. The time-course of the stance knee position and swing knee position for the three single trials in each condition are found in panels **(B,C)** respectively. Panels **(D,E)** show the time-course of the stance-leg and swing-leg knee angle, respectively. The curves in panels **(B–E)** belong to the same trial. The small circles on the curves indicate the instant at which the maximum displacement of CoP in the direction of the swing leg was reached during APA. Panels **(F,G)** show the grand means and standard deviations of the forward displacement and flexion of the knee of the swing and stance leg, respectively, measured at the instant at which CoP displacement peaked. Panels **(H,I)** portray the linear relationship between the forward displacement of CoP and stance knee flexion, and between the stance-knee flexion and ML CoP displacement, respectively.

from different initial stance width had an effect on the activity of the stance-leg TA muscle ($\chi^2 = 28$, $p < 0.001$). The Wilcoxon matched pair test indicated that the lowest activity of the stance-leg TA muscle was obtained in the Small condition ($p < 0.05$ for both comparisons) while the greatest activity was achieved in the Large condition ($p < 0.05$ for both comparisons).

Figure 7C shows the time-course of the average traces of the TFL of the swing- and stance-leg during GI in a single subject. The medians and the 25 and 75 percentiles of the amplitude of EMG activity (with respect to maximum isometric contraction) of the swing-leg TFL muscle during APA are shown in **Figure 7D**. The Friedman repeated-measures test showed no effect of initial stance width on the amplitude of EMG activity of the swing-leg TFL ($\chi^2 = 4.43$, $p = 0.11$) and gluteus medius ($\chi^2 = 2.6$, $p = 0.09$) during APA. Furthermore, ANOVA showed no difference across conditions in the amplitude of EMG activity during the step execution phase of soleus ($F_{(2,26)} = 0.36$, $p = 0.70$), gastrocnemius ($F_{(2,26)} = 1.02$, $p = 0.37$), TFL ($F_{(2,26)} = 1.97$, $p = 0.16$) and gluteus medius ($F_{(2,16)} = 1.53$, $p = 0.25$) of the stance leg.

We also investigated the complementary contribution of hip abduction of the swing side and of knee flexion of the stance side during APA. **Figure 8** shows the TA activity of the stance leg plotted against that of the swing-leg TFL (both normalized to maximum activity during isometric contraction) during APA in the three conditions. A hyperbolic relationship interpolated the data points in the Small ($r^2 = 0.25$), Medium ($r^2 = 0.23$) and Large condition ($r^2 = 0.24$). By looking closely into **Figure 8**, one can also see that the hyperbolic relationship is partly due to the fact that some subjects preferred the hip abductor activity more than stance-knee flexion and vice versa. **Figure 9** shows a scatter plot of the amplitude of the stance-leg TA activity from onset until the peak of CoP displacement and the stance-leg knee flexion at the peak of CoP displacement. A linear relationship was obtained between tibialis activity and knee flexion ($r^2 = 0.55$).

Disequilibrium Torque During Gait Initiation

Figure 10A shows the average time-course of the shear force calculated by dividing the disequilibrium torque by the instantaneous height of the CoM (black line). For comparison, the gray line indicates the average time-course of the shear force measured by the platform. During APA, the shear force produced by the distance between CoP and CoM in the frontal plane displaced the CoM in the direction of the stance leg (negative values in the Figure). Following HO of the swing leg, the torque started acting in the opposite direction.

The impulse theorem allows to quantify the amount of force generated during a certain time interval. Therefore, the impulse derived from the shear force calculated from the disequilibrium torque (see "Materials and Methods: Analysis of Biomechanical Variables" Section) has been used to describe the effect of the torque during APA and step execution on the kinematics of GI in the frontal plane. A linear relationship was obtained between the impulse values calculated from the shear force during APA and those calculated during step execution ($r^2 = 0.59$; **Figure 10B**). In addition, the impulse calculated during step execution was correlated with the instantaneous velocity of CoM ($r^2 = 0.4$; **Figure 10C**) and step width at FC ($r^2 = 0.46$; see **Figure 10D**).

Figure 10E shows the grand mean and standard deviation of the AP and ML position of the heel and hallux markers at the instants of t0 and FC. The AP position of the markers has been calculated relative to the position of the heel markers at t0 (both feet on ground). The ML position of the markers was computed with respect to the subjects' sagittal plane, calculated as the plane passing between the two anterior superior iliac spines slightly prior to t0. The position of the heel and the hallux markers at FC with respect to the medial line were not different across the three conditions ($F_{(2,26)} = 2.27$, $p = 0.12$ and $F_{(2,26)} = 0.33$, $p = 0.72$, respectively). Step length was also comparable across the three conditions ($F_{(2,26)} = 0.21$, $p = 0.81$).

DISCUSSION

Human gait is a state of controlled disequilibrium, in which anticipating the position of the body with respect to the ground is critical to avoid destabilizing torques (Bauby and Kuo, 2000). It is fragile, because it can be disturbed by many bodily conditions, including even minor degradations of the sensory information or motor output or both (Mazzaro et al., 2005; Nardone et al., 2014), as well as by cognitive tasks (Lajoie et al., 1993). Further, unlike the hopping gait of kangaroos that is characterized by symmetrical leg jumping action, human bipedal gait is asymmetrical and involves alternate single-support and double-support phases. Hence, the asymmetry of human gait requires substantial balance control in the frontal plane in order to prevent lateral falls (Thorstensson et al., 1984; MacKinnon and Winter, 1993; Orendurff et al., 2004; Sozzi et al., 2013; Wang and Srinivasan, 2014).

During GI, the CNS is confronted with the difficult task of transiting between a symmetrical quasi-static state to an asymmetrical dynamic state (Delafontaine et al., 2015). Indeed, to start walking appropriately, the CoM is moved to a position favorable to gait prior to lifting the future swing leg (Carlsöö, 1966; Brenière and Do, 1986; Brenière et al., 1987; Brenière and Do, 1991; Jian et al., 1993; Elble et al., 1994). On the one hand, the backward shift of CoP, which is responsible for the forward movement of the CoM, is caused mainly by activation of TA and decrease in soleus activity (Crenna and Frigo, 1991; Lepers and Brenière, 1995; Brenière, 2001; Honeine et al., 2013, 2014). On the other hand, the initial lateral shift of CoP in the direction of the swing leg causes the CoM to move toward the stance leg. Carlsöö (1966) and Winter (1995) argued that swing-leg abductor activity during APA unloads the stance leg and loads the other which in turn produces a lateral displacement of the CoP. However, flexing the knee of the stance leg during APA can also help unloading the swing leg. It has been already shown that the knee is moderately flexed in the stance leg during walking. This knee flexion prevents higher rate of loading during gait, and translates to attenuated rates of loading and peak vertical ground reaction force in healthy adults (Riskowski et al., 2005; Riskowski,

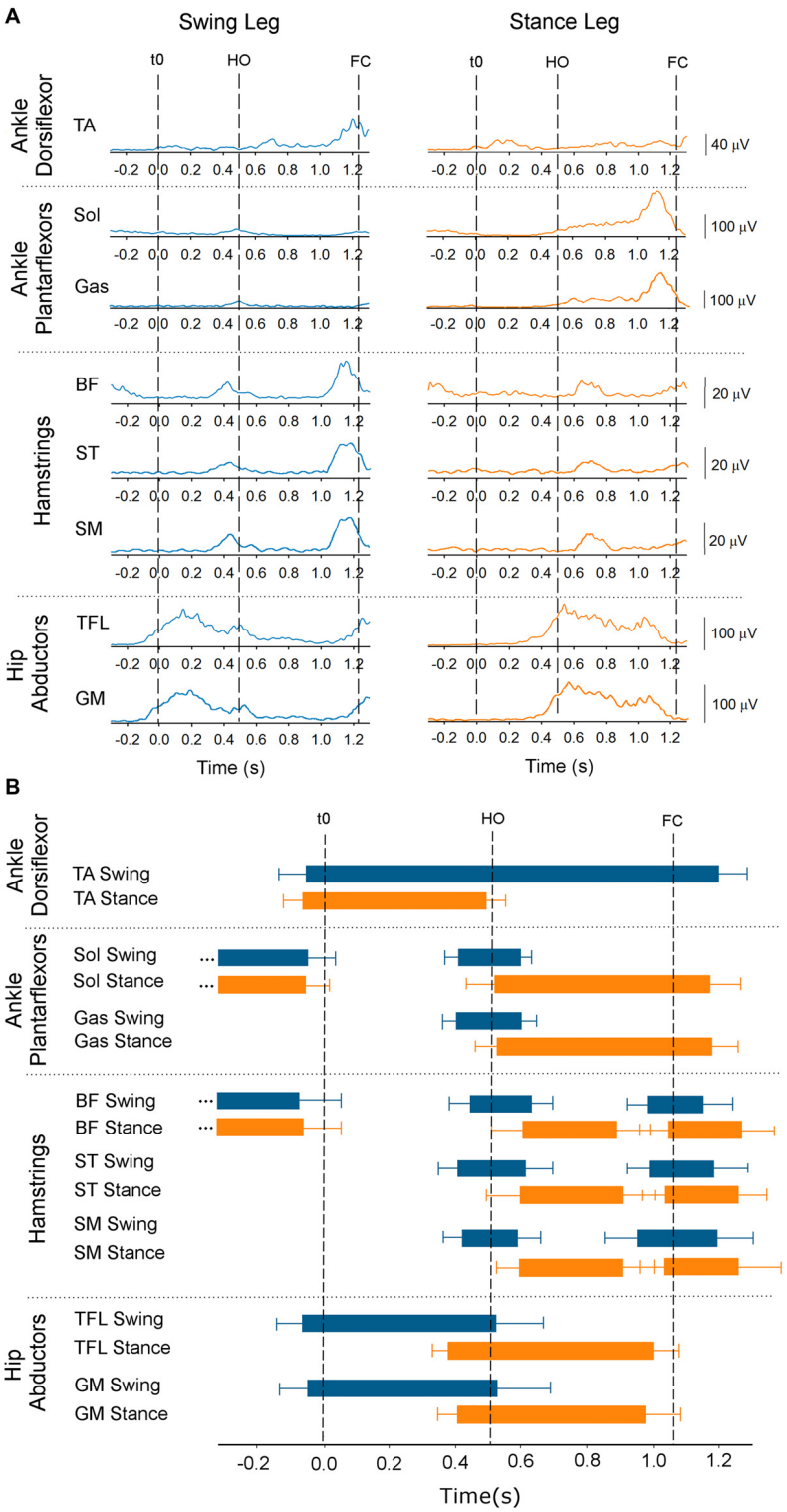

FIGURE 6 | Onset and offset of EMG activity. The figure provides temporal information about the ankle dorsi- and plantar-flexors, knee flexors and hip abductor EMG activity. Panel **(A)** shows the average time-course of one subject (Medium condition) of the rectified and low-pass filtered EMG traces (Fcut = 25 Hz) of the tibialis anterior (TA), soleus (Sol), gastrocnemius medialis (Gas), biceps femoris (BF), semitendinosus (ST), semimembranosus (SM), tensor fasciae latae (TFL) and gluteus medius muscles of the swing side (blue, left) and stance side (orange, right). t0, HO and FC are indicated by the dashed lines. Panel **(B)** shows the grand means and standard deviations of all subjects of the onset and offset across the three conditions of the same muscles' activity calculated with respect to t0.

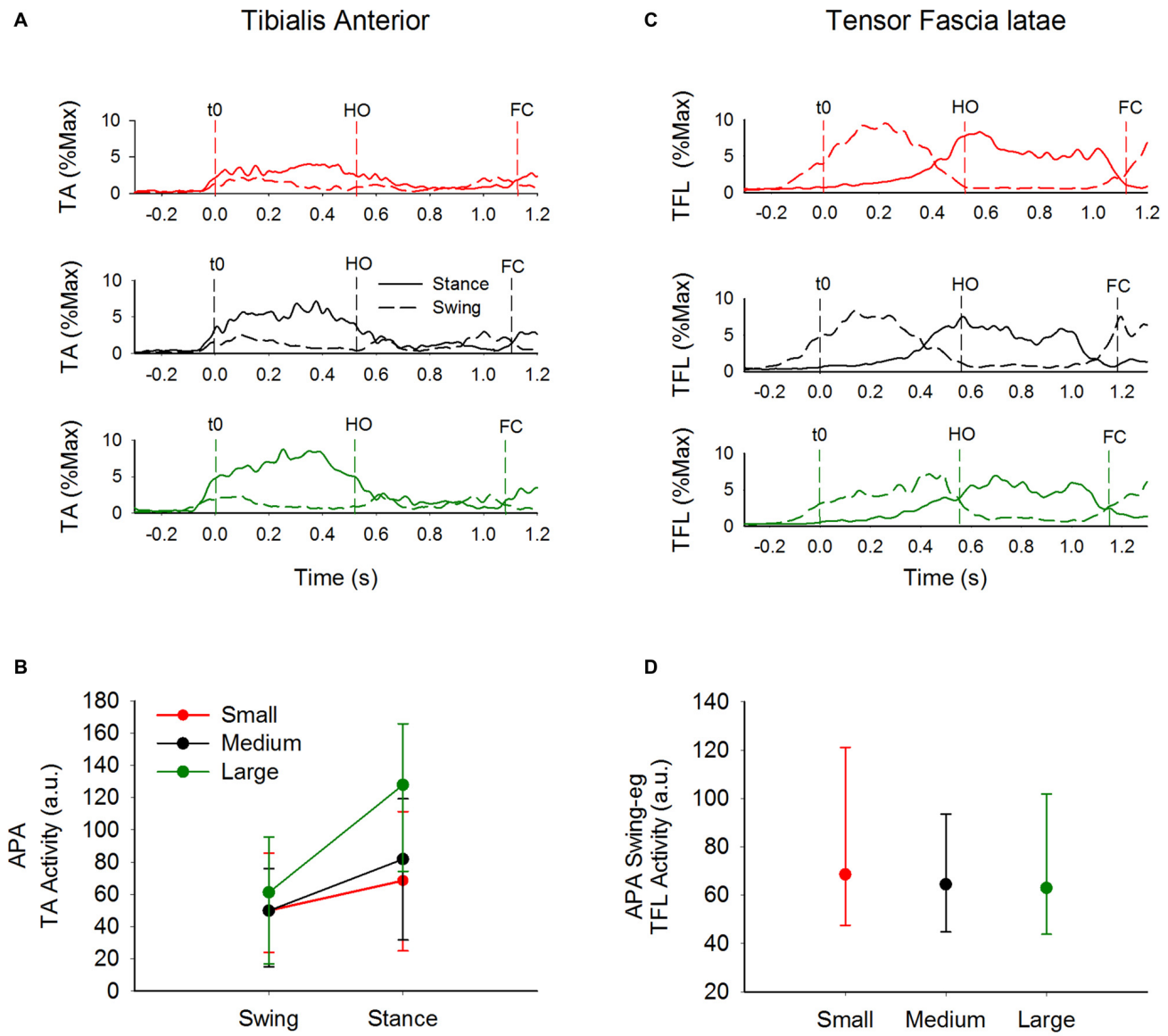

FIGURE 7 | EMG activity of TA and TFL. This figure contains information about the activity of tibialis activity and TFL muscles of both sides during GI. Panels **(A,C)** show the average envelope traces of TA and TFL, respectively, of a single subject in the three conditions (from top to bottom: Small, Medium and Large) of the swing leg (dashed line) and the stance leg (solid line). Panels **(B,D)** show the medians along with the 25th and 75th percentiles of the amplitudes of TA activity of the swing and stance legs and of TFL activity of the swing leg during APA, respectively (values are normalized to maximum isometric contraction). TA activity of the swing leg during APA was not affected by the initial stance width. However, TA activity of the stance leg was larger the greater the initial stance-width. The amplitude of TFL EMG activity was only moderately affected by the initial stance width.

2010). Hence, we hypothesized that the stance-leg knee flexion, which is part of the normal motor program for walking, could also be exploited in order to unload the stance leg during the preparation of GI.

Knee Flexion of the Stance Limb During APA

In line with Lyon and Day (1997), initiating gait at increasing stance widths causes greater displacement of the CoP in the direction of the swing leg and CoM in the opposite direction during APA. Our results also confirm the findings of Carlsöö (1966) and Winter (1995) in that the CoP displacement during APA is caused by unloading and loading the stance and swing legs, respectively (see **Figure 4**). In our hands, the greater excursions of CoP and CoM occurred without significant modifications of the global kinematic variables of GI (see **Table 1**) and most notably the duration of APA. This facilitates the comparisons across conditions without the need to normalize in time.

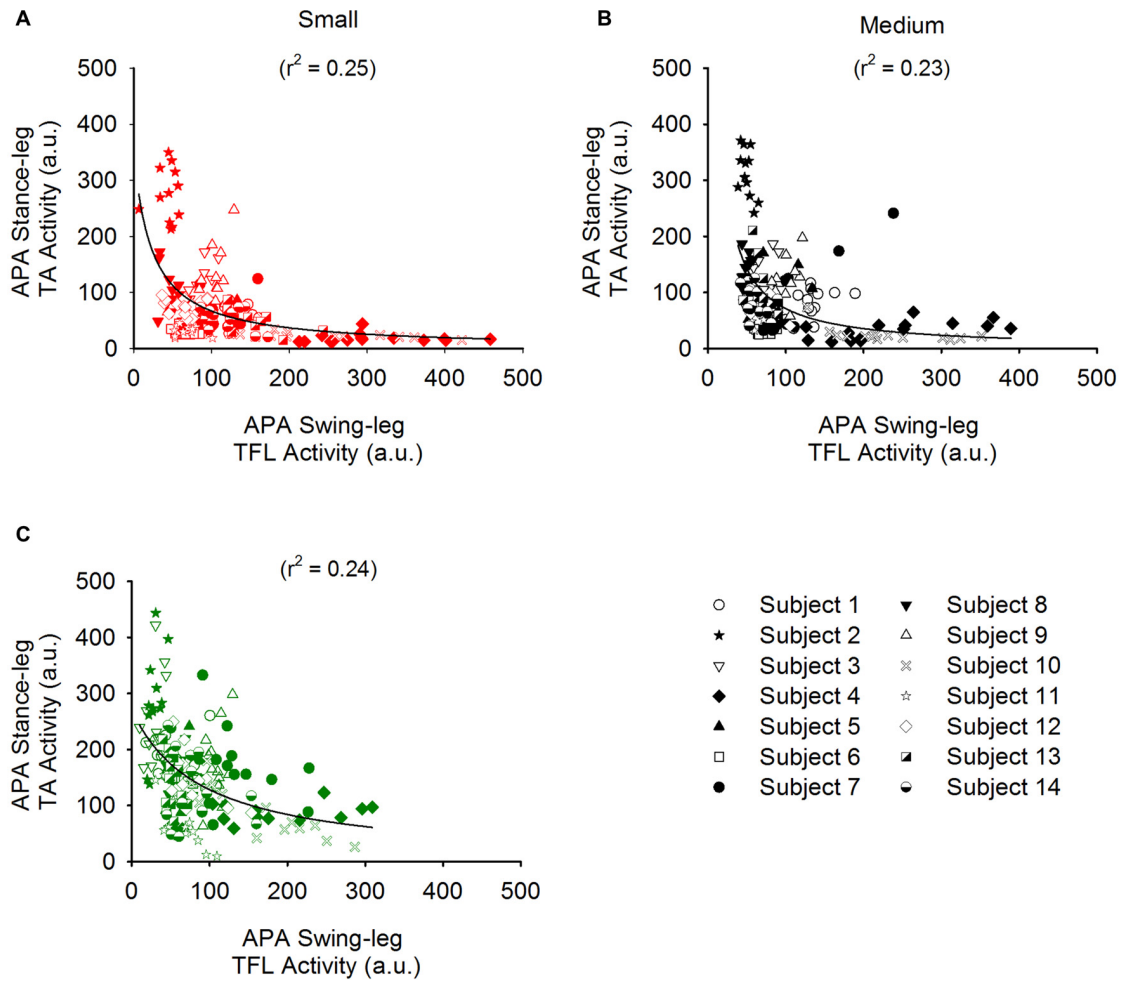

FIGURE 8 | Relationship between the EMG activity of the TA of the stance leg and that of the TFL of the swing leg. Panels **(A–C)** show the amplitude of the stance-leg TA activity plotted against that of the swing-leg TFL for all the trials of all the subjects in the Small (red), Medium (black) and Large (Green) stance-width conditions, respectively. Each subject is symbolized by a different icon. A hyperbolic *(y = ab/(b + x))* function was found to bind the activity of these muscles.

As can be seen in **Figure 5**, at t0 both knees are placed behind the vertical projection of CoM. However, during APA, the stance knee is displaced forward, placing the joint anterior to the CoM vertical projection in the sagittal plane allowing gravity to participate in flexing the knee. Meanwhile, the swing-leg knee position and angle remain more or less constant. The stance-leg knee forward advancement and flexion augmented with increasing stance width. The amplitude of the flexion of the stance-leg knee was also correlated with the lateral displacement of CoP. The linear relationship between stance-leg knee flexion and lateral displacement of CoP is in line with our hypothesis that stance knee flexion unloads the stance leg and thus participates in shifting the CoP in the direction of the swing leg.

Hamstrings and gastrocnemius activity are associated to knee flexion during the double stance phase of gait (Goldberg et al., 2004). However, none of those muscles were active during flexion of the stance-leg knee in early APA. Moreover, BF that shows tonic activity while standing becomes silent during APA (see **Figure 6**). The reason might be that hamstrings also extend the hip. Hip extension during GI should potentially slightly restrict forward movement and is therefore undesirable. Conversely, the ankle plantarflexion produced by gastrocnemius activation would impede the backward CoP displacement required for generating forward motion. Slightly prior to t0, soleus and BF muscles are silenced bilaterally followed by TA activation (**Figure 6**). As more appropriately stated by Zajac and Gordon (1989), "at times, such as in standing, muscles crossing the ankle extend (soleus) or flex (TA) the knee much more that they flex and extend the ankle". In this study, the amplitude of the TA muscle of the stance leg is greater than that of the swing leg. Furthermore, the amplitude of the stance-leg TA activity increases with larger stance-widths (see **Figure 7**). This result suggests that the reduction in soleus tonic activity and the activation of the TA of the stance leg move the stance-leg knee forward with

respect to the CoM position in the sagittal plane, thereby favoring gravity to flex the stance knee. Indeed, a linear relation between the amplitude of EMG activity of TA of the stance leg and flexion of the stance-leg knee is found here (**Figure 9**), strengthening the hypothesis that the stance-leg TA participates in displacing the CoP in the direction of the swing leg during the preparation phase of GI. It is to be noted that feet plantar afferents can influence the activity of TA and soleus during APA when raising one leg quickly (Do and Gilles, 1992). Cutaneous afferents can sense the augmentation in the shear force under the feet (Abbruzzese et al., 1996; Choi et al., 2016) that occurs with increasing stance width (Carmines and MacMahon, 1992). The changes of the cutaneous afferent input, in the different conditions, could have contributed to the modulation of stance-leg TA activity that participates in the lateral displacement of CoP during APA.

Following lift-off of the swing foot, the forward momentum of CoM places the latter anterior to the stance-leg knee, as occurs during the single-support phase of steady-state gait (Liu et al., 2008). This causes gravity to extend the stance knee thereby halting the flexion that occurred during APA. Furthermore, the activity of triceps surae and the hamstring muscles, increases during step execution. Those muscles could also be implicated in checking the knee flexion during single support.

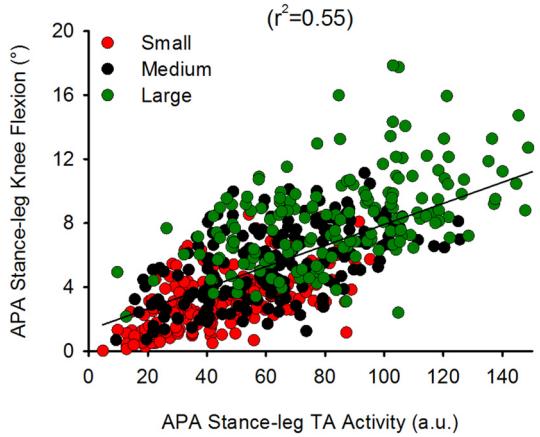

FIGURE 9 | Relationship between stance-leg TA EMG activity and knee flexion. This shows a scatter plot of the stance-leg knee flexion angle plotted against the amplitude of stance-leg TA activity during APA (normalized to maximum isometric contraction). A linear relationship was found to bind the two variables ($y = 0.07x + 1.34$) suggesting that stance-leg knee flexion might be modulated through TA activity of the same leg.

The Complementary Action of Hip Abduction and Stance Knee Flexion

Starting gait with different stance widths has no significant effect on the amplitude of hip abductor EMG activity of the swing leg during APA, albeit a slight tendency of some subjects (9 out of 14) to decrease hip abductor activity was observed when starting gait from a large stance width. Remarkably, a hyperbolic relationship binds the amplitude of stance-leg TA activity with that of the hip abductor muscles of the stance leg in each of the three conditions (see **Figure 8**). Some subjects relied more on swing-leg hip abductor activity and others on stance-leg dorsiflexor activity, while most relied on both rather equally. It is to be noted that the decrease in hip abductor activity in the Large condition of the nine subjects mentioned above is accompanied by a systematic increase in stance-leg knee flexion. A possible explanation is that due to biomechanical constraints, the hip abduction strategy is less efficient when starting from a large stance width. Conclusively, the actions of stance-knee flexion and swing-leg hip abduction appear to be complementary and synergistic in unloading the stance leg and loading the swing leg during APA. The coordination of the two strategies would result in more efficient and flexible ML displacement of the CoP in the direction of the swing leg.

The Effects of Modulation of ML CoP Displacement During APA on the Execution of the First Step

By modulating hip abduction and stance-leg knee flexion during APA, the CNS efficiently controls the distance between CoP and CoM in the frontal plane and consequently the disequilibrium torque during APA. Moreover, due to friction between the floor and the stance foot, the torque is converted into shear force that in turn displaces the CoM and places it just medially with respect to the stance foot during the single-stance phase of the execution of the first step (see **Figure 3**). In line with Lyon and Day (2005), our results show that the subjects modulate the CoP displacement during APA across conditions in order to control the ML distance between CoM and CoP during the step-execution phase. More precisely, the small displacements of CoP during the Small stance-width condition produce a small ML CoM-CoP distance during step execution, while the ample displacements of CoP during the Large stance-width condition produce a greater ML CoM-CoP distance (see **Figure 3**). Consequently, the ML disequilibrium torque and the CoM velocity during step execution are greater when larger the initial stance-width. The greater velocities of the CoM during step execution measured under larger initial stance-width causes the stepping foot to land at a larger distance with respect to the stance foot (Caderby et al., 2014). This causes the foot to be placed close to the subjects' mid-sagittal plane at the FC in all three conditions, so that subjects subsequently progressed easily along their initial straight-ahead line (see **Figure 10**). This result is interesting, because it shows that, already at the first step, subjects tend to place the foot in the appropriate position for performing the next sets, regardless of the initial postural attitude. In Honeine et al. (2014) we showed that by modulating the CoM and CoP distance in the sagittal plane the CNS sets step length, the antero-posterior velocity of CoM and the duration of the first step. Here, we complete those results by showing that by controlling the disequilibrium torque in the frontal plane during APA, the CNS determines also the ML velocity of CoM and the ML position of the swing leg at the instant of first FC.

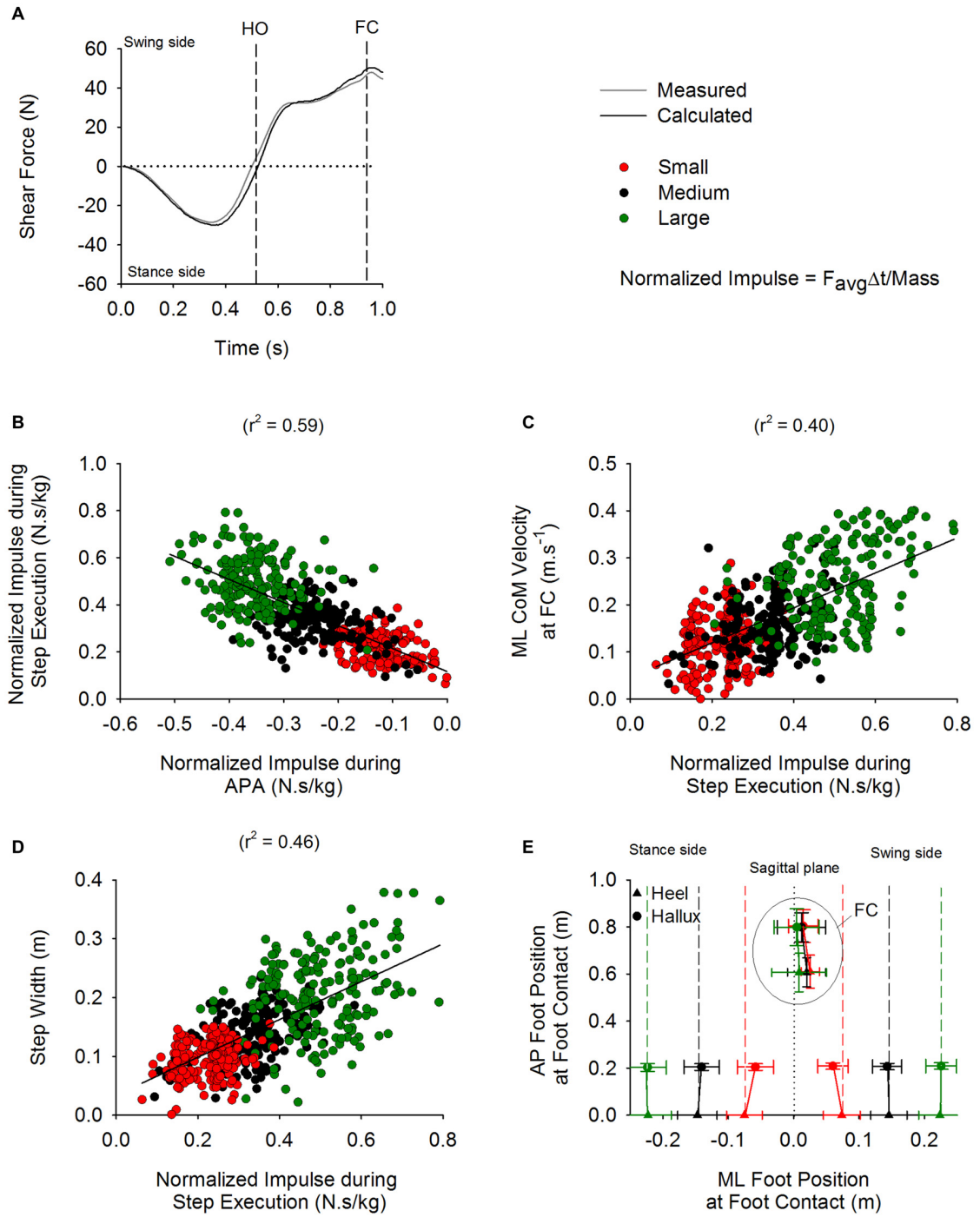

FIGURE 10 | ML disequilibrium torque and step execution parameters. The time-course of the shear force calculated from the disequilibrium torque (black trace) and measured from the platform (gray trace) are shown in panel **(A)** (average of 15 trials). The vertical dashed lines indicate HO and FC events. The negative values during APA indicate that the torque is pushing the body in the direction of the stance side. The positive values during step execution designate that the torque is acting in the direction of the swing leg. Panel **(B)** shows a scatter plot representing a linear relationship between the normalized (divided by mass) impulse calculated during APA and the normalized impulse computed during the step execution ($y = -0.98x + 0.12$). Panel **(C)** shows a scatter plot representing the linear relationship that was found between the normalized impulse during step execution and the instantaneous ML CoM velocity measured at FC ($y = 0.37x + 0.05$). Panel **(D)** shows a scatter plot representing the linear relationship found between the normalized impulse calculated during step execution and step width ($y = 0.32x + 0.03$). Panel **(E)** shows the grand means and standard deviations of the position, with respect to the sagittal plane (dotted line), of the heel and hallux markers in ML and anteroposterior (AP) direction at t0 and at FC in the three conditions. As can be seen, the subjects placed the foot at about the same position and with the same orientation close to the sagittal plane at FC in all three conditions.

Limitations

The initial stance width for each condition (15, 30 and 45 cm) was fixed for all the subjects. Due to anthropometric differences between subjects, a same width of the base of support could provoke different biomechanical constraints on the CoP displacement. Nonetheless, possibly because of the large inter-subject variability, the maximum displacement of the CoP towards the swing leg during APA was not significantly correlated with height or width of the pelvis, measured as the distance between the two anterior superior iliac spines.

Furthermore, the results of this study do not permit to make a quantitative statement about which strategy (hip abduction or stance-leg knee flexion) is mechanically more effective in displacing the CoP towards the swing leg during APA. To do so, in our opinion, this would require the calculation the contribution of the hip abduction and knee flexion torques to the CoP displacement, which is beyond the scope of this current article. One would also consider that different initial stance widths can slightly modify the angle of the tendon insertion between the hip abductors and femur. Therefore, different abduction forces could be generated for the same level of EMG activity, so that comparing EMGs across condition should be done with care.

Final Considerations

Our results support the hypothesis that both hip abduction and stance-leg knee flexion participate in unloading the stance leg and displacing the CoP in the direction of the swing leg during GI. On the one hand, hip abduction is caused by activation of the hip abductors of the swing leg (Carlsöö, 1966; Winter, 1995). On the other hand, stance-leg knee flexion is favored by the activation of TA and silencing of soleus of the same leg. The flexion of the knee during APA could be seen as an adaption of the CNS to facilitate and increase the robustness of the ML balance control process. Consequently, when ML balance control is examined in patients suffering from motor problems during GI, both hip abduction and stance knee flexion should be taken into account, in addition to initial stance width (Goodworth et al., 2014). Knee-flexion control in the frontal plane during APA could be inadequate in patients suffering from gait problems such as cerebral palsy, Parkinson's disease (Hiraoka et al., 2006; Hiraoka and Abe, 2007; Okada et al., 2011a,b; Mazzone et al., 2014), stroke, amputees (Aruin, 2016). For instance, freezing of gait in Parkinsonian patients is associated with knee trembling (Yanagisawa et al., 1991; Ueno et al., 1993; Hausdorff et al., 2003; Schaafsma et al., 2003; Bloem et al., 2004; Moore et al., 2008). Jacobs et al. (2009) found that during GI, knee trembling causes multiple APAs that are observable as a right-left leg loading-unloading cycles. Interestingly, the alternating unloading and loading of the legs was accompanied by similar alternating activation and deactivation of right-left TA (see Figure 2 in Jacobs et al., 2009). Therefore, knee trembling in Parkinson's disease patients might be preventing them from displacing CoM correctly towards the stance leg and thus not allowing them to initiate gait properly. Indeed, the smaller ML CoP displacement during APA and larger step width of the first step at GI have been observed in Parkinson's disease (Okada et al., 2011a,b). This could be in part associated with inappropriate knee flexion. Therefore, correcting the knee flexion angle of the stance leg during APA with a smart orthosis could possibly be an effective solution for enhancing GI and possibly steady-state gait in these patients.

AUTHOR CONTRIBUTIONS

J-LH contributed with project creation, data collection, data analysis and drafted the manuscript. MS contributed with project creation, data analysis. OC contributed in data collection, data analysis. M-CD contributed with project creation and data analysis. All authors discussed the results and participated in the revision of the manuscript.

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The Throw-and-Catch Model of Human Gait: Evidence from Coupling of Pre-Step Postural Activity and Step Location

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Postural activity normally precedes the lift of a foot from the ground when taking a step, but its function is unclear. The throw-and-catch hypothesis of human gait proposes that the pre-step activity is organized to generate momentum for the body to fall ballistically along a specific trajectory during the step. The trajectory is appropriate for the stepping foot to land at its intended location while at the same time being optimally placed to catch the body and regain balance. The hypothesis therefore predicts a strong coupling between the pre-step activity and step location. Here we examine this coupling when stepping to visually-presented targets at different locations. Ten healthy, young subjects were instructed to step as accurately as possible onto targets placed in five locations that required either different step directions or different step lengths. In 75% of trials, the target location remained constant throughout the step. In the remaining 25% of trials, the intended step location was changed by making the target jump to a new location 96 ms ± 43 ms after initiation of the pre-step activity, long before foot lift. As predicted by the throw-and-catch hypothesis, when the target location remained constant, the pre-step activity led to body momentum at foot lift that was coupled to the intended step location. When the target location jumped, the pre-step activity was adjusted (median latency 223 ms) and prolonged (on average by 69 ms), which altered the body's momentum at foot lift according to where the target had moved. We conclude that whenever possible the coupling between the pre-step activity and the step location is maintained. This provides further support for the throw-and-catch hypothesis of human gait.

Keywords: postural balance, gait initiation, motor activity, humans, gait, biomechanical phenomena, locomotion, walking

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INTRODUCTION

When taking a step, postural activity usually precedes the lift of the stepping foot by around half a second. It modulates the force between the feet and ground to accelerate the body sideways and forwards, and is observed during single steps as well as during locomotion (Carlsöö, 1966; Mann et al., 1979; Crenna and Frigo, 1991; Jian et al., 1993; MacKinnon and Winter, 1993). What is the function of this pre-step activity? One possibility is that its job is to move the body mass directly over the upcoming stance foot, allowing the stepping

foot to be lifted freely without compromising balance. However, this is not what is usually observed during single steps or locomotion. At the instant the stepping foot is lifted, the vertical projection of the body's center of mass (CoM) commonly lies outside and medial to the base of support formed by the stance foot (Jian et al., 1993; MacKinnon and Winter, 1993; Lyon and Day, 1997, 2005). This means that the body is not balanced, but is falling sideways under gravity during a step.

An alternative function of the pre-step activity has been proposed by the throw-and-catch model of human gait (Lyon and Day, 1997). This hypothesis states that the pre-step activity represents a "throw", which gives the body a specific position and momentum at the time of foot lift. At this point, the body enters a ballistic phase during the step where it falls under gravity along a trajectory determined by the pre-step activity, just as a ball would after being thrown. The direction and magnitude of the throw is finely tuned to take into account the initial state of the body and the intended final position of the stepping foot. Thus, during the step, the stepping foot swings towards its intended target while at the same time being optimally placed when it lands to "catch" the body and regain balance.

The throw-and-catch model predicts that the pre-step activity depends on both the body's initial conditions and the intended step location. In support of this are the findings that the resulting position and velocity of the body's CoM at the point of foot lift depend on both the initial stance width (Lyon and Day, 1997) and whether the step is to a forward or diagonal location (Lyon and Day, 1997, 2005), but are not influenced by the final position of the trailing foot (Lyon and Day, 2005). However, the predicted coupling between the pre-step activity and the intended step location has been shown to be breakable under certain circumstances. If the intended step location changes after the stepping foot leaves the ground, for example by shifting the position of a target, it is possible for the foot to land at a location different to that originally planned (Reynolds and Day, 2005, 2007; Kim and Brunt, 2009, 2013; Tseng et al., 2009; Nonnekes et al., 2010). This ability to de-couple the pre-step activity from the step location represents a challenge to the throw-and-catch hypothesis.

Here we investigate the strength of coupling between the pre-step activity and the step location under conditions previously unexplored. First, we study stepping onto five (for each foot) possible target locations, either demanding different step directions with the same step length, or demanding different step lengths with the same direction. The throw-and-catch hypothesis predicts that the pre-step activity will differ and be unique for each target location. Second, we occasionally make the central target jump to another location just after the pre-step activity has been initiated, but before the stepping foot has been lifted. This timing of target jump potentially allows the pre-step activity to be adjusted should it be advantageous to do so. The crucial question, therefore, is whether the pre-step activity is adjusted to take account of the new target location, or is unchanged such that all necessary adjustments are made later during the step, similar to that observed with later target jumps. Support for the throw-and-catch hypothesis would be obtained if: (1) the pre-step activity were modulated by the target jump; and (2) the modulation were dependent on the final location of the target.

MATERIALS AND METHODS

Ten human subjects (7 male; 24 ± 2 years; 64 ± 7 kg; mean ± standard deviation (SD)) gave written informed consent to participate in the experiment and reported no known neurological, sensory, muscular or orthopedic disorders. The experiment was approved by the UCL Research Ethics Committee and conformed to the *Declaration of Helsinki*. Participants were provided a written information sheet detailing the experimental procedures. Further to this, the experimental procedures were explained verbally. All subjects were naïve to the purpose of the study.

Protocol

Subjects performed a step onto a floor-bound target. Prior to the step, subjects stood barefoot and still with both feet parallel. The medial borders of the feet were separated by 15 cm. This starting position was chalk-marked to ensure a consistent starting location for all steps. The positions of the targets required a forwards movement, with five targets located on each of the left and right sides (**Figure 1**). Subjects were instructed to step as accurately as possible to the target, and bring the trailing foot alongside. An accurate step to each target was self-defined by all participants prior to the experiment. To achieve this, participants placed the appropriate foot over each of the 10 targets without time constraints in a manner they deemed accurate. For these accuracy trials, subjects were allowed to adjust their foot's position until they felt it represented an accurate step to a target. The step was redone if the subject or experimenter felt it necessary. Subjects were instructed to land their foot in this way for all subsequent steps and the position of their foot when it landed was compared to this ideal position. By instructing subjects to step accurately to the targets, rather than as quickly as possible, we sought to minimize variability in the placement of the stepping foot and thereby minimize variability in the step location.

The final position of the stepping foot was emphasized as being paramount and non-adjustable following foot landing. After the stepping foot landed subjects were required to step with the trailing foot and bring it alongside their stepping foot. The final position of the trailing foot does not affect the performance of the initial step (Lyon and Day, 2005) so no specific instruction was given as to where to place the trailing foot. However, subjects were encouraged to finish the step in a balanced state, similar to which they started. When a target illuminated to the left, a left-foot leading step was required and when a target illuminated to the right, a right-foot leading step was required. Multiple targets on both left and right sides were used to prevent prediction of target jump location or stepping side, thereby ensuring unbiased conditions at the time of target presentation and target jump.

A trial began with an audible beep, which was followed by a random delay and illumination of a step target. Illumination of the target acted as a cue for the subject to initiate a step

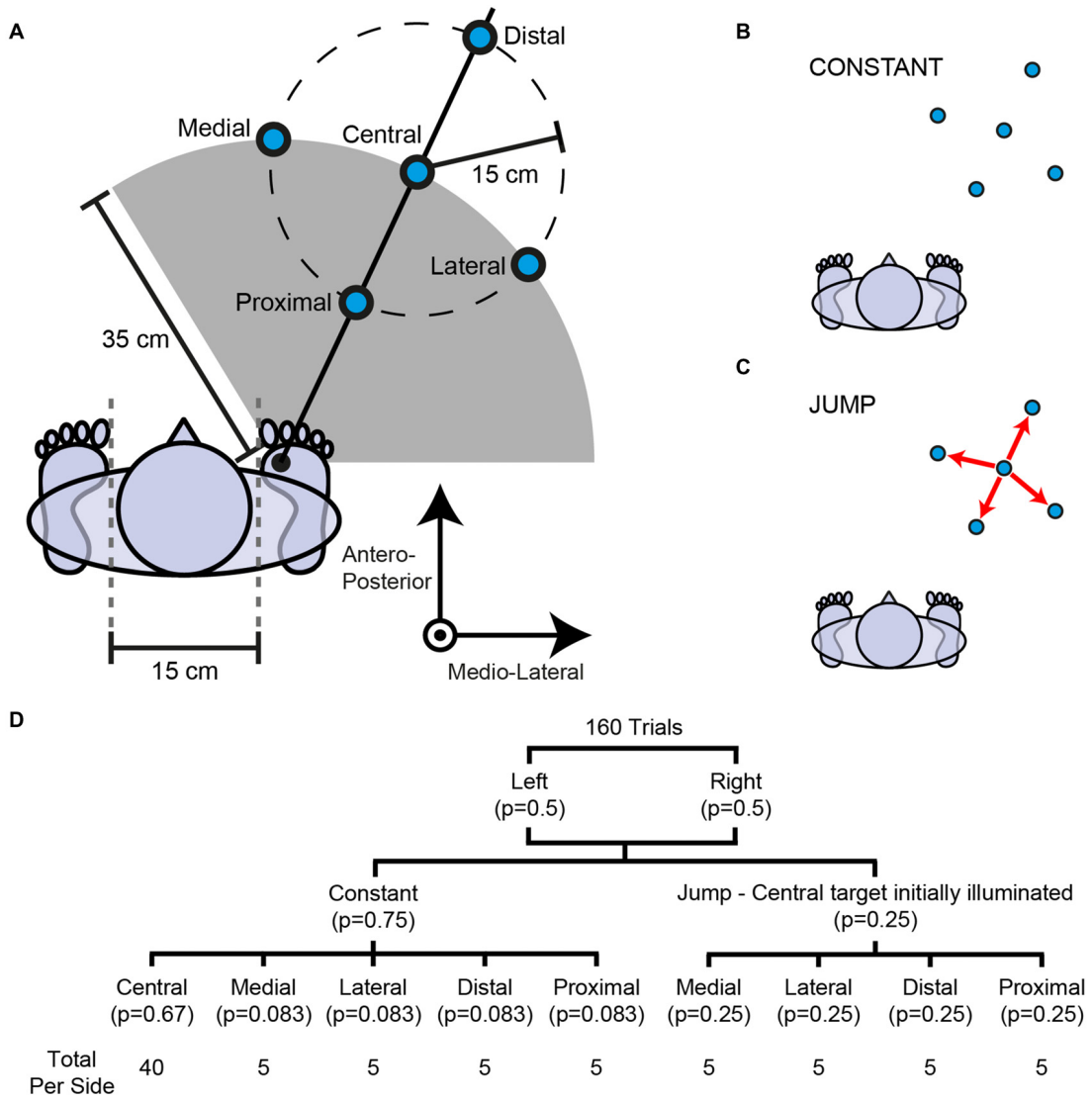

FIGURE 1 | Experimental set-up. (A) Right-sided targets are depicted; an identical configuration was present on the left side. The vertical axis protrudes directly out of the page. Subjects were instructed to step to a visually-presented target (blue circles). In most trials a target illuminated on either the left or right side and its location did not change **(B)**. In some trials the target jumped 15 cm from the central target to one of four peripheral targets (medial, lateral, distal or proximal) shortly after initiation of the pre-step activity **(C)**. **(D)** Probability tree outlining the number of trials and probability per condition. A target jump occurred with a probability of 0.33 after illumination of the central target.

to its location in their own time. The stepping targets were oriented so that step length and direction could be independently manipulated (**Figure 1A**). That is, for medial, central and lateral targets, step length was constant (35 cm) but step direction was different (0°, 25°, 50° forward of the stepping foot respectively). Equally, for proximal, central and distal targets, step direction was constant (25° forward of the stepping foot) but step length was different (20 cm, 35 cm, 50 cm respectively).

Experimental Conditions

In 75% of trials, one of the five targets on either the left or right side was selected pseudo-randomly and illuminated for the duration of the step (constant condition; **Figure 1B**). The central target was selected most frequently (probability = 0.67), whereas the peripheral targets were selected less often but each with equal frequency (probability = 0.083).

In 25% of trials, the central target was illuminated on either the left or right side and was made to unpredictably jump to one of its four peripheral targets selected pseudo-randomly (jump condition; **Figure 1C**). The peripheral targets were selected with equal frequency when a target jumped to a new location (probability = 0.25). After illumination of the central target, the probability of it jumping was 0.33.

The target jump was achieved by simultaneously extinguishing the central target and illuminating one of the four peripheral targets. Target jumps were triggered when the difference in vertical force between the stepping and trailing foot sides exceeded 80 N. This related to a mean (SD) of 7.8 (0.9)% (range: 5.7%–8.8%) of total body weight. Due to inherent electrical transmission delays, the new target would emit light 16.5 ms after the trigger signal. This delay is accounted for in all reported data. The new target appeared shortly after the initiation of the pre-step activity (mean (SD) latency: 96 (43) ms), long before the stepping foot lifted. The locations of the new targets meant that the required magnitude of foot adjustment remained constant (15 cm) but either step direction (medial- or lateral-jump) or length (distal- or proximal-jump) required modification.

A total of 160 trials were completed and performed in 10 blocks of 16 steps. The number of trials and its probability for each condition is summarized in **Figure 1D**.

Apparatus

Targets were circular (2.5 cm diameter) and illuminated via electroluminescent paper (Light Tape UK Limited, Barnsley, Yorkshire, UK) within a low-profile display on the floor in front of the subject. Ambient light conditions were dim (<0.1 Lux; Isotech 1332A Digital Illuminance Meter, Southport, Merseyside, UK) to eliminate potential distractors and ensure that the target light was compelling. Three infrared-emitting diode markers were placed at the base of the first metatarsal and head of the first (hallux) and fifth metatarsals of each foot. Marker positions were tracked at 200 Hz by two motion capture units comprising six "cameras" (Codamotion cx-1, Charnwood Dynamics, Leicestershire, UK). At the start of a trial, subjects stood with each foot over separate force platforms (9281C1, Kistler, Winterthur, Switzerland) which were embedded in the floor. Force was acquired at 1000 Hz.

Data Analysis

Both marker position and force data were digitally low-pass filtered using a zero-lag, second order Butterworth filter with 15 Hz and 30 Hz cut-off frequencies respectively. An anti-aliasing analog filter was used on force data prior to this.

The two force platforms were summed to evaluate the net force acting on the body in three-dimensions. From Newton's Second Law of Motion, the acceleration of the body's CoM was calculated by dividing net force by a subject's mass. The net acceleration of the body's CoM while the subject stood still (from the beginning of a trial until target illumination) was assumed to be zero and used as a baseline for the remainder of the trial. CoM velocity at foot lift, which has previously been shown to be an important variable in stepping (Lyon and Day, 1997, 2005), was then estimated by numerical integration of the CoM acceleration during the pre-step activity (trapezoidal method).

Typically, the center of pressure initially moves laterally towards the stepping side heel during the pre-step activity (Mann et al., 1979; Breniere et al., 1987). Therefore, the pre-step activity's initiation was calculated as the first point after target illumination that the medio-lateral (ML) center-of-pressure velocity towards the stepping foot exceeded 5 $cm.s^{-1}$ for at least 50 ms. Stepping foot lift was the first point that the stepping side's vertical force went below 1% of total body weight. Pre-step activity duration was the time from its initiation to stepping foot lift. The time the stepping foot landed was the first point after foot lift that the ML, antero-posterior (AP) and vertical speed of the stepping foot hallux marker went below 2 $cm.s^{-1}$. Speed was calculated as the absolute value of the first derivative of marker position. The final position of the stepping foot was the mean position of the three foot markers upon landing.

To investigate whether the pre-step activity was modulated when the intended step location changed, the body's horizontal (AP and ML) motion in jump trials was compared to constant-central (the initial target in a jump trial) steps over time after alignment. All trials were aligned to the initiation of the pre-step activity and CoM acceleration was differentiated to calculate jerk. Two-dimensional 95% confidence intervals (confidence ellipses) were then generated at each time point for the constant-central condition. **Figure 2** shows an example of this for one subject. The latency of any modulation was defined as the first time, at least 100 ms after a target jump, that a jump trial diverged from the constant-central confidence interval. The delay of 100 ms after a target jump was chosen as this relates to the shortest reported latencies to adjust lower limb trajectory or modulate ground reaction forces in visuomotor tasks (Reynolds and Day, 2005, 2007; Leonard et al., 2011). Modulation latency was measured for each jump condition and subject.

Sixteen jump trials (1% of total trials, 4% of jump trials) were excluded from the analysis due to the target jump being triggered

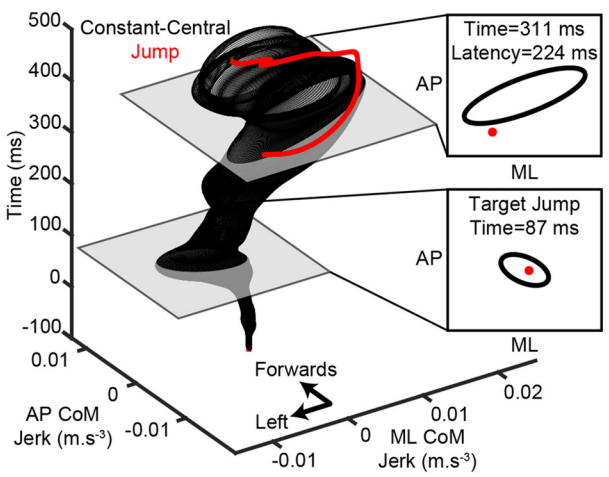

FIGURE 2 | Calculation of modulation latency. An example is shown for one subject's step to the right-side lateral target after the target jumped (red). Medio-lateral (ML) and antero-posterior (AP) center-of-mass (CoM) jerk traces were aligned to the initiation of the pre-step activity (time = 0) and 95% confidence ellipses were calculated at each time point for the constant-central steps (black). A modulation was detected when a jump trial diverged from the confidence ellipse. In this example the modulation occurred 224 ms after the target jumped and before the stepping foot lifted (time = 488).

either before the initiation of the pre-step activity or shortly before the stepping foot lifted.

Statistical Analysis

No bias was found between the left and right sides or dominant and non-dominant legs in the latency of the target jump from the pre-step activity's initiation, final position of the stepping foot, CoM velocity at foot lift, or duration of the pre-step activity (all $P > 0.05$). Therefore left-sided steps were reflected about the laboratory AP axis and combined with right-sided steps. All steps are reported as if they were right-sided.

Foot placement and CoM velocity at foot lift contained both ML and AP components and as such are multidimensional variables requiring analysis by multidimensional statistical methods. Ideally, a repeated-measures ANOVA capable of analyzing differences in multidimensional variables would be used to test whether the foot landed accurately or whether CoM velocity differed with target location. However, to the best of our knowledge, no such test exists. Therefore, paired *t*-tests for multidimensional variables (one-sample Hotelling's tests; Batschelet, 1981; Zar, 2010) were used to distinguish differences between conditions. Using multidimensional statistical methods, rather than examining the data in two dimensions separately, is advantageous as power is increased (Batschelet, 1981) and no *a priori* assumptions are required about which dimension of the data an effect is expected. CoM velocity at foot lift was paired within-subject by subtracting the mean of the constant-central condition from all other stepping conditions.

Unidimensional temporal variables (pre-step activity duration and modulation latency) were submitted to repeated-measures ANOVA with the within-subject factor of step location. ANOVAs were performed using SPSS statistical software (IBM Corporation, New York, NY, USA). Hotelling's tests and all other analyses were performed using custom written Matlab scripts (The Mathworks Inc., Natick, MA, USA). Statistical significance was set at an alpha level of 0.05 after Bonferroni correction for multiple comparisons. Greenhouse Geisser correction was used in ANOVAs when the assumption of sphericity was violated. Normality of data analyzed by Hotelling's tests was confirmed by Mardia's test of skewness and kurtosis (Mardia, 1970).

RESULTS

Steps When the Target Location Remained Constant

All subjects were able to land the stepping foot on or near the target when its location remained constant. On average, the final position of the foot was not different to each subject's self-defined ideal step, which was the case when stepping to all target locations (**Figure 3**, black symbols; all $T^2_{(2,8)} < 5.3, P > 0.7$). This indicated that a successful step was taken to all targets.

In order to land the foot in this position, all subjects produced pre-step activity that accelerated the body sideways, away from the stepping foot, and forwards. The mean (SD) time from the pre-step activity's initiation until foot lift was 561 (89) ms and was not consistently affected by the step location ($F_{(4,36)} = 0.8$, $P = 0.520$). However, the pre-step activity that accelerated the CoM differed with target location (**Figure 4**). **Figures 4A,C** depict the mean CoM acceleration for one subject and shows activity before the lift of the stepping foot. **Figures 4B,D** show that for this subject the pre-step acceleration resulted in the body gaining velocity that was specific for each intended step location. For the group analysis, each subject's mean CoM velocity at foot lift for steps to the central target was subtracted from the mean value for steps to each peripheral target. The resulting two-dimensional (AP and ML) representation of relative CoM velocity at foot lift showed a target-specific organization that resembled the relative positions of the targets in Cartesian coordinates (**Figure 4E**). The confidence ellipses of CoM velocity at foot lift for steps to medial, lateral, distal and proximal locations were all significantly different from each other (all $T^2_{(2,8)} > 82.5$, $P < 0.001$), indicating that the pre-step activity was coupled to the planned step location.

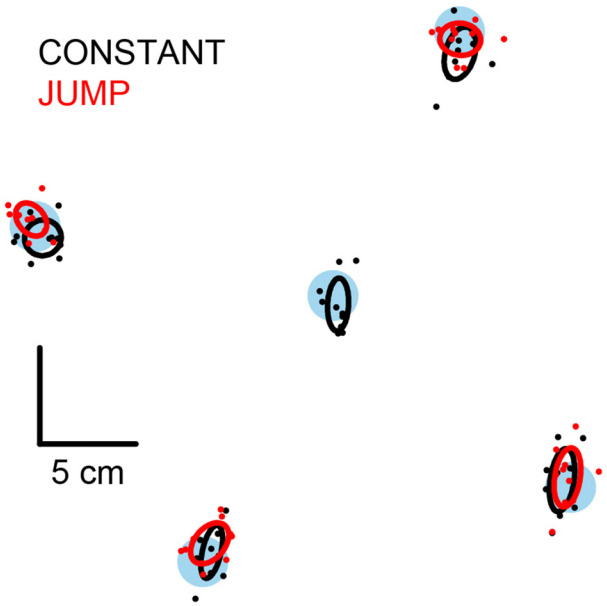

FIGURE 3 | Mean final position of the stepping foot. Filled blue circles are the stepping targets. Filled black and red circles are each subject's mean final position of the stepping foot for the constant and jump conditions respectively. Ellipses are Hotelling's 95% confidence ellipses of the group mean. The size and spacing of the stepping targets is to scale.

Steps When the Target Location Changed

All subjects adjusted their step when the target jumped to a new position shortly after initiation of the pre-step activity. This was demonstrated by the final position of the foot being different to that originally planned (constant-central steps) for steps to all target-jump locations (**Figure 3**, red symbols; all $T^2_{(2,8)} > 1900$, $P < 0.001$). Furthermore, the mean final position of the foot was not different to each subject's self-defined ideal step for any target jump location (all $T^2_{(2,8)} < 8.0$, $P > 0.3$), indicating

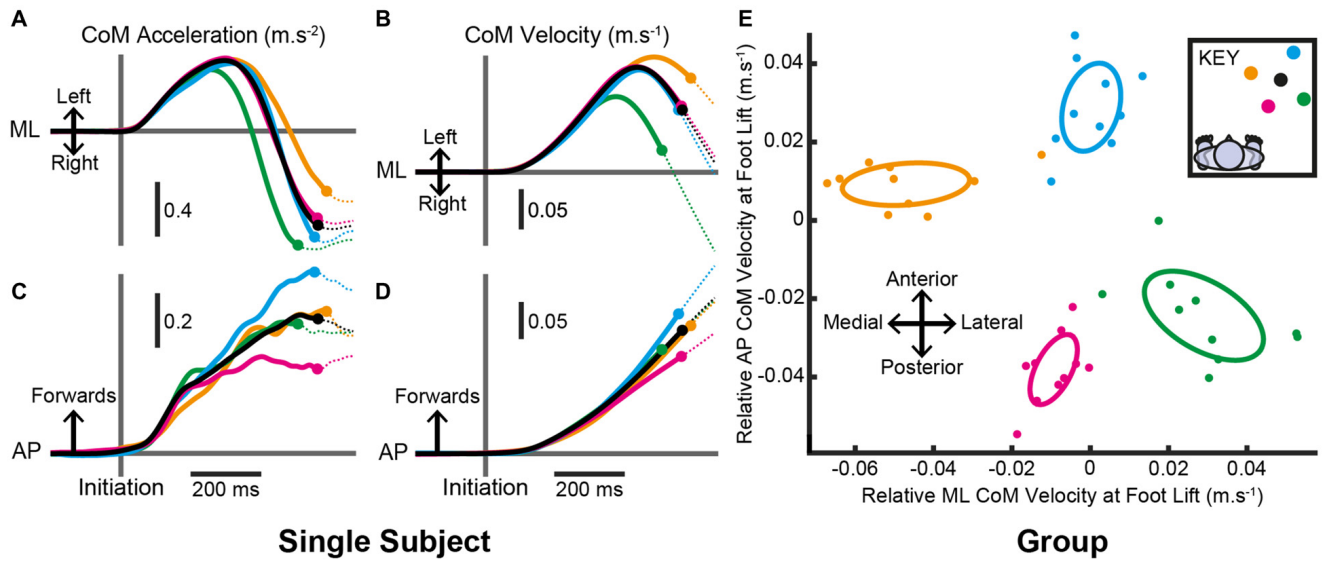

FIGURE 4 | Centre-of-mass (CoM) motion when the target location remained constant. (A–D) Mean estimated CoM acceleration **(A,C)** and velocity **(B,D)** over time from an individual subject in the ML **(A,B)** and AP **(C,D)** dimensions. Trials were aligned to the time of pre-step activity initiation. Filled circles denote the mean time the stepping foot lifted in steps to each target and the traces are dotted thereafter. **(E)** Estimated CoM velocity at foot lift for the group after within-subject pairing by subtracting the constant-central mean. Filled circles are each subject's mean estimated CoM velocity at foot lift for each target. Ellipses are Hotelling's 95% confidence ellipses of the group mean. As per the key, black= central; yellow= medial; green= lateral; blue= distal; magenta= proximal.

that the step adjustments were successful and accurate. The final position of the foot after a target jump was mostly the same as when stepping without a target jump (lateral, distal and proximal all $T^2_{(2,8)} < 10.5$, $P > 0.18$), however medial steps were modestly but significantly different from each other (mean vector distance = 1.1 cm; $T^2_{(2,8)} = 49.2$, $P = 0.002$).

To determine whether the pre-step activity was modulated in response to a change in step location, the CoM motion when subjects stepped to the constant-central target was compared with that when the target jumped (see **Figure 2** for details). An initial modulation could be reliably detected in 94% of all jump trials, with 6% of trials being excluded because their jerk trace lay outside the constant-central ellipse at the time of target jump. The first detectable modulation occurred before the foot lifted from the ground in the vast majority (93%) of the remaining trials, with a modulation after foot lift in 7% of trials (**Figure 5**). The median modulation latency was 223 ms (interquartile range = 158) and was not affected by the new target's location ($F_{(3,27)} = 1.0$, $P = 0.41$). Subjects would also delay the lift of the stepping foot to elongate the pre-step activity in response to the change of target location. When compared with steps to the constant-central target, foot lift was significantly delayed by 69 (55) ms in jump trials ($P = 0.003$), but did not depend on target-jump location ($F_{(3,27)} = 1.8$, $P = 0.178$). The stepping foot was also lifted later in jump trials than in steps to the same location without a target jump ($F_{(1,9)} = 10.9$, $P = 0.009$). The mean (SD) pre-step activity duration of steps with a target jump was 629 (129) ms.

Typically, the initial response to a change in target location acted to reduce the forward acceleration of the body, as shown for a single subject in **Figure 6C**. This "braking" effect was apparent for all target jump locations even if an increase in

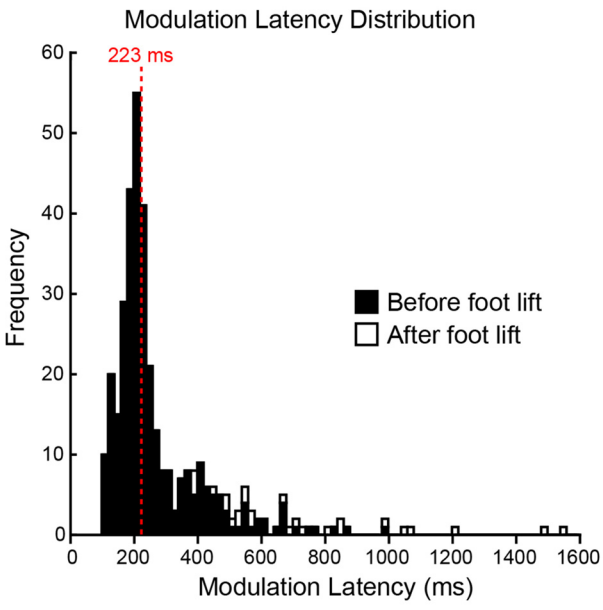

FIGURE 5 | Distribution of modulation latencies. A histogram of all jump trials for all subjects is depicted. The distribution was skewed and the average modulation latency was determined by the median (223 ms, red dashed line). Filled bars represent modulations occurring before the lift of the stepping foot and open bars represent modulations occurring after the lift of the stepping foot. Each bin is 20 ms.

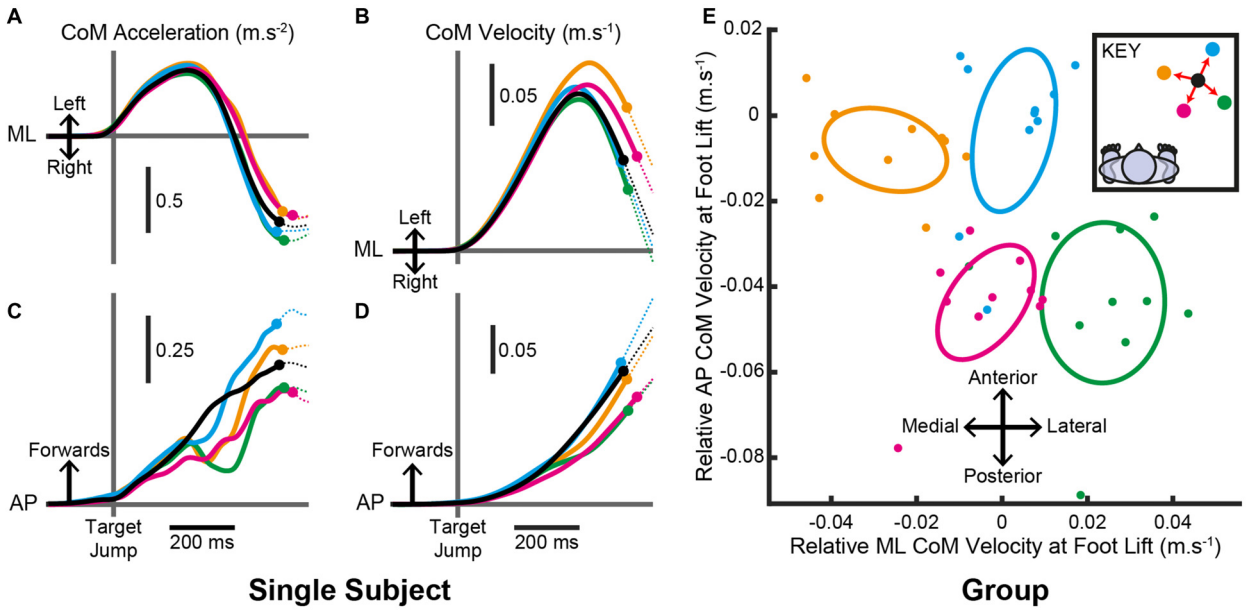

FIGURE 6 | Centre-of-mass (CoM) motion when the target location changed. (A–D) Mean estimated CoM acceleration **(A,C)** and velocity **(B,D)** over time from an individual subject in the ML **(A,B)** and AP **(C,D)** dimensions. Trials were aligned to the time a target jumped. Filled circles denote the mean time the stepping foot lifted in steps to each target and the traces are dotted thereafter. **(E)** Estimated CoM velocity at foot lift for the group after within-subject pairing by subtracting the constant-central mean. Filled circles are each subject's mean estimated CoM velocity at foot lift for each target. Ellipses are Hotelling's 95% confidence ellipses of the group mean. As per the key, black = constant-central; yellow = medial; green = lateral; blue = distal; magenta = proximal.

forward acceleration seemed more appropriate, for example during a jump that required an increased step length. The initial non-specific response was rapidly followed by a target-specific acceleration of the CoM (**Figures 6A,C**) leading to different CoM velocities at the point of foot lift (**Figures 6B,D**). For the group, the confidence ellipses of the change in CoM velocity at foot lift for steps with a medial, lateral, distal and proximal target jump were all significantly different from each other (**Figure 6E**; all $T^2_{(2,8)} > 83.9$, $P < 0.001$) demonstrating that the pre-step activity modulation was target-specific. The modulated CoM velocity at foot lift reflected the positions of the new stepping target, similar to that observed when the target position remained constant, suggesting that an attempt was made to re-couple the pre-step activity and step location.

DISCUSSION

The experiments were designed to test the throw-and-catch hypothesis of human gait. This was achieved by measuring the coupling between the pre-step activity (the throw) and the final stepping-foot position (the catch). The hypothesis states that the two actions are intimately coupled such that the pre-step activity differs with the planned step location. This was verified in the experiment where the final location was known to the subject throughout the movement. For the experiment in which the final location changed just after the throw was initiated, which effectively de-coupled the two actions, the throw was found to be adjusted so that it was re-coupled to the new step location. Together these results provide support for the throw-and-catch hypothesis of human gait.

Steps When the Target Location Remained Constant

The throw-and-catch model predicts that the pre-step activity depends on the intended step location. This is because the direction and magnitude of the body throw would need to be tuned differently in order for the body to fall towards its target during steps to different locations. Previous research identified a coupling between the pre-step activity and step location for forwards and diagonal steps (Lyon and Day, 1997, 2005). We sought to investigate whether this finding, and the throw-and-catch model, generalized to steps of different lengths and directions. The resulting data therefore required that both ML and AP body motion was analyzed together using multidimensional statistics (Hotelling's tests and confidence ellipses). The results confirmed that the pre-step activity systematically differed with target location in steps of both different lengths and directions (**Figure 4**). The net result of these changes was such that when the stepping foot lifted from the ground, the body had gained velocity, and therefore momentum, that was specific to the intended step location. Lyon and Day (1997) demonstrated that the body's momentum at the point of foot lift is a key factor that predicts the body's trajectory during the step. The coupling between the body's momentum and step location in the

present results suggests that this ballistic model generalizes and the throw is fine-tuned for steps of different lengths and directions.

In order to test the throw-and-catch model's generality, steps were initiated from an imposed initial posture which allowed both step length and direction to be precisely controlled. Although the initial posture may not have been a natural stance width or foot angle for all subjects, it is unlikely to have affected their behavior significantly. The step was otherwise natural for each subject as the initiation and duration of the step was unconstrained. This lack of temporal constraint is unlikely to have affected the use of a ballistic strategy, as it has been demonstrated both for temporally unconstrained steps (Lyon and Day, 1997, 2005) and when initiating gait as quickly as possible (Yiou et al., 2016). It is possible that differences in step duration may have influenced the throws to different targets (Zettel et al., 2002a,b; Yiou et al., 2016). However, this is unlikely to explain our data because although step duration changed with step length, it did not change with step direction (data not shown). In exploring the throw-and-catch in steps of different lengths and directions, subjects would often step beyond the force platforms. Subsequently, CoM position was unable to be reliably estimated (for a discussion of CoM position estimation from force data see Lyon and Day, 1997). The position from which the body initiates its fall is an important aspect of the throw (Lyon and Day, 1997, 2005) but, by demonstrating a step location-specific change in CoM velocity, the present results show that the pre-step activity is tuned to the future foot position.

The between-subject variability of the throw in this experiment (**Figure 4E**) and in Lyon and Day (1997) shows that there is no "one-size-fits-all" throw to achieve a successful step. Even for the same subject, different throws could successfully be caught by identical foot-landing positions. This likely reflects both the ability to make mid-step adjustments (Reynolds and Day, 2005, 2007; Kim and Brunt, 2009, 2013; Tseng et al., 2009; Nonnekes et al., 2010) and the numerous solutions that exist to catch the body without losing balance (Koolen et al., 2012). However, the present results show that there is pressure to maintain the throw within limits which differ for different step locations. This suggests there is some advantage in coupling the pre-step activity and step location.

Steps When the Target Location Changed

The pre-step activity and the step location can be uncoupled, for example by changing the location of a target. In this scenario the body throw and step location become uncoupled if the pre-step activity remains unchanged while the foot position changes. Previous work has shown that if the target is made to jump after the foot leaves the ground, so that the pre-step activity cannot be changed, the final position of the stepping foot can still be altered, albeit with varying degrees of success depending on the extent and direction of the target jump (Reynolds and Day, 2005, 2007; Kim and Brunt, 2009, 2013; Tseng et al., 2009; Nonnekes et al., 2010). This de-coupling does not necessarily disprove the throw-and-catch hypothesis, but may be interpreted as there being some flexibility in the coupling which can be exploited under certain circumstances. A better test of the hypothesis is to measure whether there is an attempt to re-couple the pre-step activity with the new step location under conditions when the pre-step activity has an opportunity to be adjusted. Here we made the target change location during the pre-step activity, long before the stepping foot left the ground, thus allowing time for a re-coupling of the pre-step activity with the new target location. The target jump was unpredictable, as more often than not the target location did not change and could be to any one of four locations when it did. This procedure resulted in substantial uncertainty and rendered attempts at anticipating the target jump unlikely to be of value to the subject. We argue that an attempt to re-couple the pre-step activity with the new step location would provide support for the throw-and-catch hypothesis given that an adjustment could be initiated after the foot leaves the ground.

Previous research is conflicted on whether the pre-step activity can be modulated. Experiments that unpredictably perturbed the trajectory of the body during the pre-step activity via mechanical pulls have returned mixed results, with muscle activity being altered to correct the body's trajectory in response to resistive (Mouchnino et al., 2012; Mille et al., 2014) but not assistive perturbations (Mouchnino et al., 2012). Additionally, stimulation of proprioceptive (Ruget et al., 2008) and vestibular (Bent et al., 2002) afferents were found not to affect the pre-step activity, suggesting it may be immutable once it has been initiated. This was not found to be the case in the present experiment, since the pre-step activity was modulated in the vast majority of trials when prompted by a visual cue. Furthermore, the precise modulation of the pre-step activity depended on the new target location. This suggests that an attempt was made to re-couple the pre-step activity to the new target location and provides causal evidence that the pre-step activity is fine-tuned to take the final position of the foot into account. According to the throw-and-catch hypothesis, re-coupling the pre-step activity to the new target location would have promoted a more appropriate fall of the body towards its intended target after the lift of the stepping foot. This does not rule out the possibility that further adjustments were made during the step.

Although the net adjustment of the pre-step activity was different depending on where the target jumped, a non-specific initial response to the perturbation was evident that reduced the forward acceleration of the body. Similar "braking" responses to visual cues have been reported after the lift of the stepping foot during both single steps and locomotion (Kim and Brunt, 2013; Potocanac et al., 2016). In the present experiment, this braking was used irrespective of where the target moved. Although the braking could have been expected when the step length required shortening, it was surprising that it was also used when a longer step was required. This is because greater forward acceleration was observed for longer steps when the target did not move (**Figure 4**). The braking may have enabled a pause whilst the necessary actions for

a successful step were reconsidered (Potocanac et al., 2016), which would explain the increase in pre-step duration that was observed when a target jumped. Mille et al. (2014) also report a similar delay in stepping after a mechanical pull to the body prior to a step. Presumably, in the current experiments, the extra time was needed to re-program and adjust the body throw so that it was re-coupled to the new final foot location.

What Advantage Does the Throw-and-Catch Coupling Offer?

Stepping can be considered a ballistic action if, as we suggest, gravity drives the fall of the body during the step with its trajectory being controlled by the pre-step activity. The ballistic nature of stepping is sometimes misinterpreted as sensory information not being attended to or usable during the step. This interpretation is clearly false given that adjustments to the step are possible both before the lift of the stepping foot, as shown in this paper, and after foot lift when suitable sensory cues are provided (Reynolds and Day, 2005, 2007; Kim and Brunt, 2009, 2013; Tseng et al., 2009; Nonnekes et al., 2010). However, the magnitude and direction of mid-step adjustments are limited by the fall of the body and the subsequent balance constraints. For example, the size of medially-directed foot adjustments cannot be made as large as laterally-directed adjustments (Reynolds and Day, 2005). This limitation may underlie the incentive to maintain the coupling between the pre-step activity and final foot location demonstrated in the present experiment. At the same time, the ability to rapidly alter the intended foot position mid-step offers a degree of flexibility in the coupling, which would be essential for responding to an unexpected environmental threat or maintaining foot landing accuracy in the presence of error in the initial throw.

CONCLUSION

We find that there is a close coupling between pre-step activity and final foot position during unperturbed steps of different lengths and directions. Furthermore, there is pressure to maintain this coupling when the demanded step location unpredictably changes shortly after initiation of the pre-step activity. We conclude that these results support the throw-and-catch hypothesis of human stepping.

AUTHOR CONTRIBUTIONS

MJB and BLD conceptualized and designed the experiment, analyzed the data, drafted and revised the manuscript and approved its final version. MJB acquired the data.

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Anticipatory Postural Control of Stability during Gait Initiation Over Obstacles of Different Height and Distance Made Under Reaction-Time and Self-Initiated Instructions

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Despite the abundant literature on obstacle crossing in humans, the question of how the central nervous system (CNS) controls postural stability during gait initiation with the goal to clear an obstacle remains unclear. Stabilizing features of gait initiation include anticipatory postural adjustments (APAs) and lateral swing foot placement. To answer the above question, 14 participants initiated gait as fast as possible in three conditions of obstacle height, three conditions of obstacle distance and one obstacle-free (control) condition. Each of these conditions was performed with two levels of temporal pressure: reaction-time (high-pressure) and self-initiated (low-pressure) movements. A mechanical model of the body falling laterally under the influence of gravity and submitted to an elastic restoring force is proposed to assess the effect of initial (foot-off) center-of-mass position and velocity (or "initial center-of-mass set") on the stability at foot-contact. Results showed that the anticipatory peak of mediolateral (ML) center-of-pressure shift, the initial ML center-of-mass velocity and the duration of the swing phase, of gait initiation increased with obstacle height, but not with obstacle distance. These results suggest that ML APAs are scaled with swing duration in order to maintain an equivalent stability across experimental conditions. This statement is strengthened by the results obtained with the mechanical model, which showed how stability would be degraded if there was no adaptation of the initial center-of-mass set to swing duration. The anteroposterior (AP) component of APAs varied also according to obstacle height and distance, but in an opposite way to the ML component. Indeed, results showed that the anticipatory peak of backward center-of-pressure shift and the initial forward center-of-mass set decreased with obstacle height, probably in order to limit the risk to trip over the obstacle, while the forward center-of-mass velocity at foot-off increased with obstacle distance, allowing a further step to be taken. These effects of obstacle height and distance were globally similar under low and high-temporal pressure. Collectively, these findings imply that the CNS is able to predict the potential instability elicited by the obstacle clearance and that it scales the spatiotemporal parameters of APAs accordingly.

Keywords: stability, anticipatory postural adjustments, obstacle clearance, mechanical modeling, temporal pressure, gait initiation, motor coordination, human

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INTRODUCTION

The control of postural stability is crucial for the efficient performance of day-to-day motor tasks. Like all terrestrial species, humans move around in a gravity field that permanently induces postural destabilization through its attracting effect towards the center of the earth. Major questions in motor control relate to the way in which humans are able to maintain stability during motor tasks that involve whole body progression, such as locomotor tasks, and how they adapt to environmental constraints, e.g., when clearing an obstacle. Gait initiation, which corresponds to the transient period between quiet standing and swing foot contact with the ground, is a classical paradigm for studying balance control mechanisms during complex whole body movement (e.g., Brenière et al., 1987; Lyon and Day, 1997, 2005; McIlroy and Maki, 1999; Yiou et al., 2012a for a recent review; Caderby et al., 2014). The act of lifting the swing foot from the ground to step in the desired direction does indeed induce a reduction in the size of the mediolateral (ML) base of support, moving from a bipedal to a unipedal stance. If the center of mass is not repositioned above (or closer to) the limits of the new base of support -i.e., the stance foot–, the body will topple towards the swing leg side during the single stance phase (or "swing phase") of gait initiation under the effect of gravity, which may cause lateral instability at foot contact. This instability is invariably attenuated during volitional stepping by the development of dynamic postural phenomena that occur before the swing phase. These dynamic phenomena correspond to "anticipatory postural adjustments" (APAs). They include a center of pressure shift towards the swing leg side which serves to accelerate the center of mass in the opposite direction, i.e., towards the stance leg side (Do et al., 1991; Jian et al., 1993; McIlroy and Maki, 1999; Nouillot et al., 2000; Caderby et al., 2014; Yiou et al., 2016). If not enough APAs are generated in the ML direction, a strategy of base of support enlarging, associated with a more lateral swing foot placement, has been shown to be triggered to maintain stability (Zettel et al., 2002; Caderby et al., 2014). In addition to this putative stabilizing function, APAs have been shown to provide the dynamic conditions for whole body progression in the desired direction. For example, during gait initiation, APAs in the anteroposterior (AP) direction include a backwards center of pressure shift that promotes the forward propulsive forces necessary to reach the intended center of mass velocity and step length (Brenière et al., 1987; Lepers and Brenière, 1995; Michel and Chong, 2004).

Postural stability during gait initiation might be further challenged by the presence of an obstacle that needs to be cleared. There has been extensive literature on the control of obstacle crossing during ongoing locomotion, especially in regards to the role of vision (e.g., Mohagheghi et al., 2004; Patla and Greig, 2006; Marigold et al., 2007). In comparison, the question how the postural and the focal components of gait initiation over an obstacle are coordinated to ensure safe body progression has received much less attention (e.g., Brunt et al., 1999; Yiou et al., 2016). Yet, it is known that gait initiation is among the motor activities associated with the highest proportion of falls in the elderly (Robinovitch et al., 2013). In addition, the most frequent cause of falling in this population is an incorrect weight transfer, which, as stated above, is one of the major functions of APAs. In addition to the risk of tripping over the obstacle, the presence of an obstacle gives rise to an increase in the duration of the swing phase and therefore an increase in the potential for lateral instability (Zettel et al., 2002; Yiou et al., 2016). Hence, it is surprising that previous studies on the influence of an obstacle on the lateral motion of the center of mass during ongoing walking have reported that lateral stability remained unchanged when the height of the obstacle was varied (Chou et al., 2001; Hahn and Chou, 2004). This result led the authors to suggest the existence of some forms of adaptive postural mechanisms aimed at compensating for the increased potential instability related to obstacle height. However, these mechanisms remain to be clarified. To date, the question of whether or not the stabilizing mechanisms of gait initiation can accommodate obstacle constraints has been investigated in only one study (Yiou et al., 2016). This study showed that the amplitude of ML APAs was larger in the obstacle condition than in the obstacle free (control) condition. It was suggested that this increase was responsible for the maintenance of postural stability at swing foot contact. Similar results were obtained by Zettel et al. (2002) during their comparison of reactive stepping over an obstacle in response to a brisk plate-form shift with the same reactive stepping in an obstacle-free condition. However, these studies are all limited by the fact that only one obstacle height and distance were tested. Thus, one can question the generalizability of these results and more specifically, the extent to which the central nervous system (CNS) is able to adjust the stabilizing features of gait initiation (including ML APAs and base of support enlargement) to match changes in obstacle height and distance and the related potential for instability. Moreover, subjects of these studies invariably increased ML APAs when stepping (voluntarily or reactively) over the obstacle; thus, it could not be established that the absence of such an increase would have necessarily led to instability at foot contact. Lyon and Day (1997, 2005) used a single-segment mechanical model in which the body falls freely under the influence of gravity to predict the magnitude of the lateral center of mass fall during the swing phase of step initiation. In the present study, we elaborated on a mechanical model that was based on these last two studies in order to investigate how changes in the parameters of ML APAs can impact on postural stability at foot contact. Such modeling may thus provide further insight into the adaptability of the postural system to environmental constraints.

This study aims to investigate how the CNS controls postural stability during gait initiation when clearing obstacles of different heights and distances. Changes in obstacle height and distance were expected to bring about modulation of the swing phase and give rise to instability. In addition, as daily motor tasks may be performed under various temporal pressure constraints, gait initiation trials were performed in reaction-time (high pressure) and self-initiated (low pressure) conditions. Our previous study (Yiou et al., 2016) showed that the duration of APAs associated with gait initiation when faced with an obstacle was shorter

under high pressure than under low pressure. This difference in duration was compensated by an increase in the amplitude of ML APAs. As only one obstacle height and distance were used (one 20 cm high obstacle, placed at a 20% body height distance from the participant), it can be questioned whether the CNS uses a similar anticipatory postural adaptation to temporal pressure when the obstacle constraints are manipulated. This is particularly the case when height and distance are increased, thereby placing a higher level of stress on the postural system.

This question might be addressed in regards to current theory on motor control, according to which our nervous system would possess neural structures (or internal models) that predict the future state of a system given the current state and the sensorimotor control signals (Wolpert and Flanagan, 2001). Such prediction would allow us to achieve rapid and accurate voluntary behavior despite the difficulties presented by motor noise, delayed sensory feedback, and a complex musculoskeletal apparatus. As stressed in Mille et al. (2012), it is clear that "the anticipatory nature of the APAs involves a role for motor prediction". Specifically, APAs structure would reflect the existence of internal models that predicts the destabilizing effect associated with the stepping (Lyon and Day, 1997, 2005). When stepping over an obstacle, it can therefore be expected that APAs will be scaled according to the potential destabilization associated with obstacle constraints. We thus hypothesize that the stabilizing features of gait initiation are scaled according to the changes in the swing phase duration that is associated with obstacle height and/or distance. More specifically, it is expected that a greater swing phase duration will be associated with larger ML APAs and eventually, a larger base of support in order to maintain unchanged postural stability at swing foot contact. Similar effects of obstacle constraints are expected under low and high temporal pressure conditions. However, APAs of larger amplitude and lower duration are expected in the high pressure condition compared with the low pressure condition. Mechanical modeling of the whole body during gait initiation is expected to reveal the extent to which postural stability at foot contact may be degraded in case ML APAs are not adequately scaled to modifications in swing duration induced by obstacle constraints.

MATERIALS AND METHODS

Participants

Fourteen subjects (eight males and six females, aged 23.2 ± 4 years [mean ± SD], height 173.4 ± 7.3 cm and weight 65.8 ± 8.7 kg) participated in the experiment. All were free of any known neuromuscular disorders. They gave written informed consent after being instructed as to the nature and purpose of the experiment, which was approved by the local ethics committee. The study conformed to the standards set by the Declaration of Helsinki.

Experimental Protocol

Participants were requested to initiate gait as fast as possible with their preferred limb while clearing an obstacle placed in front of them (**Figure 1**). Three conditions of obstacle height (2.5%, 5% and 10% of each subject's height), three conditions of obstacle distance (10%, 20% and 30% of each subject's height) and an obstacle-free control condition were used. The three obstacle distances corresponded to 21%, 42% and 63% of the step length obtained in the control condition, respectively. Each condition of obstacle height and distance was realized in two blocks, which differed in terms of their level of temporal pressure constraint: a reaction-time and a self-initiated block. In the reaction-time block (high temporal pressure), participants were instructed to initiate gait "as soon as possible" after an acoustic signal was given. In the self-initiated block (low temporal pressure), they were instructed to initiate gait when they felt ready, after receiving an "all set" signal; it was made clear that the "all set" signal was not a "go" signal and that they could take as much time as they needed to prepare their movements. The order of conditions within one given block and the order of the blocks were randomized between participants. In each condition, subjects were allowed two familiarization trials. Five trials were then recorded. A 3-min rest was imposed between two successive conditions to avoid fatigue. In each condition, the participants initially stood upright with their feet hip-width apart, their arms hanging loosely either side of their body and their body weight evenly distributed between their legs. The boundaries of their feet in the initial posture were outlined on the force plate, and participants were instructed to systematically reposition their feet within these marks under supervision. They were repeatedly reminded of the task instructions.

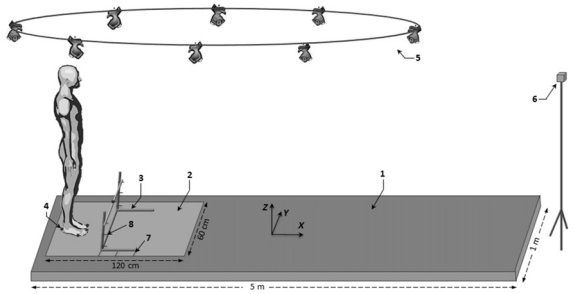

FIGURE 1 | Schematic illustration of the experimental set-up. Key: (1) walkway; (2) force-plate; (3) obstacle; (4) reflective marker; (5) Vicon camera; (6) visual target; (7) obstacle distance marker; and (8) obstacle height marker.

Materials

Gait was initiated on a force plate (600 × 1200 mm, AMTI, Watertown, MA, USA) located at the beginning of a five-meter track (**Figure 1**). The force plate was embedded in the track and was large enough to allow the participant's swing foot to systematically land on it at the end of gait initiation. After crossing the obstacle, participants walked to the end of the track, then stood still for a few seconds before returning to their starting position. The obstacle consisted of a lightweight wooden rod (length: 65 cm; diameter: 1 cm) that rested on two adjustable upright standards. The participant's toes served

as the reference point for positioning the obstacle at the various distances. Reflective skin markers (9 mm in diameter) were placed bilaterally at the hallux (toe marker), head of the fifth metatarsal (metatarsal marker), posterior calcaneus (heel marker) and at the middle of the top of the obstacle (obstacle marker). A V8i VICON eight-camera (Mcam2) motion capture system (Oxford Metrics Ltd., UK) with 64 analog channels was used to record the movement of the foot markers and to detect the position of the obstacle. Kinematic and kinetic data were collected simultaneously at a rate of 500 Hz. Data acquisition and stimulus display were controlled by a custom-made program written in Matlab™ (R2009b, The MathWorks Inc., Natick, MA, USA).

Data Analysis

Kinematic and force plate data were low-pass filtered using a Butterworth filter with a 15 Hz (Mickelborough et al., 2000) and a 10 Hz (Caderby et al., 2014) cut-off frequency, respectively. The ML (*yP*) and AP (*xP*) coordinates of the center of pressure were computed from force plate data as follows:

$$yP = \frac{Mx + Fy \times dz}{Fz} \quad (1)$$

$$xP = \frac{-My + Fx \times dz}{Fz} \quad (2)$$

where *Mx* and *My* are the moments around the AP and ML axes, respectively; *Fy*, *Fx* and *Fz* are the ML, AP and vertical ground reaction forces, respectively; and *dz* is the distance between the surface of the force plate and its origin.

Instantaneous acceleration of the center of mass along the AP and ML axes was determined from the ground reaction force according to Newton's second law. Center of mass velocity and displacement were computed by successive numerical integrations of center of mass acceleration using integration constants equal to zero, i.e., initial velocity and displacement null (Brenière et al., 1987). The following instants were determined from biomechanical traces: gait initiation onset (t_0), swing heel off, swing toe off and swing foot contact. T_0 and foot contact were determined from force plate data, whereas heel off and toe off were determined from VICON data. Two t_0 times were estimated, one for the ML axis and one for the AP axis. The t_0 times corresponded to the instants when the ML or AP center of pressure trace deviated 2.5 standard deviations from its baseline value. Heel off and toe off corresponded to the instants when the vertical position of the swing heel marker and the anterior position of the swing toe marker increased by 3 mm from their position in the initial static posture. Foot contact corresponded to the instant when the ML and AP center of pressure traces shifted abruptly laterally towards the swing leg side, and forwardly, respectively (this abrupt shift occurred at the same instant in the two traces).

Mechanical Model

In the present study, the human body was modeled during the swing phase of gait initiation (from toe off to foot contact) as a single conic inverted pendulum which rotates about a fixed point 0 (**Figure 2**). This model was based on work carried out in earlier studies (Jian et al., 1993; MacKinnon and Winter, 1993; Lyon and Day, 1997, 2005). The displacement of this cone had five degrees of freedom on the absolute referential (0, *x*, *y*, *z*), i.e., three translations and two rotations. A new referential (0, x_1, y_1, z_1) was considered after precession ψ around *z* and nutation θ around x_1, in which the inertia momentum of the body was expressed with its eigenvalues (Winter et al., 1990). The proper rotation ψ around z_1 with respect to ψ and θ was neglected. During the swing phase, we considered that the center of mass was falling laterally under the influence of two forces: the gravity force $P = mg$ (where m is the mass of the solid, and g is the gravitational acceleration) and an elastic restoring force T that reflects active muscular control of the movement (Farley and Morgenroth, 1999; Morasso and Schieppati, 1999), with $T = k|yM|$ (where k is the stiffness of the hip abductor muscles acting on the stance leg side during the swing phase (Winter, 1995) and $|yM|$ is the absolute value of the ML center of mass shift, which was systematically oriented towards the swing leg side (positive values) during the swing phase). The initial position and velocity of the cone corresponded to the position and velocity of the subject's center of mass at toe off. The addition of a restoring force on the conic model was necessary in order to control the initial velocity at toe off. Without this supplementary force, the conic pendulum would fall towards the stance leg side in most trials.

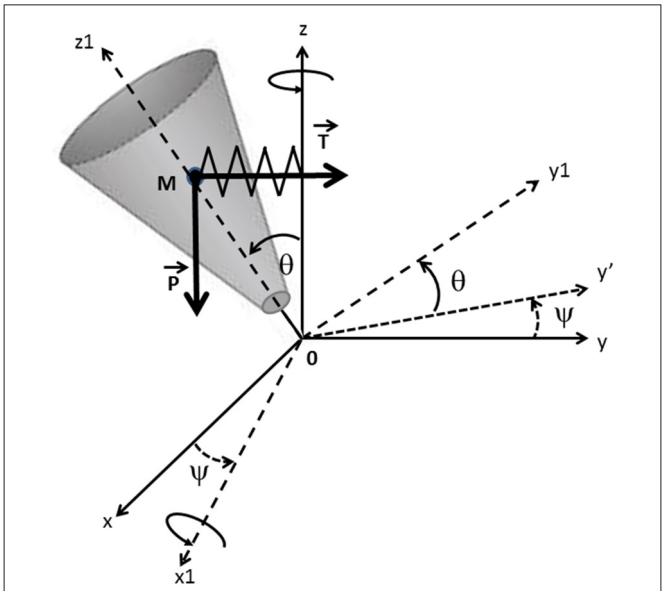

FIGURE 2 | Mechanical model. The mechanical model is represented as a conic inverted pendulum which pivots about a fixed point 0. Body displacement during the swing phase (from toe off to foot contact) presents five degrees of freedom on the absolute referential (0; *x*; *y*; *z*). (0; x_1; y_1; z_1) are the main axes of the inertia momentum of the solid body after precession ψ around *z* and nutation θ around x_1. The center of mass m falls under the influence of the gravity force *P* and the elastic restoring force *T*. The initial position and velocity of the cone correspond to the position and velocity of the subject's center of mass at toe off.

The equation of motion in $(0, x_1, y_1, z_1)$ was:

$$OM \times \left(mg + k\left|\mathrm{yM}\right|\right) = \frac{\mathrm{d}\sigma_{/0}}{\mathrm{d}t} \quad (3)$$

Where $OM = l_{\mathrm{M}}\, z_1$, with l_{M}: distance of the center of mass along z_1, and $\sigma_{/0}$: angular momentum computed as $\sigma_{/0} = I_{/0}\ \Omega$, where $I_{/0}$ is the diagonal matrix of inertia along the main axes (x_1, y_1, z_1) and Ω is the total angular velocity:

$$\Omega = \dot{\theta} x_1 + \dot{\psi} \sin\theta y_1 + \dot{\psi} \cos\theta z_1 \quad (4)$$

Finally, the differential equations of angular movement were:

$$\ddot{\theta} = \frac{mgl_{\mathrm{M}} \sin\theta + k\left|yM\right| l_{\mathrm{M}} \sin\psi \cos\theta - \dot{\psi}^2 \cos\theta \sin\theta \left(I_{oz_1} - I_{ox_1}\right)}{I_{ox_1}} \quad (5)$$

$$\ddot{\psi} = \frac{k\left|yM\right| l_{\mathrm{M}} \cos\psi \sin\theta - 2\dot{\theta}\dot{\psi} \cos\theta \sin\theta \left(I_{ox_1} - I_{oz_1}\right)}{I_{ox_1} \sin^2\theta + I_{oz_1} \cos^2\theta} \quad (6)$$

The subsequent motion of the model's center of mass was predicted by solving numerically the differential equations of motion using a fourth order Runge-Kutta algorithm. The spherical coordinates numerically computed (l_{M}, θ, ψ) were then transformed into Cartesian coordinates (x, y, z) in order to compare experimental data with the model's theoretical data.

Dependant Variables

Experimental Variables

Gait initiation was divided into three phases: APAs (from t_0 to heel off), swing foot lift (from heel off to toe off) and swing phase (from toe off to foot contact, **Figure 3**). The duration of APAs along the ML and AP axes were computed separately, because the t_0 times for these two axes did not necessarily occur simultaneously (Caderby et al., 2014). The amplitude of APAs was characterized by the peaks of the backward and lateral center of pressure shift obtained during the APAs time window. Center of mass velocity and displacement along the ML and AP axes were quantified at toe off and foot contact. The ML and AP center of mass position in the initial upright static posture was estimated by averaging the center of pressure position during the 250 ms period preceding the "all set" or the "go" signal, depending on the temporal pressure condition (Yiou et al., 2016). Spatiotemporal features of the swing phase of gait initiation that were investigated included: swing phase duration, AP center of mass velocity at foot contact, step length, step width, and dynamic stability at foot contact. Step length corresponded to the distance covered by the heel marker of the swing leg from the initial posture to foot contact. In addition, the vertical distance between the obstacle and the swing heel and swing toe markers was measured at the time when these markers passed over the obstacle. For each trial in the obstacle condition, the shorter of these two vertical distances was reported; this corresponded to the "foot clearance". An adaptation of the "margin of stability" (MOS) introduced by Hof et al. (2005) was used to quantify ML dynamic stability at foot contact (thereafter referred to as "stability"). The MOS corresponded to the difference between the ML boundary of the base of support ($\mathrm{BOS_{ymax}}$) and the ML position of the "extrapolated center of mass" at swing foot contact ($\mathrm{YcoM_{FC}}$). Thus:

$$\mathrm{MOS} = \mathrm{BOS_{ymax}} - \mathrm{YcoM_{FC}} \quad (7)$$

Because kinematic data showed that participants first landed on the force plate with the swing heel or the swing toe, $\mathrm{BOS_{ymax}}$ was estimated using the ML position of the swing heel or metatarsal marker at foot contact. The ML distance between the position of the swing foot marker at foot contact (heel or toe) and the position of the stance metatarsal marker at t_0 represented step width, and was representative of the size of the ML base of support. Based on the study by Hof et al. (2005) and the results from our previous studies (Caderby et al., 2014; Yiou et al., 2016), the ML position of the extrapolated center of mass at foot contact ($\mathrm{YcoM_{FC}}$) was calculated as follows:

$$\mathrm{YcoM_{FC}} = yM_{\mathrm{FC}} + \frac{y'M_{\mathrm{FC}}}{\omega_0} \quad (8)$$

where yM_{FC} and $\mathrm{y'M_{FC}}$ are respectively the ML center of mass position and velocity at foot contact, and ω_0 is the eigen frequency of the body, modeled as an inverted pendulum and calculated as follows:

$$\omega_0 = \sqrt{\frac{g}{l}} \quad (9)$$

where $g = 9.81\ \mathrm{m/s^2}$ is the gravitational acceleration and l is the length of the inverted pendulum, which in this study correspond to 57.5% of body height (Winter et al., 1990).

ML dynamic stability at foot contact is preserved on the condition that $\mathrm{YcoM_{FC}}$ is within $\mathrm{BOS_{ymax}}$, which corresponds to a positive MOS. A negative MOS indicates a ML instability and implies that a corrective action (e.g., in the form of an additional lateral step) is required to maintain balance.

Theoretical Variables

In order to test the validity of the model, the theoretical ML position and velocity of the center of mass at foot contact were computed by implementing the model with the initial center of mass set (ML center of mass position and velocity at foot off) and the swing phase duration obtained in each of the experimental trials. This gave theoretical values which were then compared with the experimental ones. The ML APAs were found to be scaled with swing duration in the experimental conditions (see "Results" Section); thus, these theoretical values are referred to the "theoretical conditions with APAs scaling". The model was then used to assess whether postural stability at foot contact would be degraded if the ML APAs were not scaled to swing duration, i.e., if there was no adaptation of the initial center of mass set to the obstacle height and distance. For this purpose, the theoretical ML position and velocity of

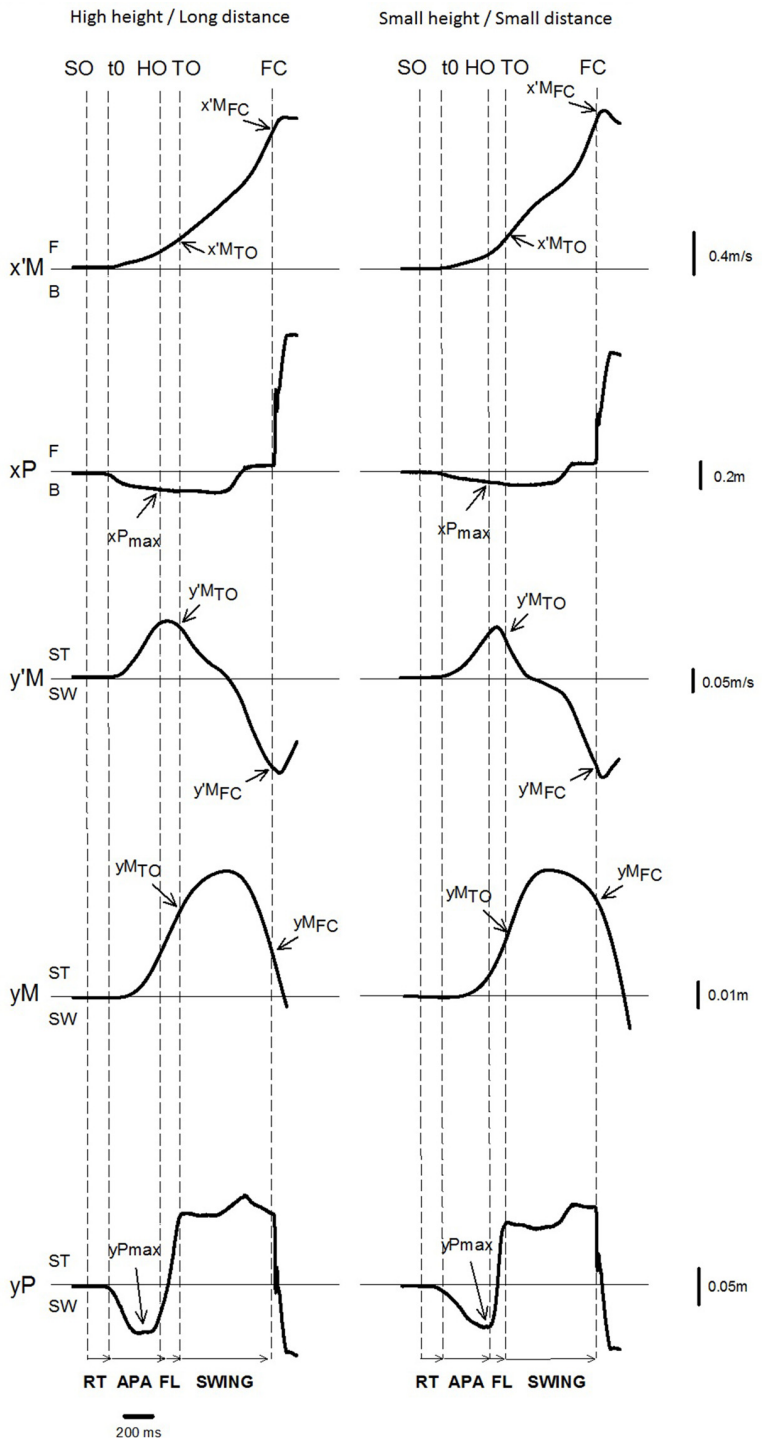

FIGURE 3 | Example of biomechanical traces and representation of the main experimental variables obtained for one representative subject initiating gait (one trial) in the reaction-time condition with the high height/long distance condition (left) and the small height/small distance condition (right). *Anteroposterior (AP) direction* x′M: center of mass (COM) velocity; $x'M_{TO}$, $x'M_{FC}$: COM velocity at foot off and at foot contact. xP: center of pressure (COP) displacement; *x*Pmax: peak of COP displacement during APAs; F: forward; B: backward. *Mediolateral (ML) direction* y′M: ML COM velocity; $y'M_{TO}$, $y'M_{FC:}$ COM velocity at foot off and foot contact; yM: ML COM displacement; yM_{FC}: COM displacement at foot contact; yP: ML COP displacement; yPmax: peak of COP displacement during APAs; and ST: stance limb; SW: swing limb. *Vertical dashed lines* SO: Go signal onset (in the reaction-time condition only); t_0 onset variation of biomechanical traces; HO: swing heel off; FO: swing foot off; FC: swing foot contact. *Horizontal arrows*: RT: time-windows for reaction-time; APA: anticipatory postural adjustments FL: foot lift; SWING: swing phase.

the center of mass at foot contact were again computed, but this time by implementing the model with: (i) the mean ML position and velocity of the center of mass at foot off obtained for each subject in the reaction-time and self-initiated obstacle-free (control) conditions; and (ii) the swing phase duration obtained in each experimental trial. The theoretical extrapolated center of mass position and the theoretical MOS at foot contact were then calculated by following the same procedure used for the experimental data. The theoretical values obtained with this procedure are referred to as the "theoretical conditions without APA scaling".

Statistics

Mean values and standard deviations were calculated for each variable in the experimental and theoretical conditions. The normality of data was checked using the Kolmogorov-Smirnov test and the homogeneity of variances was checked using the Bartlett test. To test the influence of obstacle height, obstacle distance and temporal pressure, a [3 ("obstacle height": 2.5%, 5% and 10% of the subject's height) × 3 ("obstacle distance": 10%, 20% and 30% of the subject's height) × 2 ("temporal pressure": reaction-time and self-initiated)] ANOVA with repeated measures was used on each experimental variable.

To test the validity of the model, a [3 ("obstacle height") × 3 ("obstacle distance") × 2 ("temporal pressure") × 2 ("modeling with APAs scaling": experimental conditions vs. theoretical conditions with APA scaling)] was used on the following variables: ML center of mass position and velocity, ML extrapolated center of mass, and MOS at foot contact. Linear correlations between these experimental and theoretical variables were calculated using Pearson's correlation coefficient. Finally, to test the effect of APA scaling on postural stability, a [3 ("obstacle height") × 3 ("obstacle distance") × 2 ("Modeling without APA scaling": experimental conditions vs. theoretical conditions with no APA scaling)] RM ANOVA was used on the following variables: ML center of mass position and velocity, ML extrapolated center of mass, and MOS at foot contact. The alpha level was set at 0.05. A Tukey *post hoc* test was used when necessary.

RESULTS

Description of the Biomechanical Traces in the Experimental Conditions

The time course of the biomechanical traces was globally similar in the different temporal and obstacle conditions. The traces obtained in two representative conditions are reported in **Figure 3**. Swing heel off was systematically preceded by postural dynamics that corresponded to APAs. During these APAs, the center of pressure displacement reached a peak value in a backward direction (see the negative variation of the xP trace in **Figure 3**) and towards the swing leg side (negative variation of the yP trace), while the center of mass velocity was directed forwards (positive variation of the x'M trace) and towards the stance leg side (positive variation of the y'M trace). The ML center of mass velocity trace reached a first peak value towards the stance leg side at around heel off. This trace, then fell towards the swing leg side and a second peak value towards this side was reached a few milliseconds after foot contact. The ML center of mass shift trace was bell-shaped and reached a peak value toward the stance leg side at the beginning of the swing phase. The AP center of mass velocity increased progressively until it reached a peak value a few milliseconds after swing foot contact, while the center of mass was continuously shifted forward. Differences across the conditions are reported in the paragraphs below.

Stability

Height Effect

Stability can be evaluated from foot clearance and the MOS. The risk of the swing foot striking the obstacle, which might then endanger balance, increased as foot clearance decreased. The MOS is used to quantify ML dynamic stability at foot contact. The results showed that the foot clearance significantly decreased with obstacle height ($F_{(2,26)} = 9.25$, $p < 0.001$; **Figure 4**). In contrast, there was no significant effect of the obstacle height on the MOS value ($F_{(2,26)} = 2.57$, $p > 0.05$) and related center of mass components, i.e., the ML center of mass shift ($F_{(2,26)} = 0.31$, $p > 0.05$) and velocity ($F_{(2,26)} = 0.46$, $p > 0.05$), and extrapolated center of mass position at foot contact ($F_{(2,26)} = 1.95$, $p > 0.05$).

Distance Effect

The results showed that foot clearance also significantly decreased with obstacle distance ($F_{(2,26)} = 30.07$, $p < 0.001$; **Figure 4**). There was no effect of the obstacle distance on the MOS ($F_{(2,26)} = 0.01$, $p > 0.05$), the ML center of mass shift ($F_{(2,26)} = 0.99$, $p > 0.05$) and velocity ($F_{(2,26)} = 0.64$, $p > 0.05$), and the extrapolated center of mass position at foot contact ($F_{(2,26)} = 0.11$, $p > 0.05$).

Temporal Pressure Effect

There was no significant effect of the temporal pressure on the following variables: foot clearance ($F_{(1,13)} = 3.77$, $p > 0.05$), MOS value ($F_{(1,13)} = 0.96$, $p > 0.05$), ML center of mass shift ($F_{(1,13)} = 0.95$, $p > 0.05$) and velocity ($F_{(1,13)} = 0.55$, $p > 0.05$) and extrapolated center of mass position at foot contact ($F_{(1,13)} = 0.35$, $p > 0.05$).

Postural and Foot Lift Phase

Height Effect

The results showed that there was a significant effect of the obstacle height on the duration of APAs along the ML axis ($F_{(2,26)} = 5.63$, $p < 0.01$, **Figure 5**) and the AP axis ($F_{(2,26)} = 9.38$, $p < 0.001$), and on the duration of the foot-lift phase ($F_{(2,26)} = 6.18$, $p < 0.01$). Each of these temporal variables decreased when the obstacle height increased. With regard to the spatial variables, results showed that both the peak of anticipatory ML center of pressure shift ($F_{(2,26)} = 21.44$, $p < 0.001$) and the ML center of mass velocity at toe off ($F_{(2,26)} = 4.36$, $p < 0.05$) significantly increased with obstacle height. In contrast, the peak of anticipatory backward center

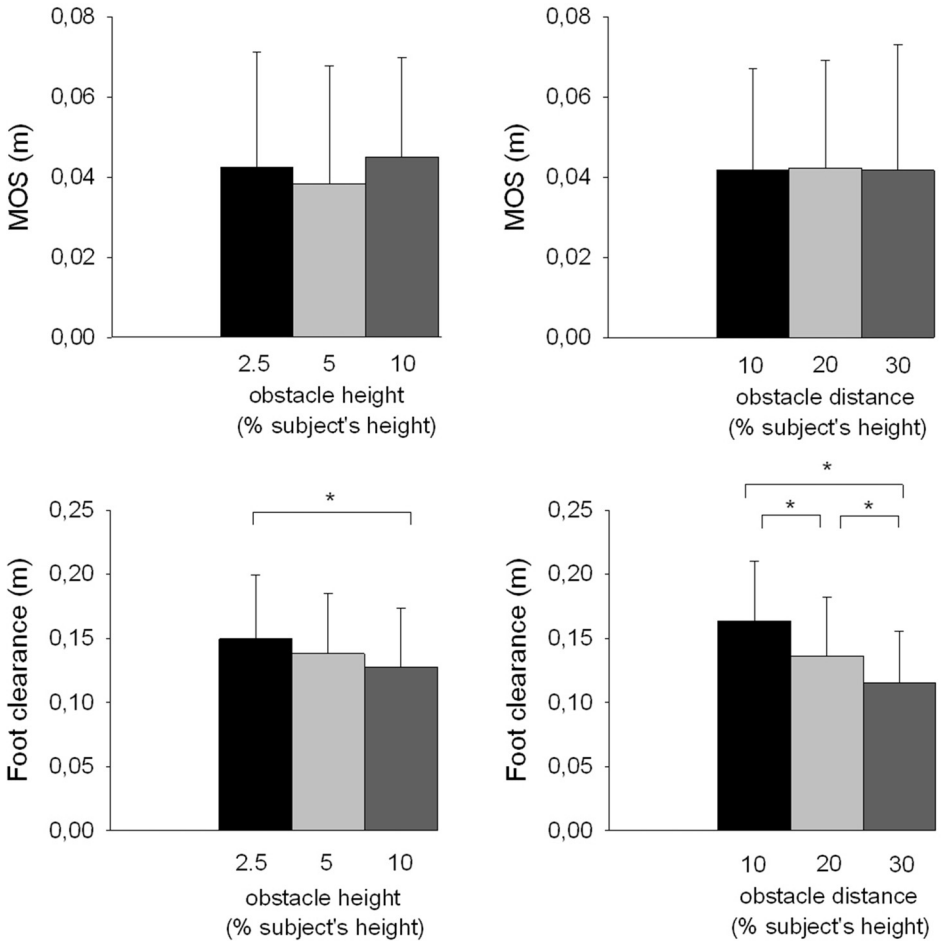

FIGURE 4 | Effects of obstacle height and distance on stability parameters. Reported are mean values (all participants together) ± 1 SD. MOS, margin of stability. *Indicates a significant difference between bars.

of pressure shift ($F_{(2,26)} = 11.43$, $p < 0.001$), the differential between the center of pressure and the center of mass position $F_{(2,26)} = 8.15$, $p < 0.01$) and the forward center of mass velocity at toe off ($F_{(2,26)} = 13.86$, $p < 0.001$) significantly decreased with obstacle height. The obstacle height constraint therefore had a similar effect on the temporal component of APAs along the AP and ML axes, but had an opposite effect on the spatial component of APAs along these two axes.

Distance Effect

Increasing the obstacle distance had a very different effect on the postural and foot lift phases compared with increasing the obstacle height. Indeed, the results showed that obstacle distance had no significant effect on the duration of APAs along the ML axis ($F_{(2,26)} = 1.44$, $p > 0.05$). However, it did have a significant effect on the APA duration along the AP axis ($F_{(2,26)} = 3.77$, $p < 0.05$) and on the duration of the foot lift ($F_{(2,26)} = 21.53$, $p < 0.001$). Specifically, these two variables increased with obstacle distance. The results further showed that there was no significant effect of the obstacle distance on the following spatial variables: peak of anticipatory ML ($F_{(2,26)} = 0.62$, $p > 0.05$) and AP center of pressure shift ($F_{(2,26)} = 1.00$, $p > 0.05$), ML ($F_{(2,26)} = 1.78$, $p > 0.05$) and AP ($F_{(2,26)} = 2.18$, $p > 0.05$) center of mass shift at toe off, and ML center of mass velocity at toe off ($F_{(2,26)} = 1.30$, $p > 0.05$). In contrast, the forward center of mass velocity at toe off increased significantly with obstacle distance ($F_{(2,26)} = 30.51$, $p < 0.001$).

Temporal Pressure Effect

The results showed that the following temporal variables were significantly shorter in the reaction-time block than in the self-initiated block: duration of APAs along the AP axis ($F_{(1,13)} = 61.63$, $p < 0.001$) and ML axis ($F_{(1,13)} = 31.6$, $p < 0.001$), and duration of foot lift ($F_{(1,13)} = 16.99$, $p < 0.01$). The following spatial variables reached a significantly larger value in the reaction-time block than in the self-initiated block: peak of anticipatory ML ($F_{(1,13)} = 20.04$, $p < 0.001$) and AP ($F_{(1,13)} = 41.82$, $p < 0.001$) center of pressure shift, and ML center of mass velocity at foot off ($F_{(1,13)} = 11.60$,

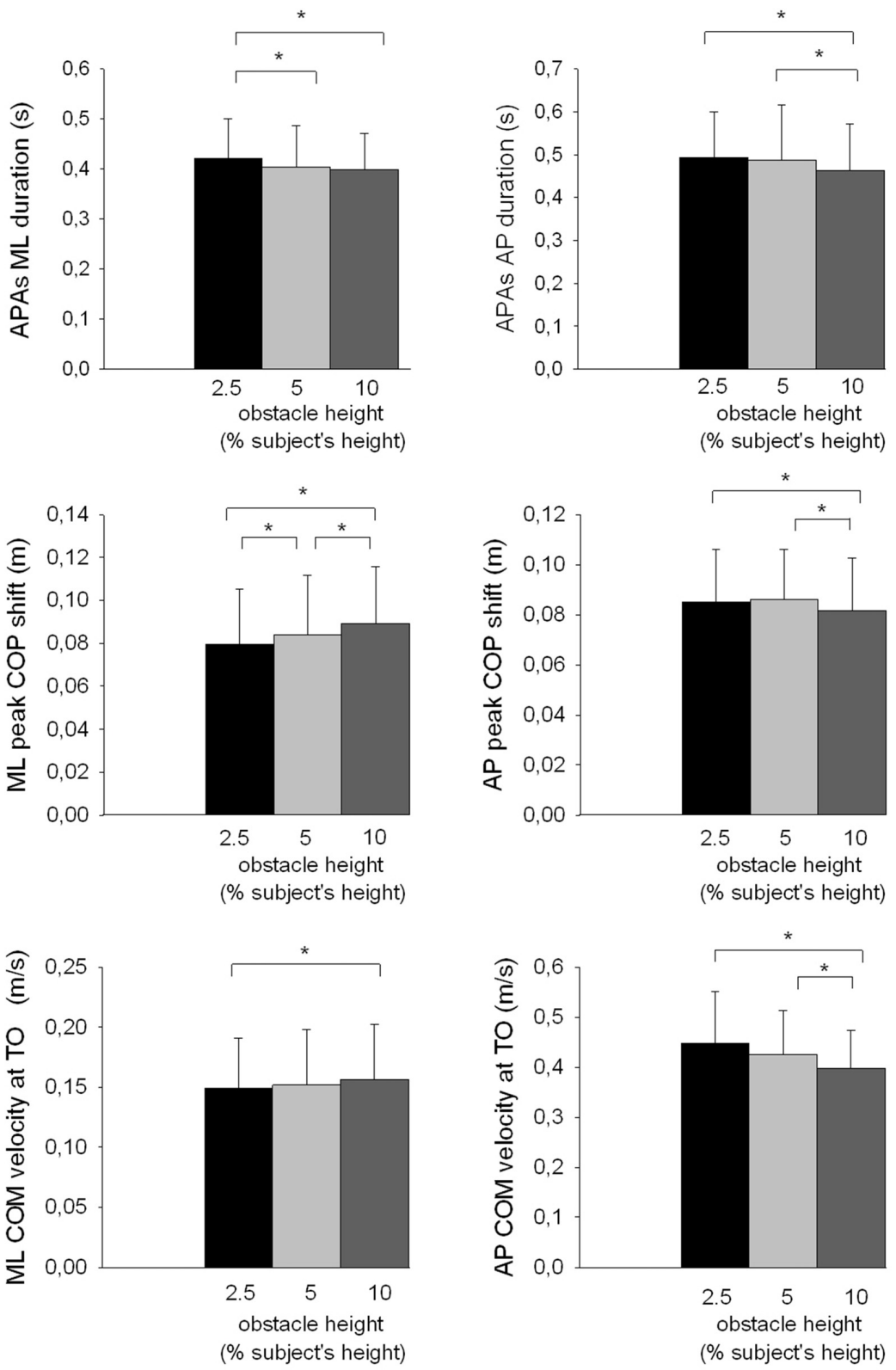

FIGURE 5 | Effects of obstacle height on selected ML and AP postural parameters. Reported are mean values (all participants together) ± 1 SD. APAs, anticipatory postural adjustments; TO, toe off; COP, center of pressure; COM, center of mass. *Indicates a significant difference between bars.

$p < 0.01$). In contrast, the ML ($F_{(1,13)} = 1.98$, $p > 0.05$) and AP ($F_{(1,13)} = 2.45$, $p > 0.05$) shift of the center of mass at foot off were not significantly different for the two temporal pressure blocks.

Swing Phase

Height Effect

The results showed that the duration of the swing phase significantly increased with obstacle height ($F_{(2,26)} = 58.07$, $p < 0.001$). In contrast, there was no significant effect of the obstacle height on the step length ($F_{(2,26)} = 2.77$, $p > 0.05$), step width ($F_{(2,26)} = 0.59$, $p > 0.05$) and motor performance (in terms of forward center of mass velocity at swing foot contact; $F_{(2,26)} = 0.74$, $p > 0.05$). Finally, the results showed that there was no change in swing foot strike patterns with changes to obstacle height; here, subjects landed on the force plate with the heel first in 85% of the trials.

Distance Effect

The results showed that there was no effect of the obstacle distance on the duration of the swing phase ($F_{(2,26)} = 2.57$, $p > 0.05$) and step width $F_{(2,26)} = 0.05$, $p > 0.05$). In contrast, there was a significant effect of the obstacle distance on the step length ($F_{(2,26)} = 23.05$, $p < 0.001$) and motor performance ($F_{(2,26)} = 6.72$, $p < 0.01$). Both variables increased with distance. Finally, the results showed that there was a significant effect of obstacle distance on the foot strike pattern, with the ratio of forefoot strike increasing with obstacle distance ($F_{(2,26)} = 7.37$, $p < 0.01$). This ratio increased from 6.7% for the small distance obstacle condition to 20.7% for the long distance obstacle condition.

Temporal Pressure Effect

The results showed that there was a significant effect of the temporal pressure on the duration of the swing phase ($F_{(1,13)} = 10.81$, $p < 0.01$). This duration was longer in the reaction-time block than in the self-initiated block. In contrast, there was no effect of the temporal pressure on the following variables: step length ($F_{(1,13)} = 0.58$, $p > 0.05$), step width ($F_{(1,13)} = 0.20$, $p > 0.05$), motor performance ($F_{(1,13)} = 0.04$, $p > 0.05$) and foot strike pattern (the mean percentage of the heel-strike pattern was 86%).

Validation of the Mechanical Model

A visual analysis of **Figure 6** illustrates the excellent fit between the experimental traces and those obtained with the mechanical model. The best fit between experimental (dashed line) and theoretical (full line) data was obtained for a stiffness of the hip abductor muscles of about 1000 N/m. This value corroborates with previous data in the literature (Morasso and Schieppati, 1999). This corresponds to a restoring force of approximately $T = 50$ N, applied at the center of mass. This close fit was further strengthened by the finding that there was no significant effect of the factor "modeling with APA scaling" on the MOS and on the related center of mass components. In addition, there was no interaction between this factor and obstacle height, obstacle distance and temporal pressure for any of these variables. In contrast, there was a significant positive correlation between the theoretical data (obtained in the conditions with ML APA scaling) and the experimental data for the MOS ($r = 0.42$, $p < 0.05$), the ML center of mass position ($r = 0.94$, $p < 0.001$) and the ML center of mass velocity ($r = 0.72$, $p < 0.001$) at foot contact. Collectively, these results validate the mechanical model.

Comparison of Experimental Data and Theoretical Data Obtained in the Conditions Without Mediolateral APA Scaling

In the theoretical conditions without ML APA scaling, the same initial ML center of mass set used in the control condition (obstacle-free condition) was introduced into the conditions where an obstacle had to be cleared (see "Materials and Methods" Section). The results showed there was a significant effect of the factor "modeling without APA scaling" on the MOS ($F_{(2,26)} = 4.77$, $p < 0.05$) and with the exception of the ML center of mass position at foot contact ($F_{(2,26)} = 1.63$, $p > 0.05$), on each of the MOS-related center of mass components, i.e., peak of ML velocity ($F_{(2,26)} = 8.73$, $p < 0.001$) and extrapolated center of mass ($F_{(2,26)} = 4.84$, $p < 0.05$) at foot contact. Specifically, the mean MOS value was significantly lower in the theoretical conditions compared with the experimental conditions, and the extrapolated center of mass reached positions closer to the lateral boundary of the base of support. In addition, the peak of ML center of mass velocity at foot contact—which was directed towards the swing leg side—reached a greater value in the theoretical conditions than in the experimental conditions. Also, there was a "modeling without APA scaling" × "obstacle height" interaction on the MOS ($F_{(2,26)} = 4.77$, $p < 0.05$) and on each related variable. Most interestingly, the difference in the MOS value between the experimental and theoretical conditions without APA scaling increased progressively when the obstacle height increased (**Figure 7**). A negative MOS value was even reached for the middle height obstacle. Finally, the results showed that there was no significant "modeling without APA scaling" × "obstacle distance" interaction ($F_{(2,26)} = 0.22$, $p > 0.05$) or "modeling without APA scaling" × "temporal pressure" interaction ($F_{(2,26)} = 0.16$, $p > 0.05$). These results thus illustrate how postural stability can be expected to degrade in cases where ML APAs are not scaled according to swing duration.

DISCUSSION

The goal of the present study was to investigate how the CNS controls postural stability during gait initiation when negotiating obstacles of different heights and distances under low and high temporal pressure constraints. Based on a mechanical model of the body falling laterally under the

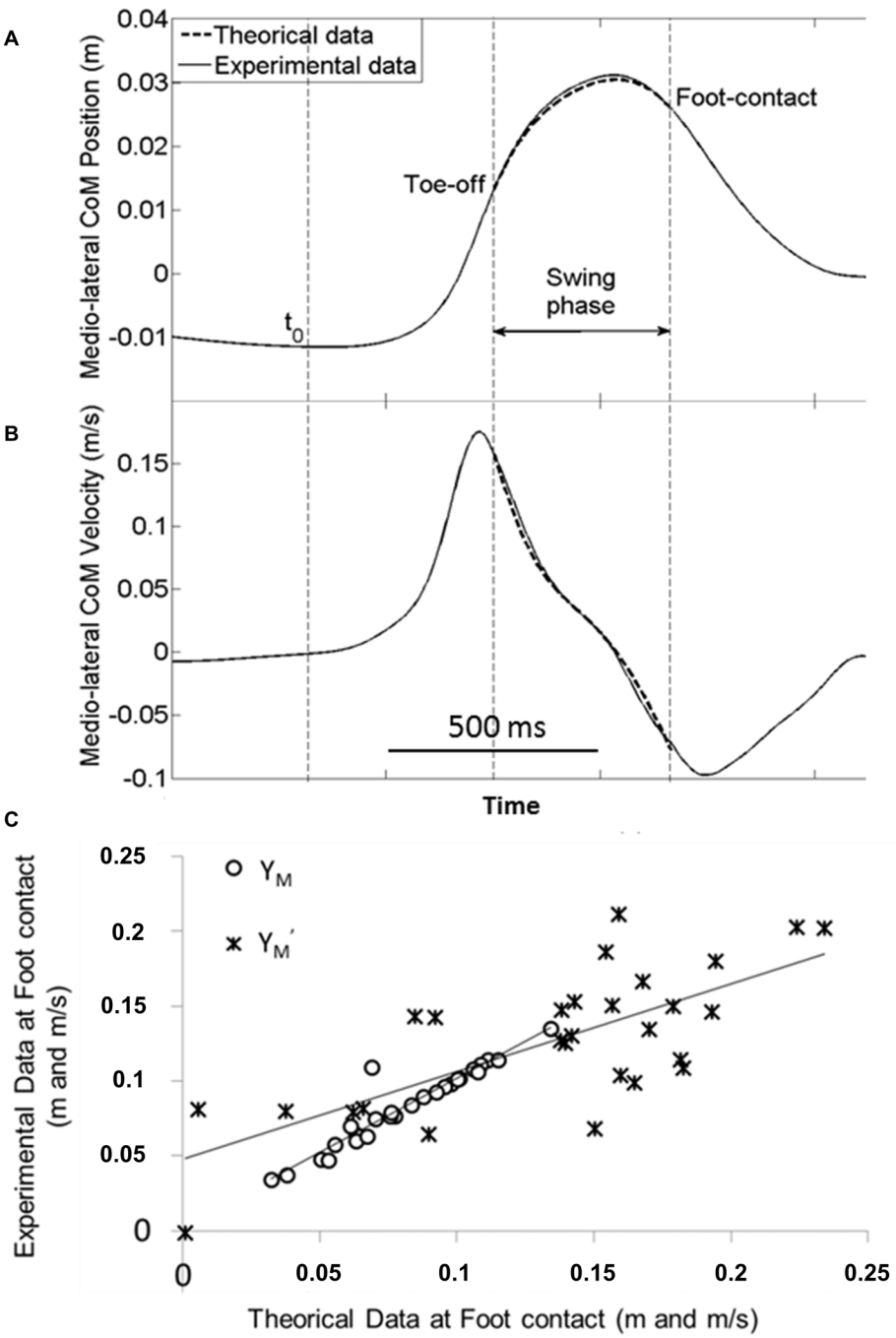

FIGURE 6 | Validation of the mechanical model. Typical experimental (full line) and theoretical (dash line) time-course traces of the ML center of mass shift **(A)** and velocity **(B)** are superimposed during the swing phase (from swing foot off to foot contact). Traces are obtained from one representative subject in the reaction-time condition with the medium height and short distance obstacle. **(C)** Example of linear regression between experimental vs. theoretical data obtained in the obstacle free (control) condition. Each point represents the average value of the ML center of mass position (Y_M) and velocity (Y'_M) at foot contact in the control conditions (self-initiated and reaction-time conditions pooled together) for each of the 14 subjects. Note the excellent fit between the experimental and theoretical data.

influence of gravity and submitted to an elastic restoring force, the functional link between the observed ML APA scaling and the maintenance of postural stability across the experimental conditions was first discussed. This was followed by a discussion of the way in which the AP and ML components of APAs need to be coordinated to ensure safe body progression. Globally, the results illustrate the capacity of the CNS to adapt coordination between the postural and focal

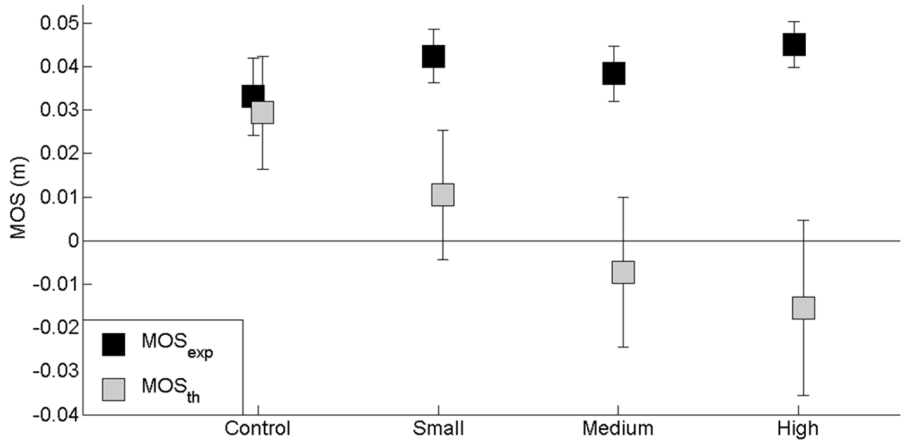

FIGURE 7 | Effects of obstacle height on the experimental (MOS_{exp}) and theoretical (MOS_{th}) "margin of stability" (MOS) values computed in the conditions with no APA scaling. The height of the obstacle is indicated in the abscissa (small, medium and high). In the control condition, there was no obstacle. Reported are mean values (all participants together) ± 1 SD. Note that the experimental MOS values remained unchanged, while theoretical MOS values decreased with obstacle height.

components of a motor task to meet various spatial and temporal constraints.

Scaling Mediolateral APAs to Swing Duration Allows the Maintenance of Postural Stability

As expected, increasing the obstacle height resulted in a significant increase in swing duration (Chou et al., 2001; Hahn and Chou, 2004), thereby mechanically increasing the potential for lateral imbalance during the swing phase of gait initiation. Indeed, previous studies have reported that the swing phase of gait initiation could be assimilated to a ML (Lyon and Day, 1997, 2005) and forward (Lepers and Brenière, 1995) ballistic center of mass fall around the stance ankle, with gravity being the main motor of action. Increasing the duration of this phase may therefore theoretically lead to a larger center of mass motion and velocity at the end of this ballistic phase, i.e., at foot contact. The original model of the whole body falling towards the swing leg side after swing foot off, which was developed in the present study, is in accordance with this statement. Indeed, when the initial center of mass set (i.e., center of mass shift and velocity at foot off) remained the same as in the obstacle-free condition, it was found that artificially increasing the swing phase duration directly impacted on the center of mass set at foot contact. As a consequence, postural stability at this instant was degraded, as revealed by a decrease in the theoretical MOS values. In contrast to this effect of obstacle height, increasing the obstacle distance did not result in any significant change in the swing phase duration. This is coherent with the finding that both step length and step velocity increased with obstacle distance. Thus, as expected, the theoretical center of mass set at foot contact and the related degree of postural stability remained unchanged when this distance increased.

Although the theoretical model revealed the potential for increased instability with obstacle height, the results obtained in the experimental conditions showed that there was no main effect of obstacle height on the center of mass set at foot contact and on the related level of stability. Similar findings were observed in recent studies (Chou et al., 2001; Hahn and Chou, 2004) that examined the clearance of obstacles of varying height during steady walking. This led the authors to suggest the existence of some forms of adaptive postural mechanisms, although these mechanisms were not described. The present results show that the anticipatory peak of ML center of pressure shift increased along with obstacle height. This increase is responsible for a subsequent increase in the ML center of mass velocity at toe off. As stated above, it is clear from the theoretical model that if such an increase in the initial center of mass set had not occurred when the obstacle height increased, a lower state of postural stability would have been reached at foot contact, as shown by the lower theoretical MOS values. Thus, in order to maintain an equivalent stability in the experimental conditions, the additive strategy would be needed to compensate for insufficient APAs, e.g., in the form of lateral stepping so as to increase the base of support width (Zettel et al., 2002; Caderby et al., 2014). If this is still insufficient, because not enough time is available to position the swing foot laterally, a strategy of lateral leg crossover stepping, linked with a high risk of lateral falling (Patton et al., 2006), may be necessary to recover balance. Our results thus show that the CNS precisely scales the ML APAs to the duration of the swing phase, so as to maintain an equivalent postural stability at foot contact across the experimental conditions. The finding that obstacle distance had no influence on ML APAs parameters and the related initial center of mass set (in contrast with obstacle height) is in line with this statement, because swing duration did not vary with this obstacle feature.

The present findings are in accordance with the notion that postural stability at the end of a voluntary leg movement is a

major parameter taken into account during the programming of APAs (Do et al., 1991; Nouillot et al., 2000). Do et al. (1991) used a lower limb flexion-extension executed as fast as possible to test the influence of final stability on APAs. The initial body posture was bipedal, while the final one was either bipedal (stable posture) or unipedal (unstable posture). The biomechanical and electromyographic data showed that ML APAs were larger when the final posture was unstable, because of the need to propel the center of mass further (i.e., above the stance foot) to maintain stability in the final posture. Similarly, the amplitude of the ML APAs in the present study increased along with the potential for instability at foot contact, which corresponded to the end of the gait initiation process. In contrast to the study by Do et al. (1991), the potential for increased instability at the end of gait initiation was masked in our study, because the MOS remained the same across the experimental conditions. A similar remark can be made with regard to previous studies which focused on the effect of various environmental (Chou et al., 2001; Hahn and Chou, 2004; Yiou et al., 2011, 2016) or temporal constraints (Yiou et al., 2012b; Hussein et al., 2013; Caderby et al., 2014) on the control of ML stability during dynamic tasks (e.g., leg flexion, gait initiation and steady walking). In the present study, this potential for instability was revealed in the theoretical trials, where it was found that without APA scaling the MOS values decreased when obstacle height was increased. The present results thus demonstrate the imperative need to adequately scale the ML APAs features to the swing phase duration in order to maintain an optimal stability. Moreover, the invariance of the MOS value across the experimental conditions, despite the presence of potential instability, adds to the growing evidence that this parameter may function as a balance control parameter, as previously suggested in the literature (e.g., Yiou et al., 2011, 2012b; Caderby et al., 2014; Nakano et al., 2016).

This invariance implies that the CNS is able to precisely predict the potential instability elicited by obstacle clearance and that it scales the spatiotemporal parameters of the ML APAs accordingly. The results of this study are thus in accordance with the view that in programming APAs, the CNS uses internal models that takes into account the dynamic consequences of an expected perturbation and generates responses to counter their effect (e.g., Flanagan and Wing, 1997; Wing et al., 1997). More specifically, internal models would be used to predict the effect of the gravitational forces acting on the whole-body during obstacle clearance. This prediction would serve to program, adaptive APAs so as to maintain unchanged stability despite the variations in obstacle constraints. The notion that internal models integrate external forces (such as gravity or Coriolis forces) acting on body segments to plan and execute movements, has been classically proposed for various voluntary upper limb movements, such as grip force with load during object manipulation (e.g., Johansson and Cole, 1992; Flanagan and Wing, 1997; Kawato, 1999; Wolpert and Flanagan, 2001), arm movement in the vertical plane (e.g., Papaxanthis et al., 2005; Gaveau and Papaxanthis, 2011), arm reaching (Cohn et al., 2000) etc. The results of the current study further suggest that such internal models of gravity may also be used to plan and execute the postural component of a whole body motor task.

Coordination Between Mediolateral and Anteroposterior Components of APAs Allows Safe Body Progression

Surprisingly, the results also showed that the duration of both the ML APAs and the foot lift phase decreased with obstacle height. Less time was therefore allocated by participants to propelling the center of mass laterally before triggering the ballistic phase of gait initiation. This reduction in time may seem at odds with the need to increase the ML center of mass set at foot off, as argued above. We propose that it is linked to the spatial constraints exerted on the progression velocity in the AP direction. It can indeed reasonably be speculated that delaying the time of swing foot off in the presence of a high obstacle would increase the forward fall of the center of mass (allowing participants to get closer to the obstacle), as well as the amplitude of the forward center of mass velocity at foot off (Lepers and Brenière, 1995). By so doing, less time would then be allocated for clearing the obstacle with the trailing leg during the following swing phase, with a consequent increased risk of tripping over the obstacle. Instead, the results showed that the forward center of mass shift and velocity at foot off both decreased with obstacle height, which might be a combined effect of this shortened delay for swing foot off with the reduced amplitude of the anticipatory backward center of pressure shift. The amplitude of AP and ML APAs were thus both scaled according to swing duration but in an opposite way. Note that a similar strategy for AP APAs attenuation has already been reported in a study that compared stepping over an obstacle in reaction to rapid surface translation with stepping when there is no obstacle to be cleared (Zettel et al., 2002). The reduction in time taken to lift the swing foot might reflect a protective strategy directed to clear the obstacle safely by reducing the chances of contact between the trailing leg and the obstacle. It is however noteworthy that the vertical distance between the swing foot and the top of the obstacle at the time of obstacle clearance (i.e., the "foot clearance") decreased with obstacle height. In our trials, we did not observe any obstacle contact; thus, we believe that the obstacle (height and distance) and the velocity constraints of the present study were not putting young, healthy participants at risk of forward tripping.

Given the precise scaling of the initial ML center of mass set required to maintain stability across the obstacle conditions (see **Figure 7**), the present findings suggest that the CNS must necessarily have taken into account the reduction in time allocated to lift the swing foot to program the ML APAs' amplitude. Part of the observed increase in the peak of anticipatory ML center of pressure shift may therefore serve to compensate for this shortened duration so that an adequate initial ML center of mass set can be reached to maintain stability. In other words, it is likely that constraints imposed on the progression direction (which are likely responsible for the reduction in time allocated for swing toe off, as argued above) were integrated into the programming of APAs in the ML direction. This statement adds to the growing evidence that the CNS exerts a global control over the anticipatory postural dynamics in the horizontal plane (Caderby et al., 2014) rather than an independent control of APAs along the AP and ML

axes and on the associated postural function (forward body progression and ML stability, respectively). This coordination between the ML and AP components of APAs thus seems to be an imperative condition for both safely clearing the obstacle and reaching a stable state at foot contact. Thus, in addition to the need to coordinate each postural component of the task (the AP and the ML postural components) with the focal one, the CNS also needs to coordinate the postural components between them so that participants can safely clear the obstacle.

Temporal Pressure-Induced Adaptive Changes of Mediolateral and Anteroposterior APAs

Compensation for a reduced ML APAs duration by an increase in the ML APAs amplitude was found in the present study when comparing the high and low temporal pressure conditions. Specifically, the duration of APAs in the high pressure condition was shorter and the peaks of anticipatory ML and AP center of pressure shift were larger than in the low pressure condition. A similar effect of temporal pressure was previously reported in the literature for various stepping tasks such as gait initiation with or without an obstacle to clear (Yiou et al., 2016), or rapid leg flexion (Yiou et al., 2012b; Hussein et al., 2013). It is presumed that these changes in the spatiotemporal APAs parameters under high temporal pressure reflect a strategy to hasten the onset of the voluntary movement (swing foot off) so as to meet the instruction to initiate the step as soon as possible after the GO signal, while maintaining the same stability and progression velocity. Obstacle height and temporal pressure, thus induced similar adaptive changes in the ML APAs parameters. This similitude could be explained by the fact that increasing the obstacle height and the temporal pressure level both required an earlier swing foot off and induced a longer swing phase duration. For this reason, combining these two constraints in one single condition (i.e., clearing a high obstacle within a high temporal pressure) may have been particularly challenging for the postural control system. The fact that postural stability was maintained in such a challenging condition further reveals the adaptability of this system.

The present results may be discussed in regards to recent studies which focused on the effect of temporal pressure on ML stability during ongoing walking with the goal to cross an obstacle (e.g., Moraes et al., 2007; Nakano et al., 2015, 2016). In these studies, participants avoided a virtual planar obstacle that could suddenly appear one step before the obstacle crossing, thus inducing a temporal pressure. In the condition without temporal pressure (control condition), the obstacle could be seen by participants when they stood in their initial posture. Under temporal pressure, the authors found that the extrapolated center of mass position at the swing foot contact was located further toward the swing leg side as compared to the control condition. The MOS however, remained unchanged because of a greater lateral step placement. In the present study, no such effect of temporal pressure on the actual and extrapolated center of mass position or on foot placement was observed. The MOS and the related center of mass components remained, however the same as in the low temporal pressure condition. This invariance was due to the above reported changes in APAs parameters with temporal pressure. These discrepancies between the present study and the literature might possibly be ascribed to the time allocated to plan an efficient anticipatory strategy to maintain postural stability. In the present study, participants could indeed visually catch the features of the obstacle largely before the imperative "go" signal in the high pressure condition. In other words, they had plenty of time to predict the postural disturbance associated with the forthcoming task, and they could thus plan the APAs parameters accordingly. In line, MacKinnon et al. (2007) reported that the spatiotemporal features of APAs for gait initiation were progressively assembled before the deliverance of the "go" signal. In contrast, in the above reported studies, the obstacle appeared just one step before it had to be cleared. Participants had therefore much less time than in the present study to plan in advance the level of anticipatory postural dynamics required to maintain stability at foot-contact. Such a situation may potentially be detrimental to stability since it is known that vision is used in a feedforward rather than in on-line mode to regulate obstacle clearance during ongoing locomotion (Patla and Vickers, 1997). To maintain stability, participants in these studies thus needed to use an additive strategy of lateral foot placement to maintain stability. Future studies will investigate this hypothesis by enabling participants to catch the obstacle features with various delays before and after the deliverance of the "go" signal.

CONCLUSION

The results of this study show that the CNS is able to scale and coordinate the ML and AP components of APAs according to obstacle constraints and related variations in swing duration. This capacity allows participants to safely clear the obstacle and maintain optimal postural stability. These results were strengthened by the findings obtained with the mechanical model, which revealed how stability would be degraded if the ML APAs were not scaled to swing duration. These findings imply that the CNS is able to precisely predict the potential instability elicited by obstacle clearance and that it scales the spatiotemporal parameters of APAs according to this prediction. The results offer a better understanding of how the body adapts to environmental constraints in order to ensure safe and efficient whole-body progression. In a future study, we will investigate the strategies of young, healthy adults and compare them with those adopted by older adults (fallers and non-fallers) in the maintenance of stability in a similarly complex environment.

AUTHOR CONTRIBUTIONS

EY, RA, CT, OL, PF: designed the study; collected, analyzed and interpreted the data; drafted and revised the manuscript; gave final approval.

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Effects of Changing Body Weight Distribution on Mediolateral Stability Control during Gait Initiation

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During gait initiation, anticipatory postural adjustments (APA) precede the execution of the first step. It is generally acknowledged that these APA contribute to forward progression but also serve to stabilize the whole body in the mediolateral direction during step execution. Although previous studies have shown that changes in the distribution of body weight between both legs influence motor performance during gait initiation, it is not known whether and how such changes affect a person's postural stability during this task. The aim of this study was to investigate the effects of changing initial body weight distribution between legs on mediolateral postural stability during gait initiation. Changes in body weight distribution were induced under experimental conditions by modifying the frontal plane distribution of an external load located at the participants' waists. Fifteen healthy adults performed a gait initiation series at a similar speed under three conditions: with the overload evenly distributed over both legs; with the overload strictly distributed over the swing-limb side; and with the overload strictly distributed over the stance-leg side. Our results showed that the mediolateral location of center-of-mass (CoM) during the initial upright posture differed between the experimental conditions, indicating modifications in the initial distribution of body weight between the legs according to the load distribution. While the parameters related to the forward progression remained unchanged, the alterations in body weight distribution elicited adaptive changes in the amplitude of APA in the mediolateral direction (i.e., maximal mediolateral shift of the center of pressure (CoP)), without variation in their duration. Specifically, it was observed that the amplitude of APA was modulated in such a way that mediolateral dynamic stability at swing foot-contact, quantified by the margin of stability (i.e., the distance between the base of support boundary and the extrapolated CoM position), did not vary between the conditions. These findings suggest that APA seem to be scaled as a function of the initial body weight distribution between both legs so as to maintain optimal conditions of stability during gait initiation.

Keywords: anticipatory postural adjustments, postural stability, gait initiation, external load, weight bearing asymmetry, margin of stability, balance

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INTRODUCTION

Gait initiation, which corresponds to the transition from an upright stance to walking, is a locomotor task that is frequently executed in daily life. This task can be decomposed into two successive phases: a "postural phase", which precedes the swing heel-off time, followed by a "step execution phase" (Brenière et al., 1987; Brunt et al., 1999). During the postural phase, dynamic phenomena known as "anticipatory postural adjustments" (APA) are developed along the progression (or anteroposterior) axis (Brenière et al., 1987; Crenna and Frigo, 1991). These APA are manifested by a backwards shift in the center of pressure (CoP), which acts to propel the center of mass (CoM) forwards. It is acknowledged that these anticipatory dynamic phenomena create the conditions that are needed to reach the intended gait speed at the end of the first step (Brenière et al., 1987; Lepers and Brenière, 1995; Michel and Do, 2002).

APA are also described along the mediolateral axis. They are characterized by a CoP shift towards the swing-leg side, which propels the CoM towards the stance-leg side prior to swing foot-off (Jian et al., 1993; Elble et al., 1994). These postural dynamics are known to be crucial for stabilizing the whole body during step execution (McIlroy and Maki, 1999; Rogers et al., 2001; Yiou et al., 2012a). Indeed, the act of lifting the swing foot may create a mediolateral "gap" between the CoM and the CoP, which is then located in a new position beneath the stance foot. This gap may be responsible for a disequilibrium torque, which accelerates the CoM towards the swing-leg side and can potentially lead to a sideways fall. During gait initiation, this disequilibrium torque is invariably attenuated by the CoM displacement towards the stance leg-side during APA. Mediolateral APA are thus generally considered a feed-forward mechanism; one that is responsible for controlling mediolateral stability during gait initiation (McIlroy and Maki, 1999; Mille et al., 2014). Nevertheless, it is noteworthy that the mediolateral swing-foot placement (i.e., step width) may also be modulated in order to control mediolateral stability during gait initiation (Zettel et al., 2002a,b; Caderby et al., 2014). Modulating the swing-foot placement allows the CoM to be repositioned inside the base of support, thus ensuring postural stability.

The question of whether and how the initial body weight distribution between both legs may influence the gait initiation process in able-bodied subjects has been addressed in recent studies (Patchay and Gahéry, 2003; Azuma et al., 2007). In these studies, weight distribution between both legs were experimentally modified by asking subjects to shift their weight either onto the stance leg-side or swing leg-side prior to gait initiation, thus yielding an asymmetrical body weight distribution between the legs. Overall, these studies reported that an increase in the weight distribution over the swing leg-side induced APA of a longer duration, a shorter duration of step execution, and faster forward progression velocity compared with gait initiation performed with a posture with symmetrical body weight distribution over both legs. This effect was reversed when subjects shifted their weight over the stance leg-side. Despite the efforts made by the aforementioned authors, there is still an overall lack of understanding of how initial body weight distribution between the legs influences mediolateral postural stability during gait initiation. Such knowledge would be particularly significant for the prevention of falls, because mediolateral instability is known to be responsible for sideways falls and serious hip fractures (Nevitt and Cummings, 1993; Kannus et al., 2006).

When body weight is positioned closer to the stance leg-side in the initial upright posture, the amplitude of the mediolateral postural dynamics generated during APA needs to be scaled down (when compared with posture with symmetrical body weight distribution) to maintain postural stability during step execution. If it is not, the CoM may be propelled beyond the base of support with the risk of an imbalance towards the stance leg-side. Conversely, when body weight is positioned closer towards the swing leg-side in the initial posture, the amplitude of the mediolateral postural dynamics during APA needs to be scaled up to maintain postural stability during step execution. If it is not, the tendency of the CoM to fall towards the swing leg-side during step execution will be exacerbated, with a potential risk of imbalance. A strategy of increasing step width may then be required to maintain balance. Thus, body weight distribution between both legs can influence mediolateral stability during gait initiation, according to the loaded limb side. Nevertheless, recent results have suggested that the central nervous system is able to modulate the stabilizing features of gait initiation, i.e., mediolateral APA and swing-foot placement, so as to maintain an invariant mediolateral stability in situations with a postural constraint, e.g., induced by a lateral arm motion (Yiou and Do, 2011), an obstacle to clear (Yiou et al., 2016b) or a faster gait speed (Caderby et al., 2014). Therefore, the question arises as to whether such adaptations occur when gait initiation is performed and body weight distribution between both legs is modified.

It should be noted that, in contrast with some specific cases of pathological patients (e.g., patients that have suffered a stroke Marigold and Eng, 2006; Tessem et al., 2007), healthy adults evenly distribute their body weight between both legs during quiet standing (Bouisset and Maton, 1995; Hill and Vandervoort, 1996). In able-bodied subjects, natural posture with asymmetrical body weight distribution between the legs can be found in ecological situations, typically when one side of the body is loaded with an additional mass (e.g., carrying an object with a single hand or a backpack on one shoulder, etc.). Some authors have reported that, under such conditions, CoM location during quiet stance is shifted towards the overloaded limb side (Wu and MacLeod, 2001; Haddad et al., 2011). To our knowledge, although recent studies have investigated the effect of changes in body weight distribution induced by load carriage and by overweight on postural control during various motor tasks (e.g., Li and Aruin, 2007, 2009; Robert et al., 2007; Cau et al., 2014; Chen et al., 2015), no study has sought to examine the effect of changes in body weight distribution between the legs induced by load carriage on postural stability during gait initiation.

Thus, the aim of this study was to investigate the effect of changes in body weight distribution between both legs induced by an external load on mediolateral stability control during gait initiation. Based on previous findings from the literature (Yiou and Do, 2011; Caderby et al., 2014; Yiou et al., 2016b), we hypothesized that healthy young adults would modulate the stabilizing features of gait initiation (i.e., mediolateral APA and/or step width) as a function of initial body weight distribution so that the mediolateral stability remains unchanged.

MATERIALS AND METHODS

Subjects

Fifteen healthy subjects (13 males, 2 females; mean age: 21 ± 2 years, height: 176 ± 9 cm, weight: 70 ± 10 kg) participated in this experiment. All gave written consent after being fully informed of the test procedure, which was approved by the Institutional Review Board for the Protection of Human Research of the University of La Réunion and conducted in accordance with the Declaration of Helsinki.

Experimental Set-Up and Procedure

Gait initiation was performed from a first force-plate located at the beginning of a 5-m walkway. A second force-plate was located immediately in front of this initial force-plate so that the first step naturally landed on it. The two force-plates (40 × 60 cm, AMTI, Watertown, MA, USA), embedded in the walkway, recorded the ground reaction forces and moments at 1000 Hz. Beforehand, a foot switch sensor (25 mm, Biometrics, France) was secured to the first force-plate, under the heel of the subject's swing leg. Force-plate and foot switch signals were synchronized and transmitted to an acquisition system.

Initially, subjects were instructed to stand barefoot in a comfortable and natural upright posture with their arms alongside their trunk. They were asked to stand as still as possible and to fixate their gaze on a target placed at eye level, at a distance of 6 m. After receiving a verbal "all set" signal, subjects initiated gait on their own initiative and continued walking straight ahead to the end of the walkway. The swing leg was selected by the subject and was maintained throughout the experiment. After each trial, the subjects repositioned themselves in the standardized foot position (see McIlroy and Maki, 1997) previously marked on the first force-plate. The experimenter triggered the data acquisition when the subjects were motionless and at least 1 s before the "all set" signal.

Each subject performed a gait initiation series under three experimental conditions (**Figure 1**): with a load symmetrically distributed around the waist (Symmetrical condition), with an asymmetrical load strictly placed over the stance-limb side (Stance condition), and with an asymmetrical load strictly placed over the swing-limb side (Swing condition). The overload consisted of a belt positioned at a height that was close to the subject's body CoM, which in this study corresponded to 57% of the subject's height (Winter, 1990). Weights were attached to this belt ventrally and dorsally in order to reach the desired load. The chosen mass was 10% of the subject's body mass, because this was shown to be sufficient to modify the CoM location in quiet standing (Wu and MacLeod, 2001). In all conditions, the weights were placed symmetrically with respect to the sagittal plane so as avoid modifying the anteroposterior CoM location during the upright posture (Caderby et al., 2013a).

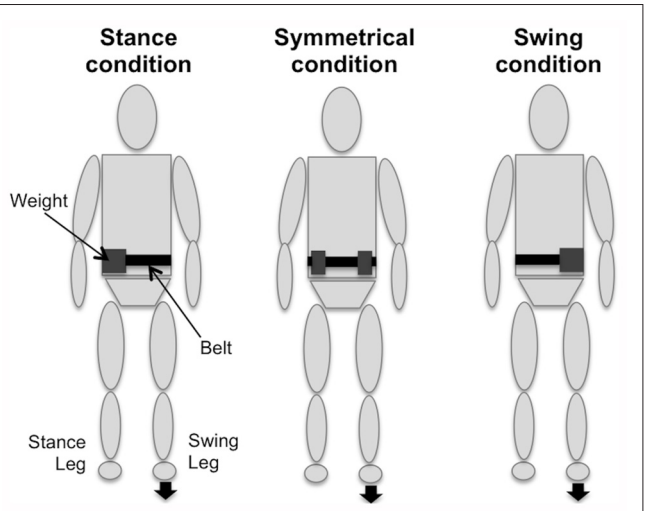

FIGURE 1 | Schematic representation of the various experimental conditions (Stance, Symmetrical and Swing). Note that the weights were ventrally and dorsally added.

To enable a comparison to be made between the various experimental conditions, the subjects were instructed to maintain a similar self-selected gait speed in all conditions. The order of the experimental conditions was randomized across subjects. In each condition, the subjects performed two familiarization trials, followed by eight trials from which data were collected. The subjects rested for 3 min between each condition.

Data Analysis

Before analysis, the force-plate signals were filtered using a low-pass Butterworth filter with a 10 Hz cut-off frequency. The anteroposterior and mediolateral CoP coordinates were calculated from force-plate data in accordance with the manufacturer's instructions (AMTI Manual). The anteroposterior (x"CoM) and mediolateral (y"CoM) accelerations of the CoM were determined from ground reaction forces according to Newton's second law. The anteroposterior and mediolateral CoM velocities and displacements were computed by successive numerical integrations of the corresponding acceleration using the trapezoidal rule. Calculations were performed with integration constant null, i.e., initial velocity and displacement equal to zero (Brenière et al., 1987). By convention, the CoM displacement and velocity and the CoP displacement were considered positive when directed forwards and towards the swing leg-side.

Several temporal events were determined to calculate our various dependent variables. The APA onset was detected when y"CoM deviated 2.5 standard deviations from its baseline value (Yiou et al., 2012b). Time of heel-off was detected from the

foot switch sensor (Caderby et al., 2013b). The instant of swing foot-contact was determined when the vertical force signal of the second force-plate exceeded 10 N. The instant of swing foot-off was identified from the mediolateral CoP displacement (Melzer et al., 2007; Uemura et al., 2011), at the precise point when the slope of the CoP shift toward the stance leg suddenly changed (absolute CoP slope <100 mm/s, 2 samples in a row). The instant of stance foot-off was determined when the vertical force signal of the first force-plate dropped below 5 N.

Dependent Variables

The main dependent variables are illustrated in **Figure 2**. Initial anteroposterior and mediolateral CoM locations were estimated by averaging respectively the anteroposterior and mediolateral CoP positions during the 250 ms period preceding the "all set" signal (McIlroy and Maki, 1999). These initial locations also served as initial constants for computing the CoM position from its displacement during the time course of the gait initiation movement.

APA duration corresponded to the delay between APA onset and the heel-off of the swing leg. Step execution duration corresponded to the time between the swing heel-off and the swing foot-contact. Anteroposterior and mediolateral APA amplitudes were characterized respectively by the maximal backwards CoP shift and the maximal mediolateral CoP shift towards the swing leg during APA. The anteroposterior and mediolateral CoM velocities to time of heel-off and foot-contact were analyzed. Both the peak of mediolateral CoM displacement towards the stance leg during gait initiation and the mediolateral distance between the CoM and the CoP at this instant were calculated. Progression velocity was quantified at the peak of the anteroposterior CoM velocity reached at the end of the first step (Brenière et al., 1987). Step length was calculated as the anteroposterior distance between the CoP position at the swing foot-off time and the stance foot-off time (Gélat et al., 2006).

The concept of "margin of stability" (MoS) introduced by Hof et al. (2005) was used to quantify mediolateral dynamic stability in the present study. The MoS corresponded to the difference between the mediolateral boundary of the base of support (BoS_{ymax}) and the mediolateral position of the "extrapolated CoM" at foot-contact ($YcoM_{FC}$), i.e., $MoS = BoS_{ymax} - YcoM_{FC}$. As in Hof et al. (2005), BoS_{ymax} was determined from CoP data. Specifically, BoS_{ymax} was defined as the mediolateral CoP position at the time of stance foot-off, which at this point was located beneath the swing-foot (Hof et al., 2005). The mediolateral distance between the CoP position at this time (i.e., stance foot-off) and the mean CoP position over the single stance period of the leg stance represented the step width, and was representative of the size of the mediolateral base of support.

Based on the study of Hof et al. (2005), the mediolateral position of the extrapolated CoM at foot-contact ($YcoM_{FC}$) was calculated as follows:

$$YcoM_{FC} = yCoM_{FC} + \frac{y'CoM_{FC}}{\omega_0},$$

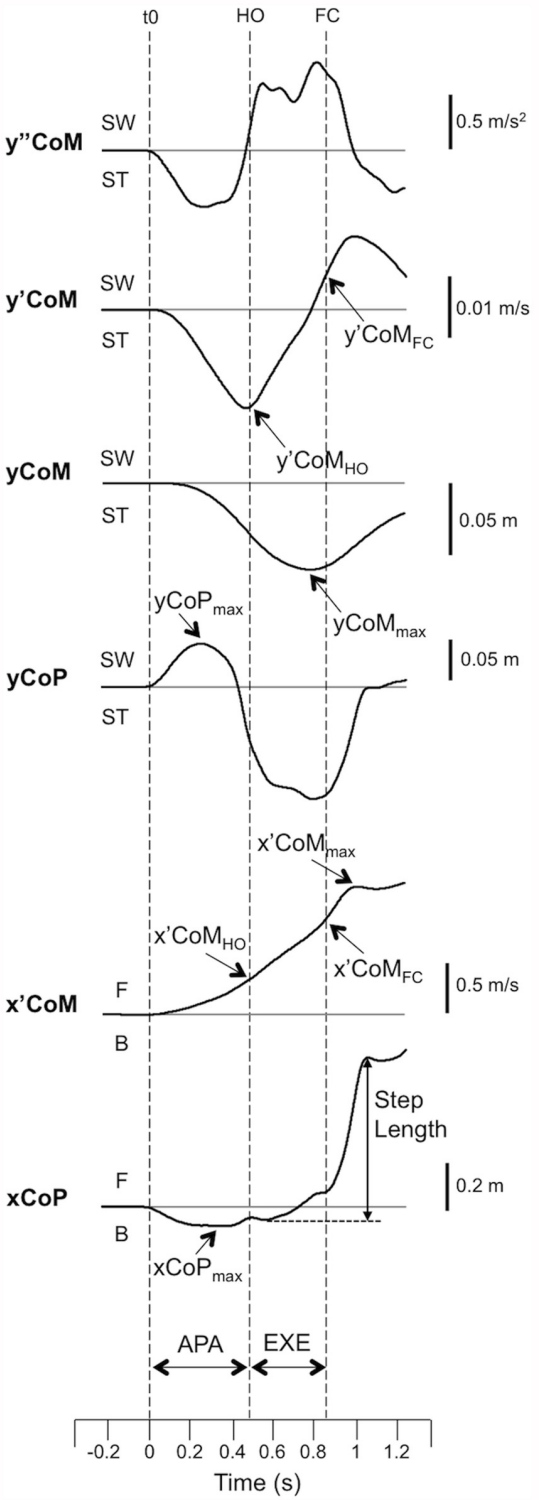

FIGURE 2 | Example of the main biomechanical traces obtained for one subject during gait initiation gait (one trial) under the Symmetrical condition. y"CoM, y'CoM, yCOM, yCoP: mediolateral center-of-mass (CoM) acceleration, velocity and displacement, mediolateral center-of-pressure (CoP) displacement, respectively. x'COM, xCoP: anteroposterior CoM velocity and

(*Continued*)

FIGURE 2 | Continued
anteroposterior CoP displacement, respectively. T0 indicates the onset variation of the y"CoM trace from the baseline. HO and FC: swing heel-off and swing foot-contact, respectively. F and B indicate forward and backward movement, respectively. ST and SW indicate stance limb and swing limb, respectively. $x'CoM_{HO}$, $x'CoM_{FC}$, $x'CoM_{max}$, $xCoP_{max}$: anteroposterior CoM velocity at heel-off, at foot-contact, at the end of the first step and maximal backwards CoP shift, respectively. $y'CoM_{HO}$, $y'CoM_{FC}$, $yCoM_{max}$, $yCoP_{max}$: mediolateral CoM velocities at heel-off, at foot-contact, maximal mediolateral CoM displacement towards the stance leg and maximal mediolateral CoP displacement towards the swing leg during anticipatory postural adjustments (APA). APA and EXE: time windows for APA and step execution.

where $yCoM_{FC}$ and $y'CoM_{FC}$ are respectively the mediolateral CoM position and velocity at foot-contact, and ω_0 is the eigenfrequency of the body modeled as an inverted pendulum, calculated as:

$$\omega_0 = \sqrt{\frac{g}{l}},$$

where g = 9.81 m/s^2 is the gravitational acceleration and l is the length of the inverted pendulum, which in this study corresponded to 57.5% of the body height (Winter, 1990).

Mediolateral dynamic stability at foot-contact is ensured on condition that $YcoM_{HC}$ is within BoS_{ymax}, which corresponds to a positive MoS. A negative MoS indicates mediolateral instability and implies that a corrective action (e.g., in the form of an additional lateral step) has to be undertaken to maintain balance.

Statistical Analysis

Mean and standard deviation values for each dependent variable were calculated over the eight trials performed in each experimental condition. Repeated measures ANOVA with the load distribution condition (Stance, Symmetrical and Swing) as within-subject factors were conducted on each of these variables in turn. For each ANOVA, partial eta-squared value (η_p^2) was presented as a measure of effect size. When a significant statistical difference was found, *post hoc* comparisons were performed using pairwise comparisons with a Holm-Bonferroni correction (Holm, 1979). The level of significance was set at $\alpha = 0.05$.

RESULTS

Description of the Biomechanical Traces

Gait initiation movement globally followed a similar pattern under the various load distribution conditions. This pattern is illustrated in **Figure 2**. The heel-off of the swing leg was systematically preceded by postural dynamics that corresponded to APA. During APA, CoP shifted backwards and laterally towards the swing leg. In the mediolateral direction, CoP displacement reached a peak value towards the swing leg, while CoM displacement and velocity were directed towards the stance leg. The mediolateral CoM velocity trace reached the first peak value towards the stance-leg side at around heel-off. This trace then dropped towards the swing-leg side. The second peak value towards this side was reached a few milliseconds after foot-contact. The CoM displacement reached a peak value towards the stance-leg side during the execution phase. The CoM then fell towards the swing-leg side. In the anteroposterior direction, the CoM velocity increased progressively until it reached a peak value a few milliseconds after foot-contact.

Initial Posture

Load distribution significantly affected the initial CoM location in the mediolateral direction $F_{(1,14)} = 73.34$, $P < 0.001$, $\eta_p^2 = 0.84$), but not along the anteroposterior direction ($P > 0.05$, $\eta_p^2 = 0.02$). *Post hoc* analysis revealed that the initial mediolateral CoM location differed significantly between the three experimental conditions ($P < 0.001$). In the Symmetrical condition, the initial mediolateral CoM location was 0.1 ± 0.7 cm on the swing-leg side with respect to the midline between both feet. This initial mediolateral CoM position (with respect to the midline between both feet) was significantly closer to the swing leg in the Swing condition (0.8 ± 0.7 cm at the swing-leg side), and significantly closer to the stance leg in the Stance condition (0.8 ± 0.8 cm at the stance-leg side) compared with the Symmetrical condition.

Anticipatory Postural Adjustments

No effect of the load distribution was found on APA duration ($P > 0.05$, $\eta_p^2 = 0.17$, **Figure 3**). Similarly, statistical analysis indicated that the load distribution did not affect the maximal backward CoP shift ($P > 0.05$, $\eta_p^2 = 0.02$, **Figure 4**) and the anteroposterior CoM velocity at heel-off ($P > 0.05$, $\eta_p^2 = 0.05$, **Figure 4**), indicating that the anticipatory postural dynamics in the anteroposterior direction were not modified by changes in body weight distribution. In contrast, with regard to the mediolateral postural dynamics, a significant effect of the load distribution was found for the peak of the mediolateral CoP shift during APA ($F_{(1,14)} = 13.46$, $P < 0.001$, $\eta_p^2 = 0.49$) and the mediolateral CoM velocity at heel-off ($F_{(1,14)} = 20.42$, $P < 0.001$, $\eta_p^2 = 0.59$). *Post hoc* analysis indicated that these parameters differed significantly between all of the conditions (**Figure 3**). More specifically, when compared with the Symmetrical condition, these parameters were significantly higher in the Swing condition, and lower in the Stance condition.

Mediolateral Stability

A significant effect of the load distribution was found for the maximal mediolateral CoM displacement towards the stance leg during step execution ($F_{(1,14)} = 22.53$, $P < 0.001$, $\eta_p^2 = 0.62$). Compared with the Symmetrical condition, this parameter was significantly higher in the Swing condition, and significantly lower in the Stance condition (**Figure 5**). Despite these variations, both the mediolateral CoP position ($P > 0.05$, $\eta_p^2 = 0.10$) and the mediolateral gap between the CoP and CoM at the time of maximal mediolateral CoM displacement were unchanged in all of the conditions ($P > 0.05$, $\eta_p^2 = 0.13$, **Figure 5**). A significant effect of the load distribution was also found for the mediolateral CoM velocity at foot-contact ($F_{(1,14)} = 4.65$, $P < 0.05$, $\eta_p^2 = 0.25$). Specifically, the mediolateral CoM velocity was significantly higher in the Stance condition

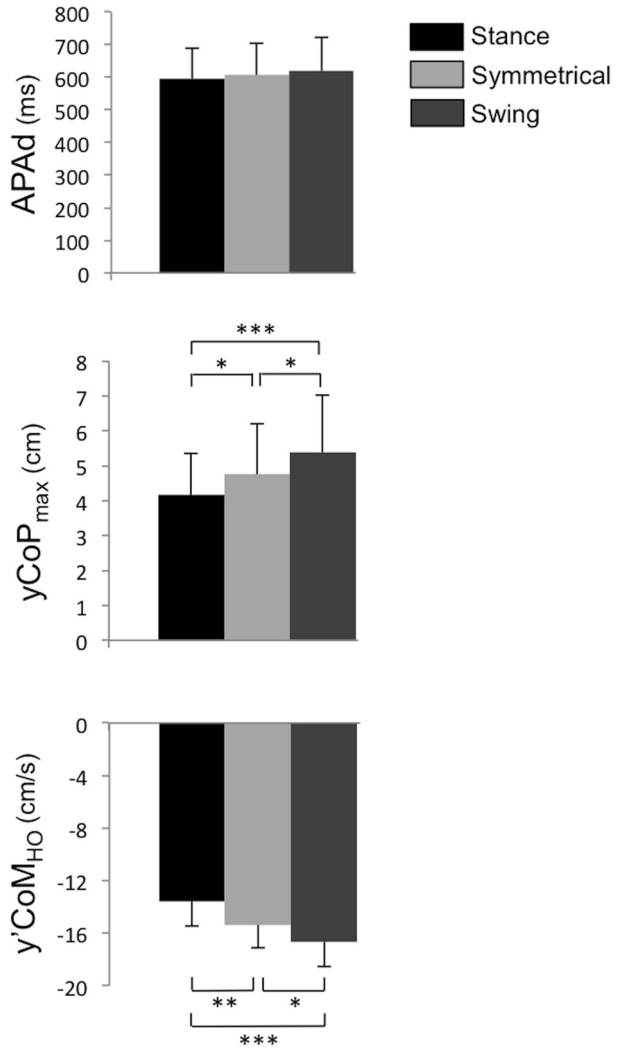

FIGURE 3 | Mean of temporo-spatial features of APA under the Stance, Symmetrical and Swing conditions. APAd: APA duration; $yCoP_{max}$: peak of mediolateral CoP shift towards the swing leg during APA. $y'CoM_{HO}$: mediolateral CoM velocity at heel-off. Negative values indicate a displacement or velocity directed towards the stance leg. *,**,***Significant difference with $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

than in the Swing condition (**Figure 5**), whilst the *post hoc* analysis revealed no other difference. Finally, there was no effect of load distribution on the mediolateral CoM position at foot-contact ($P > 0.05$, $\eta_p^2 = 0.06$, **Figure 5**), the mediolateral position of the extrapolated CoM at foot-contact ($P > 0.05$, $\eta_p^2 = 0.07$, **Figure 5**), the margin of stability ($P > 0.05$, $\eta_p^2 = 0.14$, **Figure 5**), and step width ($P > 0.05$, $\eta_p^2 = 0.03$, **Figure 5**).

Motor Performance

Our results showed that the load distribution had no effect on the parameters related to forward progression (**Figure 4**): the anteroposterior CoM velocity at foot-contact ($P > 0.05$, $\eta_p^2 = 0.17$), the peak of the anteroposterior CoM velocity at the end of the first step ($P > 0.05$, $\eta_p^2 = 0.08$), the duration of step execution ($P > 0.05$, $\eta_p^2 = 0.15$), and the step length ($P > 0.05$, $\eta_p^2 = 0.13$).

DISCUSSION

The aim of this study was to investigate the effects of changing the initial body weight distribution between both legs on the control of mediolateral dynamic stability during gait initiation. Changes in body weight distribution were experimentally induced by modifying the distribution along the frontal plane of an external load located at the participants' waists.

External Load Induced Changes in Body Weight Distribution between Both Legs

The changes in body weight distribution induced by the external load were attested by the significant differences observed in the initial mediolateral CoM location between the various experimental conditions. In the Symmetrical condition, the CoM was almost located at the midline between both feet (0.1 cm from the swing leg), reflecting a quasi-symmetrical body weight distribution between both legs. In the asymmetrical loading conditions (Stance and Swing conditions), we observed that the initial CoM location was significantly shifted towards the overloaded leg side, which is in accordance with previous studies on quiet standing (Wu and MacLeod, 2001; Haddad et al., 2011). This indicates an increase in the body weight distribution over the overloaded leg side. To be precise, the CoM was displaced by ∼0.8 cm on the overloaded side (stance or swing leg) compared with the Symmetrical condition. This finding is in accordance with the deviations observed in the study by Wu and MacLeod (2001) for an asymmetrical load of 10% of body weight (≈1 cm in this previous study). The initial anteroposterior CoM location, in contrast, was not affected by changes in the external load distribution. This suggests that, in the present study, the distribution of body weight along the sagittal plane did not change between the various experimental conditions.

Effects of the Changes in Body Weight Distribution on Mediolateral Dynamic Stability Control

In accordance with our hypothesis, our results showed that the mediolateral dynamic stability at swing foot-contact, quantified by the margin of stability, was unaffected by the changes in the initial body weight distribution. This finding suggests that the subjects developed adaptive postural strategies in order to reach an equivalent mediolateral stability when the initial body weight distribution was modified. It has been shown that mediolateral stability during gait initiation is mainly regulated by the mediolateral APA and the mediolateral swing foot-placement, i.e., the step width (McIlroy and Maki, 1999; Caderby et al., 2014; Yiou et al., 2016a). In the present study, the step width was not

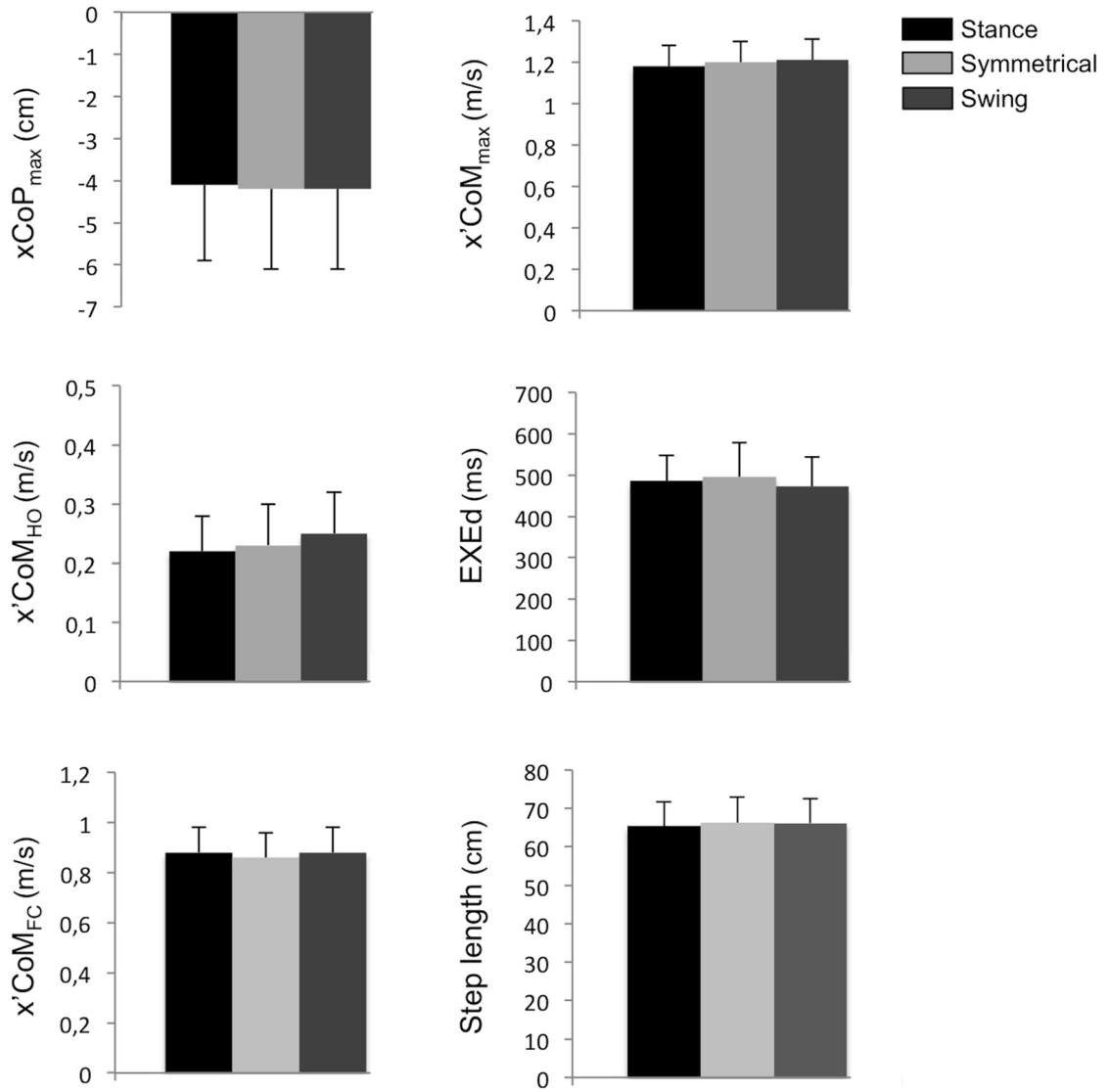

FIGURE 4 | Mean of parameters related to the forward progression under the Stance, Symmetrical and Swing conditions. $xCoP_{max}$: maximal backward shift of the CoP during APA. $x'CoM_{HO}$: anteroposterior velocity of the CoM at heel-off. $x'CoM_{FC}$: anteroposterior CoM velocity at foot-contact. $x'CoM_{max}$: peak of the anteroposterior CoM velocity at the end of the first step. EXEd: duration of step execution. Negative values indicate a displacement or velocity directed backwards.

modified between the various experimental conditions. This implies that other forms of postural adaptations occurred in order to maintain an invariant mediolateral dynamic stability when the body weight distribution between the legs was modified.

It is well known that mediolateral APA, often considered as a lateral thrust exerted on the ground (Mouchnino and Blouin, 2013), serve to propel the CoM towards the stance foot prior to swing foot-off. Although the CoM is never repositioned over the stance foot, mediolateral APA help to minimize the extent to which the body subsequently falls towards the swing-leg side during step execution, i.e., mediolateral instability (Jian et al., 1993; Winter, 1995; Lyon and Day, 1997; McIlroy and Maki, 1999; Rogers et al., 2001; Yiou et al., 2016a). In the present study, the results showed that APA duration, i.e., the time allocated to propel the CoM toward the stance foot, did not differ between the various conditions. In contrast, the amplitude of mediolateral APA, characterized by the peak of mediolateral CoP shift towards the swing leg during APA, varied as a function of the body weight distribution over both legs. Specifically, when compared with the Symmetrical condition, mediolateral APA amplitude increased when body weight was further distributed onto the swing leg (in the Swing condition), and

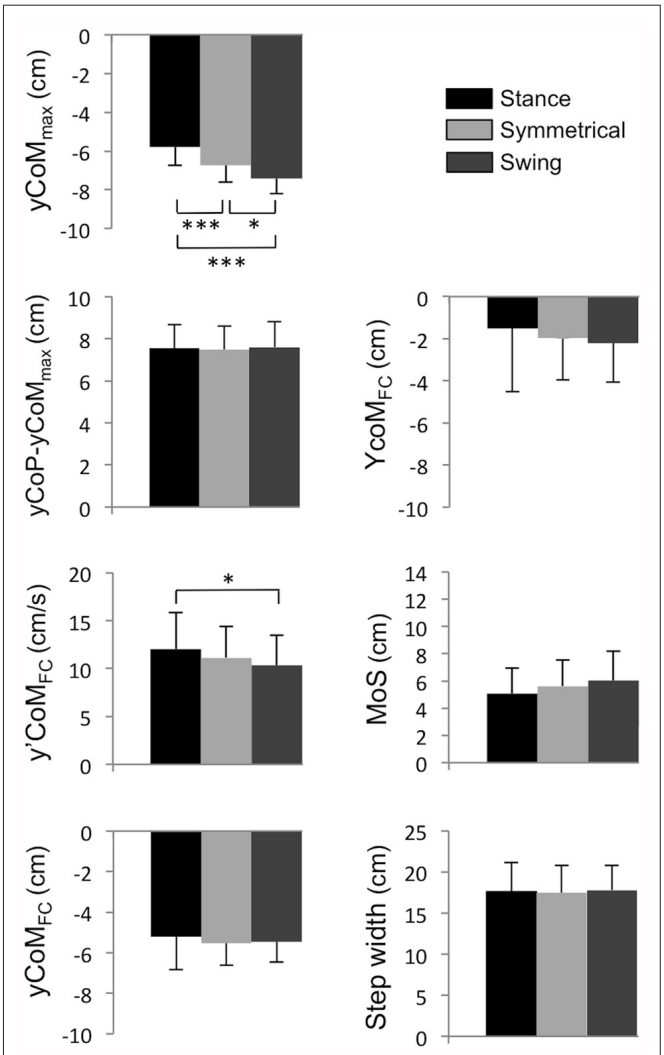

FIGURE 5 | Mean of parameters related to the mediolateral stability under the Stance, Symmetrical and Swing conditions. yCoM$_{max}$: maximal CoM displacement towards the stance leg. yCoP-yCoM$_{max}$: mediolateral distance between CoP and CoM at the instant when the CoM reaches its maximal displacement towards the stance leg. y'CoM$_{FC}$: mediolateral CoM velocity at foot-contact. yCoM$_{FC}$: mediolateral CoM position at the time of foot-contact. YcoM$_{FC}$: mediolateral extrapolated CoM position at the time of foot-contact. Margin of stability (MoS). Negative values indicate a displacement or velocity directed towards the stance leg. *,***Significant difference with $P < 0.05$ and $P < 0.001$, respectively.

decreased when body weight was further distributed onto the stance leg (Stance condition). It has been shown that this anticipatory CoP shift towards the swing leg generates the propulsive forces responsible for accelerating the CoM in the opposite direction, i.e., towards the stance leg (Brenière et al., 1987; Jian et al., 1993; Winter, 1995). Consequently, these modulations in the mediolateral amplitude of APA influenced the propulsion of the CoM towards the stance foot, as attested by the differences in mediolateral CoM velocity at heel-off and the peak of mediolateral CoM displacement towards the stance foot during step execution. To be precise, compared with the Symmetrical condition, both the displacement and velocity of the CoM directed towards the stance leg increased in the Swing condition, and decreased in the Stance condition. Similar findings were observed in previous studies that investigated the effect of body weight distribution between both legs on the gait initiation process (Patchay and Gahéry, 2003; Azuma et al., 2007). However, none of these existing studies established the link between these postural adaptations and mediolateral dynamic stability during gait initiation.

Our results suggest that mediolateral APA changes in the present study aimed to compensate for the differences in the initial CoM location during the upright posture. By modulating the mediolateral APA amplitude, the subjects were able to adapt the propulsive forces so that the CoM reached a similar position relative to the stance foot during the step execution phase. Indeed, we observed that the gap between the CoP and CoM at the time of the maximal mediolateral CoM displacement towards the stance foot during step execution did not vary. This indicates that the CoM was propelled at a similar distance from the stance foot during step execution. As a consequence, the extent that the body fell laterally towards the swing leg, reflected by the mediolateral CoM position at the time of foot-contact, did not change between the various conditions. Thus, we were able to achieve an equivalent extrapolated CoM position at foot-contact in the various conditions, although the mediolateral CoM velocity at foot-contact was slightly higher in the Stance condition than in the Swing condition. In short, these adaptive changes in the mediolateral APA avoided the eventual modulation of the step width to maintain the extrapolated CoM inside the base-of-support. In addition, they helped to maintain the mediolateral stability invariant in the various conditions. These results are in line with findings from previous studies, which have shown that healthy subjects are able to modulate the features of APA in order to maintain an unchanged mediolateral stability when confronted with postural perturbation (Yiou et al., 2012a, 2016b; Caderby et al., 2014). Furthermore, these results reinforce the hypothesis that the extrapolated CoM could be a robust parameter for human balance control (Hasson et al., 2008; Yiou et al., 2012a; Caderby et al., 2014).

Our findings, which show that APA are scaled as a function of body weight distribution between the legs, are congruent with findings from the existing literature on gait initiation (Patchay and Gahéry, 2003; Azuma et al., 2007) for a task that combines stepping and pointing (Robert et al., 2007), and on a leg flexion task (Mille and Mouchnino, 1998). Recent data has provided evidence that cutaneous mechanoreceptors in the sole of the foot may be involved in the setting of APA associated with gait initiation (Mouchnino and Blouin, 2013). These receptors are sensitive to changes in pressure plantar distribution (Kavounoudias et al., 1998), which may be induced by modifications in the body weight distribution between both legs. Thus, it may be assumed that the adaptive APA changes observed in our study were associated with the integrity of these receptors in our healthy young subjects. Further investigations are required to determine

whether the present results are applicable in populations that suffer from a decline in the sensitivity of these plantar receptors, such as elderly people (Wells et al., 2003; Perry, 2006). Specifically, future studies should investigate whether, like young healthy adults, the elderly are able to adapt the APA to changes in body weight distribution between the legs so as to maintain unchanged the mediolateral stability during gait initiation. Such studies may allow to identify abnormalities in the generation of APA under conditions requiring postural adaptation and may thus offer a better understanding of the causes of the frequent falls that occur among the elderly during gait initiation (Robinovitch et al., 2013).

Effects of the Changes in Body Weight Distribution on Motor Performance

Our results indicate that changes in body weight distribution between both legs did not influence the temporal (i.e., duration of APA and step execution) and spatial (i.e., amplitude of anteroposterior APA, step length and anteroposterior CoM velocities at the various selected events) variables related to forward progression. These results are in marked contrast with those from previous studies (Patchay and Gahéry, 2003; Azuma et al., 2007; Dalton et al., 2011), which noted changes in these variables as a function of body weight distribution between both legs. This discrepancy may be explained by the fact that, contrary to these previous studies, the participants of the present study were instructed to maintain a similar progression velocity under the various experimental conditions, as attested by the absence of change in the peak of anteroposterior CoM velocity at the end of the first step. Thus, in our study, it may be assumed that the subjects scaled the temporo-spatial features of gait initiation in such way that forward progression velocity remained equivalent across all conditions. These results support the hypothesis that young healthy adults are able to independently create the conditions for both forward progression and mediolateral stability during gait initiation (Caderby et al., 2014). Interestingly, a recent study has shown that modifications in the body weight distribution over the legs along the anteroposterior direction led to scaling of the amplitude of anteroposterior APA without consistent changes in the amplitude of mediolateral APA (Hansen et al., 2016). These findings suggest that changes in the body weight distribution along the anteroposterior direction might affect the biomechanical organization of gait initiation in that direction, but not in the mediolateral direction. Further investigation is however required to confirm this hypothesis.

Conclusion

The results of the present study highlight that young healthy adults are able to modulate mediolateral APA so as to maintain optimal conditions of dynamic stability during gait initiation with the modification of the initial body weight distribution between both legs. Bearing in mind the fact that elderly people's falls frequently occur during gait initiation, the present findings may provide a basis for future studies that aim to better understand the mechanisms of falls in this population.

AUTHOR CONTRIBUTIONS

TC, EY and GD designed the study. TC, GD and BB collected the data. TC, EY, NP, XV, BB and GD analyzed and interpreted the data, drafted the manuscript and gave final approval.

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frontiers in Human Neuroscience

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Rigid Ankle Foot Orthosis Deteriorates Mediolateral Balance Control and Vertical Braking during Gait Initiation

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Rigid ankle-foot orthoses (AFO) are commonly used for impeding foot drop during the swing phase of gait. They also reduce pain and improve gait kinematics in patients with weakness or loss of integrity of ankle-foot complex structures due to various pathological conditions. However, this comes at the price of constraining ankle joint mobility, which might affect propulsive force generation and balance control. The present study examined the effects of wearing an AFO on biomechanical variables and electromyographic activity of tibialis anterior (TA) and soleus muscles during gait initiation (GI). Nineteen healthy adults participated in the study. They initiated gait at a self-paced speed with no ankle constraint as well as wearing an AFO on the stance leg, or bilaterally. Constraining the stance leg ankle decreased TA activity ipsilaterally during the anticipatory postural adjustment (APA) of GI, and ipsilateral soleus activity during step execution. In the sagittal plane, the decrease in the stance leg TA activity reduced the backward displacement of the center of pressure (CoP) resulting in a reduction of the forward velocity of the center of mass (CoM) measured at foot contact (FC). In the frontal plane, wearing the AFO reduced the displacement of the CoP in the direction of the swing leg during the APA phase. The mediolateral velocity of the CoM increased during single-stance prompting a larger step width to recover balance. During step execution, the CoM vertical downward velocity is normally reduced in order to lessen the impact of the swing leg with the floor and facilitates the rise of the CoM that occurs during the subsequent double-support phase. The reduction in stance leg soleus activity caused by constraining the ankle weakened the vertical braking of the CoM during step execution. This caused the absolute instantaneous vertical velocity of the CoM at FC to be greater in the constrained conditions with respect to the control condition. From a rehabilitation perspective, passively- or actively-powered assistive AFOs could correct for the reduction in muscle activity and enhance balance control during GI of patients.

Keywords: ankle-foot orthosis, ankle rigidity, gait initiation, balance control, vertical braking

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INTRODUCTION

Ankle joint plays a critical role during locomotion and is frequently prone to injury (Fuchs et al., 2003). The "traditional" ankle-foot orthoses (AFO) are rigid and designed to immobilize the ankle joint at a right angle. Such an approach is effective for preventing foot drop during swing phase ensuring toe clearance and proper contact with the heel (Yamamoto et al., 1997; Shorter et al., 2013; Alam et al., 2014). Immobilization of the ankle joint, henceforth referred to as ankle rigidity, has also been documented to reduce pain (Leung and Moseley, 2003; Thoumie et al., 2004; Richie, 2007), stimulate proprioception (Feuerbach et al., 1994; Nigg, 2001; Richie, 2007) and enhance gait for a wide range of patients suffering from severe locomotive disorders (Danielsson and Sunnerhagen, 2004; Lucareli et al., 2007; Wang et al., 2007; Brehm et al., 2008; Abe et al., 2009; Fatone et al., 2009). The current modern design of AFOs include articulated devices capable of assisting plantarflexion during stance. Whereas some studies confirmed the benefits of assistive AFOs (Guillebastre et al., 2009; Bregman et al., 2011; Eddison and Chockalingam, 2013; Petrucci et al., 2013; Kerkum et al., 2014; Kim et al., 2015), other studies have asserted a minimal effect of traditional AFOs on global gait kinematics in hemiplegic patients (Yamamoto et al., 1997; Mulroy et al., 2010). Therefore, taken into consideration the economic cost and the bulkiness of some articulated AFOs, the standard rigid model is still commonly used in rehabilitation practices.

While the effects of wearing AFOs on the general kinematic of gait during steady-state walking have been studied to a certain extent, little is known about their effects on the kinematics and EMG parameters of gait initiation (GI). GI is now a well-established experimental paradigm which has led to numerous fundamental findings. It comprises of an anticipatory postural adjustment (APA) phase and step execution phase (Carlsöö, 1966; Brenière and Do, 1986, 1991; Brenière et al., 1987). In GI, an APA has two objectives. The first is to create a disequilibrium torque in the sagittal plane which allows to initiate forward movement of the center of mass (CoM) from immobile posture. The motor strategy involves inhibition of antigravity background muscle activity of soleus (Sol) and bilateral activation of tibialis anterior (TA) which induce backward displacement of the center of pressure (CoP) relative to CoM, creating the disequilibrium torque (Crenna and Frigo, 1991; Lepers and Brenière, 1995). The magnitude of the disequilibrium torque plays a crucial role in determining global kinematic of GI (Honeine et al., 2014). The second objective of APA is to displace the CoM in the direction of the stance leg prior to step execution (Mille et al., 2014). The CoM lateral displacement towards the swing leg allows modulating the disequilibrium torque in the frontal plane to prevent a rapid medial fall and control mediolateral kinematic variables (Lyon and Day, 1997; Honeine et al., 2016; Yiou et al., 2016a,b). The CoM displacement during APA has been shown to result from loading the swing leg whilst unloading the other (Carlsöö, 1966; Winter, 1995). Loading the swing leg causes the ipsilateral movement of the CoP and contralateral movement of CoM. Honeine et al. (2016) showed that during APA, stance leg TA activity ipsilaterally flexes the knee, contributing to hip abductor activity in loading the swing leg which produces the typical displacement of CoP in the frontal plane. During step execution, stance leg Sol is activated in order to resist the action of gravity and brake the fall of the CoM (Honeine et al., 2013, 2014). Braking the fall of CoM could ease the impact of the swing limb at foot contact (FC), reducing the stress on the leg joints and providing postural stability during the subsequent double-stance phase (Kuo, 2007; Welter et al., 2007; Chong et al., 2009).

Lower leg proprioceptive afferent inputs play a major role in modulating lower leg activity during the APA phase of GI (Ruget et al., 2008, 2010; Mouchnino and Blouin, 2013). By constraining the ankle joint, an AFO would necessarily alter this somatosensory information and could thus have a deteriorating effect on motor performance during APA. Delafontaine et al. (2015) showed that ankle hypomobility induced by means of strapping the joint deteriorated both the APA and step execution phases. In addition, strapping the ankle had a tendency to impair mediolateral balance control and braking of CoM fall during single-stance.

In the present study, we investigated the effect of firm ankle rigidity caused by wearing a solid "standard" AFO on GI. We hypothesized that immobilizing the ankle should cause an ipsilateral reduction in TA dorsiflexor muscle activity during APA and Sol plantarflexor muscle activity during step execution. The reduction in TA activity during APA is expected to produce a reduction in forward and lateral CoM velocity throughout GI (Honeine et al., 2013, 2014, 2016). We also postulate that the reduction in stance leg Sol activity during step execution should impede the braking of the CoM downward fall (Honeine et al., 2013, 2014). If our hypothesis is confirmed, then this study would favor the use of articulated plantar-flexion-assisting AFOs in order to enhance dynamic balance during locomotive tasks of patients.

MATERIALS AND METHODS

Subjects

Nineteen healthy adults (10 men and 9 women, mean age 30.3 ± 4.4 years, height 1.7 ± 0.07 m and body-mass 69.8 ± 6.2 kg) participated in this study. All subjects gave informed written consent as required by the Declaration of Helsinki. The experiment was approved by the local ethic committee of the University Paris-Saclay (EA 4532).

Experimental Protocol

Subjects stood on a force platform (0.9 × 1.80 m, AMTI, Watertown, MA, USA). They were asked to initiate gait at a self-paced speed following an acoustic signal. Subjects were specifically instructed not to start walking in a reaction-time mode, but to start when they felt ready (this usually occurred following an interval of 0.5–1 s). They performed GI under three experimental conditions: GI without wearing an orthosis

(Ctrl), GI while wearing the orthosis on the stance leg ankle (O-St), and GI while wearing the orthoses on both ankles (O-Bi). The order of the conditions was randomly assigned. Before recording, preferential starting leg of the subjects was established. Subjects were asked to stand still eyes closed, and a small thrust was applied to their back forcing them to make a step forward. This was repeated three times. Subjects were instructed to initiate gait with the stepping leg that was used during this test. Each experimental condition comprised 10 trials. Biomechanical variables, obtained from each trial, were calculated (see below). The mean of the 10 trials for each variable was then computed. Subjects were asked to wear everyday sneaker shoes. In the O-St conditions, subjects kept wearing the shoe on the swing side in order to match the elevation of the orthosis and mimic real life situation. A rigid "standard" short ankle foot orthosis ("botte de marche courte MaxTrax® Ankle", Donjoy®) was used in this study (**Figure 1**). The orthosis was designed to prevent plantar/dorsi flexion and eversion/inversion movements of the ankle (Thoumie et al., 2004).

Acquisition and Measurements

Ground reaction forces and CoP data were obtained from the force platform. Surface EMG activity of TA and Sol was recorded using bipolar Ag-AgCl electrodes via wireless preamplifiers (Zero-wire, Aurion, Milan, Italy). Electrode sites and preparation was performed according to the SENIAM protocol (Merletti and Hermens, 2000). EMG raw traces were bandpass filtered (10–500 Hz) with a second order Butterworth no-lag filter. Force platform and EMG data were digitized with an analog to digital converter at a sampling frequency of 1000 Hz and saved on a PC for off-line analysis.

The mediolateral (ML) CoP instantaneous position curve was used to determine the onset of GI ($t0$), first foot off (FO1) and FC, in addition to the second foot off (FO2; **Figure 2**). The instant of $t0$ was determined as the instant when the ML CoP trace deviated 2 standard deviations from its baseline value. The moments of foot offs and that of FC were determined as the local minimums of the second derivative of the ML CoP trace. Visual inspection was conducted on all trials to verify the correctness of the algorithm.

FIGURE 1 | "Standard" short ankle foot orthosis. The figure portrays a frontal and side view of the rigid orthosis that was used in this study. The orthosis can block dorsi- and plantarflexion of the ankle in addition to reducing the eversion and inversion of the foot.

The APA phase was considered to be the time-window spanning from $t0$ until FO1. The step execution phase was considered as the period between foot off and FC. Step length was approximated as the distance between the anteroposterior (AP) position of CoP at the instants of $t0$ and the FO2 (**Figure 2**). Step width was considered to be the distance between the ML position of the CoP at the instants of the FO1 and FO2 (**Figure 2**). The CoM acceleration in the ML and AP directions were calculated by dividing the respective ground reaction forces by the subjects' mass. The CoM vertical acceleration was obtained by subtracting the subjects' bodyweight from the vertical ground reaction force and dividing by the subjects mass. The CoM velocity in all three directions was then obtained by integrating the respective acceleration with respect to time. The magnitude of the vertical braking during step execution was measured as the difference between the minimum vertical velocity of CoM during single support and its vertical velocity at FC (**Figure 3**).

EMG raw traces were rectified and then low-pass filtered at a cut-off frequency of 25 Hz with a no-lag second order Butterworth filter. Amplitudes of EMG activity of each muscle were calculated by integrating the respective EMG filtered trace. Amplitudes of TA activity of both legs were calculated from the moment of onset until the instant of foot off. Amplitudes of stance leg Sol activity were calculated from the moment of onset until the instant of FC. The moment of muscle onset was calculated using a custom-made algorithm based on continuous (Morlet) wavelets transform (see Honeine et al., 2016).

Statistical Analyses

The Shapiro-Wilk test was used to determine if the studied variables were normally distributed. If ShapiroWilk test was significant (i.e., SW-$p < 0.05$), then the hypothesis that the data is normally distributed should be excluded. In the result section, the normality distribution tests are presented in the following condition order: Ctrl, O-St and O-Bi. Repeated-measures analysis of variances (ANOVAs) were used to test the effect of the three experimental conditions on the kinematics and EMG parameters. A significant outcome was followed up with the Bonferroni correction *post hoc* test. The threshold of significance was set at $p < 0.05$.

RESULTS

We first analyzed general kinematic variables of GI. **Table 1** contains the grand mean and standard deviation of the duration of APA and step execution. Wearing the AFO, i.e., in the O-St and O-Bi conditions, had a significant effect on the durations of both the APA and step execution phases (SW-p: 0.16, 0.44, 0.22—$F_{(2,36)} = 38$, $p < 0.001$; SW-p: 0.24, 0.11, 0.82—$F_{(2,36)} = 55$, $p < 0.001$, respectively). *Post hoc* analyses showed that wearing

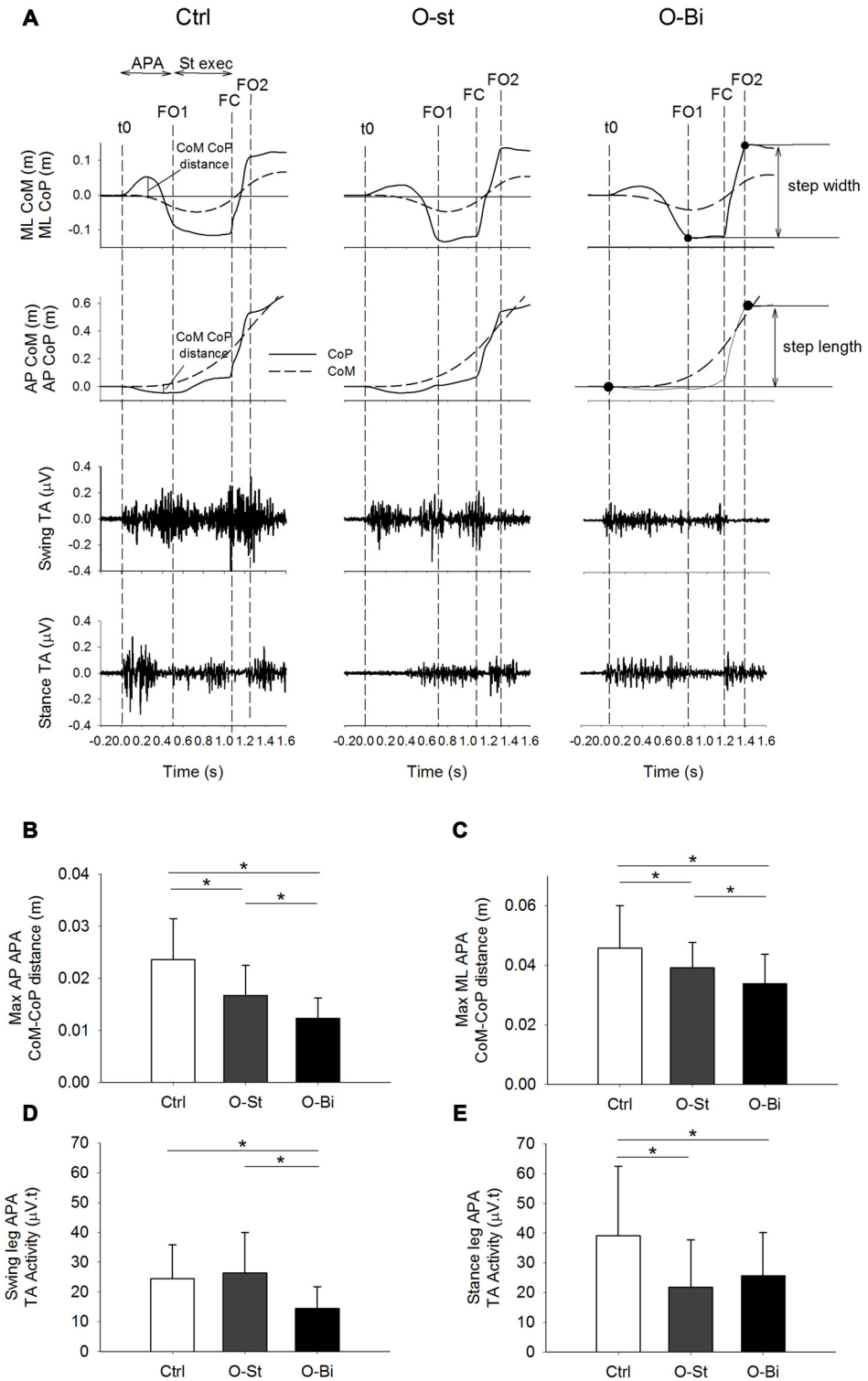

FIGURE 2 | Anteroposterior (AP) and mediolateral (ML) center of mass (CoM)-center of pressure (CoP) distance and the bilateral tibialis anterior (TA) activity. Panel **(A)** shows, from top to bottom the timelines of the ML and AP CoP (solid lines) and CoM (dashed lines) trajectories in addition of the raw traces of swing and stance TA activity during gait initiation (GI). The traces were obtained from a single trial of a representative subject in the Ctrl (left), O-St (middle) and O-Bi (right) conditions. The vertical dash lines represent the instant of *t*0, first foot off (FO1), foot contact (FC) second foot off (FO2). Panels **(B–E)** show the grand means (N = 19) and standard deviations of the maximum AP and ML distance between the CoM and CoP, the swing and stance TA activity. The histograms show that wearing the ankle-foot orthoses (AFO) decreases the activity of TA and ML and AP CoP and CoM excursions. *Indicates significant difference ($p < 0.05$).

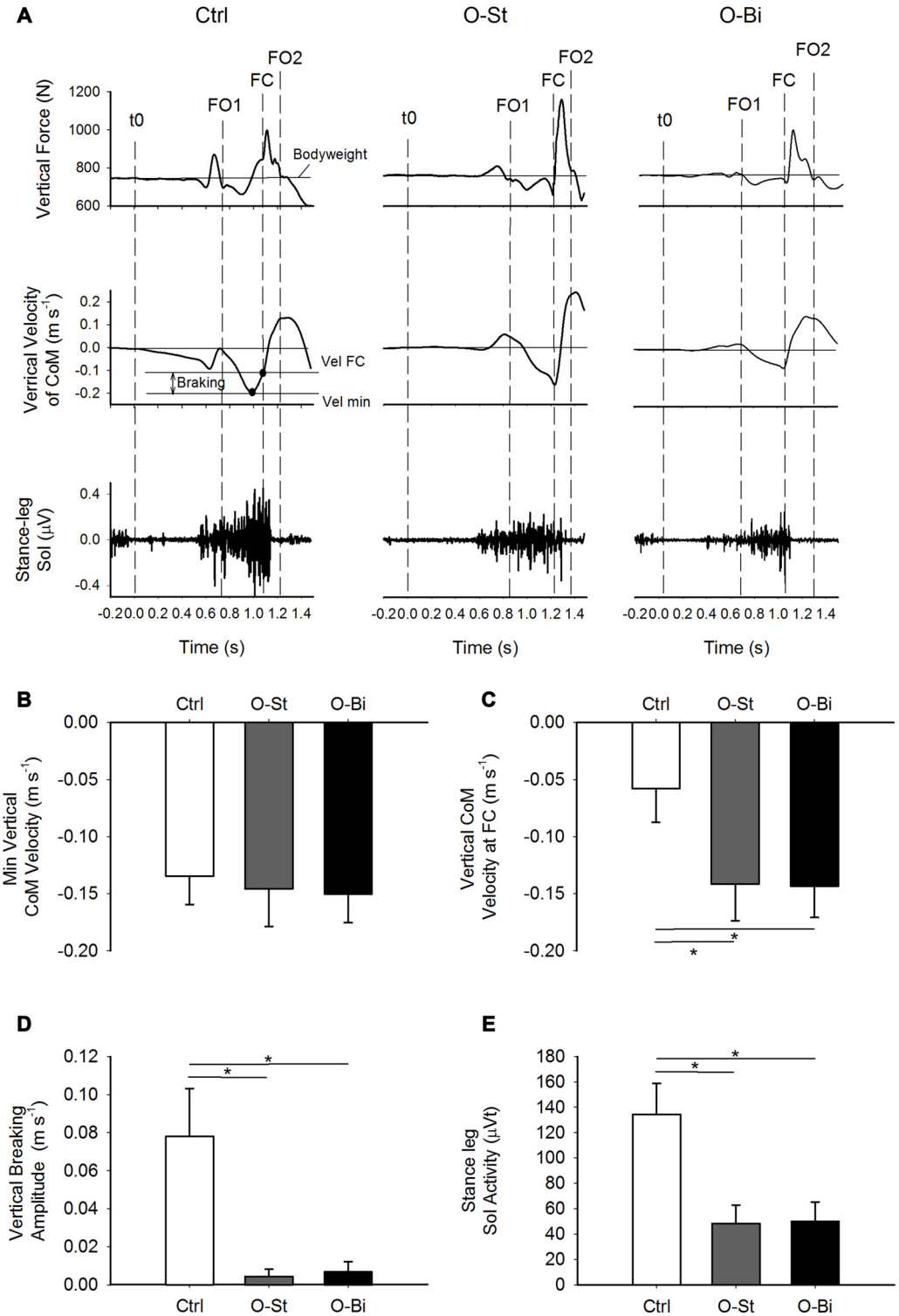

FIGURE 3 | Vertical ground reaction force and CoM velocity and the stance leg Sol activity. Panel **(A)** shows, from top to bottom) the timelines of the vertical ground reaction forces and vertical CoM velocity in addition of the raw traces of stance Sol activity during GI. The traces were obtained from a single trial of a representative subject in the Ctrl (left), O-St (middle) and O-Bi (right) conditions. The vertical dash lines represent the instant of *t*0, first foot off (FO1), FC second foot off (FO2). Panels **(B–E)** show the grand means ($N = 19$) and standard deviations of the minimum vertical velocity of CoM, the vertical velocity of CoM at FC, the vertical braking of CoM vertical fall and the stance Sol activity during step execution. It can be noted that wearing the AFO decreases the activity of Sol, which affects the braking action on the CoM vertical fall. *Indicates significant difference ($p < 0.05$).

TABLE 1 | Grand means (*N* = 19) and standard deviations of the durations of gait initiation (GI) phases.

	Duration of APA (s)	Duration of step execution (s)
Ctrl	0.62 ± 0.04	0.37 ± 0.02
O-St	0.74 ± 0.05*	0.31 ± 0.03*
O-Bi	0.67 ± 0.05*◇	0.38 ± 0.03◇

*Significantly different than Ctrl, ◇significantly different than O-St.

the orthosis increased the duration of APA, more so when the AFO was worn on the stance leg than bilaterally ($p < 0.001$ for both comparisons). The duration of step execution decreased only in the O-St condition ($p < 0.001$).

APA in the Anteroposterior Direction

The time-profiles of the CoM (dashed line) and CoP (solid line) during the first step in the sagittal plane in addition to the TA activity of both legs are presented in **Figure 2A** top panels. The traces were obtained from one subject during all three conditions: Ctrl (left), O-St (middle) and O-Bi (left). As seen in the figure, CoP is displaced backwards during APA. The displacement is accompanied by bilateral activation of the TA muscles. Grand mean and standard deviation of the maximal distance between CoM and CoP during APA in AP direction in addition to the amplitude of EMG activity of both TA muscles are shown in the **Figures 2B,D,E**.

ANOVA showed a significant effect of wearing the orthosis on the maximum CoM-CoP distance in the AP direction during the APA phase (SW-*p* for the Ctrl, O-St and O-Bi respectively: 0.95, 0.18, 0.24—$F_{(2,36)} = 30.3$, $p < 0.001$). *Post hoc* analyses showed that the maximum AP CoM-CoP distances observed during APA were greatest in the Ctrl condition and smallest in the O-Bi condition ($p < 0.05$ for all comparisons). ANOVA also showed an effect of wearing the orthosis on the activity of TA (swing leg: SW-*p*: 0.67, 0.72, 0.15—$F_{(2,36)} = 18.7$, $p < 0.001$; stance leg: SW-*p*: 0.14, 0.31, 0.38—$F_{(2,36)} = 24.4$, $p < 0.001$). *Post hoc* analyses showed that the activity of TA was always smaller when the ankles were constrained by the orthosis with respect to not wearing it ($p < 0.001$ for all comparisons).

APA in the Mediolateral Direction

Figure 2A also portrays the displacement time profiles of the CoM (dashed line) and CoP (solid line) in the frontal plane in all three conditions. During APA, CoP is displaced laterally in the direction of the swing foot. The displacement of CoP causes a movement of the CoM in the opposite direction. ANOVA showed a significant effect of wearing the orthosis on the maximum ML CoM-CoP distance during the APA phase (SW-*p*: 0.16, 0.4, 0.73—$F_{(2,36)} = 21.6$, $p < 0.001$, respectively). *Post hoc* analyses showed that the maximum ML CoM-CoP distances measured during APA were greatest in the Ctrl condition and smallest in the O-Bi condition ($p < 0.05$ for all comparisons). Grand means and standard deviations are shown in **Figure 2C**.

Kinematic Variables of Step Execution

Grand means and standard deviations of the AP and ML velocity of CoM measured at FC, as well as step length, and step width are shown in **Table 2**. Wearing the orthosis significantly changed the instantaneous AP velocity measured at the instant of FC (SW-*p*: 0.19, 0.75, 0.28—$F_{(2,36)} = 37.9$, $p < 0.001$). *Post hoc* tests revealed that the AP velocity of the CoM decreased in both the O-St and O-Bi conditions ($p < 0.001$ in both comparisons). However, the AP CoM velocity was higher in the O-Bi condition with respect to O-St ($p < 0.05$). The orthosis did not modify step length (SW-*p*: 0.46, 0.21, 0.11—$F_{(2,36)} = 0.32$, $p = 0.74$). Wearing the rigid AFO also changed the ML velocity of CoM measured at FC (SW-*p*: 0.07, 0.12, 0.39—$F_{(2,36)} = 60.3$, $p < 0.001$). *Post hoc* analyses showed an increase in ML velocity of the CoM, more so when it was applied bilaterally than to the stance leg alone ($p < 0.05$ for all comparisons). Step width was also significantly affected as a result of wearing the AFO (SW-*p*: 0.47, 0.69, 0.67—$F_{(2,36)} = 55$, $p < 0.001$). *Post hoc* analyses showed that step width increased in O-St with respect to Ctrl and was largest in the O-Bi condition ($p < 0.01$ for both comparisons).

Active Vertical Braking during Step Execution

The time-*p*rofiles of the vertical ground reaction force, the CoM vertical velocity curves (upper panels) and of the EMG activity of the stance leg soleus (lower panels) obtained from one trial of a single subject in the Ctrl (left), O-St (middle) and O-Bi (left) conditions are shown in panel A of **Figure 3**. As can be seen in the figure, following foot off, the CoM accelerated downward (negative velocity indicates downward movement of CoM) and then reversed. In fact, during single support, the CoM velocity shows a "V" shape indicating that the CoM fall was braked. In Ctrl condition, the braking action, which is accompanied by a surge in stance soleus activity, caused a reduction in the absolute of vertical velocity of the CoM measured at FC. In the O-St and O-Bi conditions,

TABLE 2 | Grand means (*N* = 19) and standard deviations of general kinematics variables of GI.

	AP velocity at foot contact (m/s)	ML velocity at foot contact (m/s)	Step length (m)	Step width (m)
Ctrl	1.05 ± 0.10	0.16 ± 0.05	0.55 ± 0.04	0.17 ± 0.04
O-St	0.87 ± 0.11*	0.19 ± 0.06*	0.53 ± 0.05	0.21 ± 0.05*
O-Bi	0.912 ± 0.12*◇	0.23 ± 0.06*◇	0.55 ± 0.07	0.24 ± 0.05*◇

*Significantly different than Ctrl, ◇significantly different than O-St.

the soleus activity of stance leg was reduced and minimum absolute velocity at FC, in most cases, was recorded at FC. This reveals that constraining the stance leg with a rigid AFO has a deteriorating effect on the active vertical braking that occurs during unconstrained GI.

Grand means and standard deviations of the minimum vertical velocity of CoM during single-support, the vertical velocity of CoM measured at the instant of FC, the active vertical braking of CoM and the amplitude of the stance leg Sol activity during single-support are shown in **Figure 3** (lower panels). ANOVA showed no effect of the orthosis on the absolute minimum vertical velocity of CoM during single-support across the conditions (SW-p: 0.34, 0.52, 0.14—$F_{(2,36)} = 0.28$, $p = 0.54$). However, wearing the orthosis had an effect on the vertical velocity of CoM measured at the instant of FC (SW-p: 0.12, 0.6, 0.19—$F_{(2,36)} = 106.7$, $p < 0.001$) and the magnitude of vertical braking of CoM during single-stance (SW-p: 0.52, 0.57, 0.07—$F_{(2,36)} = 266.1$, $p < 0.001$). *Post hoc* analyses revealed that both the absolute vertical velocity of CoM at FC and the amplitude of vertical braking of CoM were significantly smaller in the O-St and O-Bi condition with respect to the Ctrl conditions ($p < 0.001$). *Post hoc* analyses showed that the absolute vertical minimum velocity of CoM and the absolute velocity at FC measured in O-St and O-Bi conditions were comparable ($p > 0.05$). Wearing the orthosis also had an effect on the amplitude of the stance leg Sol activity during single-support (SW-p: 0.18, 0.31, 0.26—$F_{(2,36)} = 101.4$, $p < 0.001$). *Post hoc* analyses showed that the amplitude of the stance leg Sol activity was lowest in the O-St and O-Bi ($p < 0.001$).

DISCUSSION

The results of the present study show that AFOs cause an ipsilateral reduction in TA activity during APA, and ipsilateral decrease of Sol activity during step execution. The decrease in muscle activity is accompanied by a decrease in AP CoM velocity and an increase in ML CoM velocity. In addition, constraining the stance leg ankle joint reduced the vertical braking of the CoM fall that is observed in the single-stance phase of normal GI.

Foot and ankle proprioceptive inputs are known to play a role in modulating lower leg activity during the APA phase of GI (Ruget et al., 2008, 2010; Mouchnino and Blouin, 2013). The modification of lower limb muscle activity in this study may be linked to alteration in the proprioceptive foot and ankle inputs that are caused by constraining the ankle with a rigid AFO. In line with Delafontaine et al. (2015), the reduction in AP velocity measured at FC, with respect to control, is greater in the O-St than in the O-Bi condition. Delafontaine et al. (2015) suggested that the higher AP CoM velocity in the double-constrained condition is probably due to the better capacity of the brain to deal with a symmetrical change of proprioceptive inputs, as opposed to the asymmetrical somatosensory modification that occurs when only one ankle is constrained. The increase in AP velocity in the O-Bi condition could also be caused by adjusting trunk position in order to advance the position of the CoM relative to the base of support and increase forward momentum, which is thought to occur in lower limb amputees (Michel and Do, 2002).

Our evidence that induced stance leg ankle rigidity reduces the activity of the TA is consistent with the results of Geboers et al. (2002). During the APA phase of GI, the bilateral increase in TA activity accompanied by the silencing of both Sol muscles is responsible for generating a forward momentum (Crenna and Frigo, 1991; Honeine et al., 2013, 2014). It may be noted that the decrease in TA activity was compensated by an increase in the duration of APA in order to allow the gravitational torque to accumulate more pace and reach higher forward velocity. Nonetheless, the forward velocity reached at FC when the stance leg was constrained is lower than in the control condition. In addition, Honeine et al. (2016) have shown that TA activity during APA is greater in the stance leg than the contralateral limb. This causes a slight stance leg knee flexion which assists the hip abductor activity in loading the future swing leg and displacing the CoP in the direction of the swinging leg (Carlsöö, 1966; Winter, 1995). In the present study, reduction of the activity of stance TA activity also results in a decrease in ML CoP displacement during APA, corroborating the results of Honeine et al. (2016). In line with Caderby et al. (2014) and Honeine et al. (2016), for the same initial stance width, a smaller CoP displacement during APA causes the ML distance between the CoM and CoP to be larger during the subsequent step execution. This produces a larger gravitational torque during the single-support phase. As a result, the velocity of the medial fall during single-stance increases, prompting a rise in step width to restore stability in the frontal plane.

The results of this study also show that wearing the AFO on the stance leg (i.e., in the O-St and O-Bi condition) reduces the activity of the stance leg soleus EMG during single-support, as shown in studies investigating steady-state walking (Yamamoto et al., 1993; Boninger and Leonard, 1996; Miyazaki et al., 1997; Akizuki et al., 2001). In normal gait, during the single-stance phase, the body rotates around the ankle-forefoot articulation system causing the CoM to accelerate downwards. In healthy individuals, the CoM downward velocity is reduced prior to FC (Chong and Do, 2003). This active braking of CoM during single-stance is the result of triceps-surae activity (Honeine et al., 2013, 2014). In our study, the decrease of the stance leg soleus activity reduces the effectiveness of vertical braking of the CoM fall during the step-execution phase and substantially increases the shock between the swing leg and the ground at FC. In other words, the downward fall of the CoM is halted mechanically by the impact of the swing foot with the ground. On the one hand, Chong and Do (2003) and Welter et al. (2007) state that the main aim of the active braking is to reduce the shock between the heel of the swing leg and the ground. On the other hand, the dynamic inverted pendulum model provided by Kuo (2007) suggest that the vertical braking action observed in late single-stance is required to minimize the work that is necessary to lift the CoM during the subsequent double-support phase. Hence, the triceps surae braking action is necessary for the proper execution of the step-to-step transition.

Furthermore, it should be kept in mind that AFOs are traditionally designed with the main objective of preventing foot-drop in order to allow for toe clearance and promote contacting the floor with the heel instead of the metatarsals (Yamamoto et al., 1997; Shorter et al., 2013; Alam et al., 2014). Nonetheless, many "modern" AFOs have been designed in order to assist plantarflexion. Such devices can be broadly classified into two categories: passive and active devices. Passive AFOs generally employ spring mechanisms in order to store energy during single-stance, later releasing it in order to assist plantarflexion. The types of springs in passive AFO vary from mechanical (Guillebastre et al., 2009), pneumatic (Ferris et al., 2005), carbon composites material (Zou et al., 2014), oil damper (Ohata et al., 2011), and magneto reological damper (Svensson and Holmberg, 2008). Active AFOs operate an actuator in order to perform a torque across the ankle joint. Most common actuators are small electric motors (Bai et al., 2015) or pneumatic pumps (Chin et al., 2009). Furthermore, some actively-powered AFOs are designed to be controlled through EMG activity (Ferris et al., 2005; Cain et al., 2007; Wentink et al., 2013). Such a control system is thought to increase the efficiency of the AFO by enhancing the timing during which the assistive torque is generated (Alam et al., 2014).

Assistive AFOs have been shown to enhance push-off which restores active braking during late single-stance. The effect of those assistive AFOs have been shown to be beneficial for cerebral palsy patients (Eddison and Chockalingam, 2013; Kerkum et al., 2014) and hemiplegic patients following a stroke (Kim et al., 2015). In addition, Bregman et al. (2011) have shown that wearing a spring-assisted AFO decreases the energy cost of gait in stroke patients by about 10%. Their result corroborates with the hypothesis of Kuo (2007) who states that vertical force applied during late single-stance helps to reduce the energetic cost required to raise the CoM during double stance. In addition, Petrucci et al. (2013) showed that mechanically-generating plantarflexion across the swing leg ankle during APA increases the mediolateral displacement of the CoP. It is important to note that the negative effects that were induced by the rigid AFO are comparable to those described in impaired gait consecutive to different diseases. For instance, in hemiparetic stroke subjects, the preparatory ML displacement of CoP is reduced when gait is initiated with the affected limb (Hesse et al., 1997). In addition, progressive supranuclear palsy patients (Welter et al., 2007), parkinsonians (Chastan et al., 2009a,b) and elderly subjects (Chong et al., 2009) have been already documented to have deficits in braking the downward acceleration of the CoM during single-stance. It is thought that such locomotive symptoms are due to supraspinal complications affecting the central command responsible for the proper generation of APA (Rocchi et al., 2012) and step execution (Demain et al., 2014). In this study, a population of healthy young subjects was tested and the effects were obtained by mechanically constraining the ankle joint. Based on our data alone it is not possible to state whether constraining the stance leg further deteriorates the central command of patients which could worsen balance control and the active braking of gait. For instance, Chen et al. (2015) have shown that wearing an anterior (flexible) AFO improves lateral CoM displacement in stroke patients during upright stance. Further research should be performed in order to investigate whether rigid AFO could have an increased negative effect on patients and whether assistive AFO could restore balance control and active braking.

Limitations

Wearing AFO enlarges the area of the base of support of the subjects. In addition, the same AFO was used regardless of the subjects' shoe size. Our present data do not allow to differentiate between the influence of the enlargement of the base of support and that of constraining the ankle. In addition, wearing the AFO also increases the volume of the whole shank. Therefore, it could be possible that the increase in step-width in the O-St and O-Bi conditions is a precautious strategy aimed at preventing the ankle to bump into the AFO or a collision between the two AFOs during the execution of the second step. Future experiments including a variation of initial feet-width and/or wearing slimmer AFOs should untangle this problem. In impaired locomotive neurological patients such as Parkinsonians, this technical problem could have two ambivalent effects. Indeed, it could further deteriorate balance control or improve it, as subjects should walk with enlarged step-width. Future experiments should shed light on this question.

CONCLUSIONS

Blocking ankle movement or limiting it disturbs kinematics gait parameters, balance control in the frontal plane and deteriorates the vertical braking action during single-stance. It would be interesting to test whether utilization of assistive AFO devices could permit to regain normal or nearly normal gait, i.e., walking with normal equilibrium and without ankle pain.

AUTHOR CONTRIBUTIONS

AD contributed with project creation, data collection, data analysis and drafted the manuscript. OG contributed with project creation, data analysis. SC contributed with project creation, data analysis. M-CD and J-LH contributed with project creation, data collection, data analysis. All authors discussed the results and participated in the revision of the manuscript.

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Effect of Experimentally-Induced Trunk Muscular Tensions on the Sit-to-Stand Task Performance and Associated Postural Adjustments

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It has been shown that increased muscular activity along the trunk is likely to impair body balance, but there is little knowledge about its consequences on more dynamic tasks. The purpose of this study was to determine the effect of unilateral and bilateral increases of muscular tension along the trunk on the sit-to-stand task (STS) performance and associated anticipatory postural adjustments (APAs). Twelve healthy females (23 ± 3 years, 163 ± 0.06 cm, 56 ± 9 kg), free of any neurological or musculoskeletal disorders, performed six trials of the STS at maximum speed, in seven experimental conditions varying the muscular tension along each side of the trunk, using a specific bimanual compressive load paradigm. A six-channel force plate was used to calculate the coordinates of the center of pressure (CP) along the anterior-posterior and medial-lateral axes, and the kinematics of the head, spine and pelvis, were estimated using three pairs of uni-axial accelerometers. The postural and focal components of the task were assessed using three biomechanical parameters calculated from CP signals: the duration and magnitude of APAs, and the duration of focal movement (dFM). Results showed that beyond a given level, higher muscular tension along the trunk results in longer APAs, but with a stable duration of the focal movement. In addition, no significant variation of APAs and FM parameters was found between bilateral and unilateral increases of muscular tension. It was suggested that restricted mobility due to higher muscular tension along the trunk requires an adaptation of the programming of APAs to keep the same level of performance in the STS task. These findings may have implications in treatment strategies aimed at preserving functional autonomy in pathologies including a rise of muscular tension.

Keywords: muscular tension, mobility, trunk, sit-to-stand, focal movement, postural adjustments

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INTRODUCTION

According to the seminal work of Bouisset and Zattara (1981), voluntary movement induces a perturbation to balance, and a counter-perturbation must be developed for the movement to be performed efficiently. This counter-perturbation starts prior to the onset of the voluntary movement, and serves to create in the rest of the body a movement whose forces of inertia would, when the times comes, balance the inertia forces due to the voluntary movement. This early postural activity, termed anticipatory postural adjustments (APAs), is organized according

to a reproducible pattern for a given movement and for every subject (Bouisset and Zattara, 1981, 1983). According to the hypotheses developed by Gelfand et al. (1966), the voluntary movement may be broken up into two components, one focal and one postural. The former refers to the voluntary movement itself, and the latter to the associated stabilizing activity of the body (Bouisset and Do, 2008). These two components require the mobility of a focal and a postural chain, which are usually located in distinct parts of the musculo-skeletal system. For example, the antepulsion of the upper limb is preceded by an acceleration of the shank (Bouisset and Zattara, 1983), and a bimanual isometric push task involves the mobility of the pelvis (Le Bozec and Bouisset, 2004). Consequently, restricted mobility of the bony chain may impair motor performance, even though its source is located in a part remote from the focal movement (FM).

According to Bouisset and Le Bozec (2002), postural chain dynamic mobility results from anatomical and physiological factors. The former ones refer to the structural properties of the bony chain (ligaments, bony stops. . .) which determine the articular range of motion, and can be considered as inherently passive. The latter and active factors are related to the pattern of muscular excitation, which can either generate or restrict bony segment displacements, depending on the agonist or antagonist function of the active muscles, respectively. In a pathological context, it has been assumed that a pain-related rise in muscular tension in low back pain is likely to impair the dynamic mobility capacity of the postural chain through a slowing-down effect (Hamaoui et al., 2004). Still for this pathology, it has also been shown an alteration of the APAs when performing upper limbs movements (Hodges and Richardson, 1999).

To date, a number of experiments have explored the effect of passive restrictions of postural chain mobility on voluntary movements. For example, a lower performance was shown to be associated with restricted pelvis mobility in a pointing task (Lino and Bouisset, 1994), in isometric pushing efforts (Le Bozec and Bouisset, 2004), or in the sit-to-stand task (STS; Diakhaté et al., 2013). However, few data are available on the influence of higher muscular tensions, although they represent a frequent symptom in a number of pathologies (hemiplegia, Parkinson's disease, back pain, muscular spasms in sports medicine. . .). Based on different bimanual isometric pushing paradigms varying muscular activity along the trunk while seated (Hamaoui et al., 2007) and standing (Hamaoui et al., 2011; Hamaoui and Le Bozec, 2014), a number of studies support the view that muscular tension impairs body balance when it exceeds a given level, with a more significant effect in case of asymmetrical tensions. In line with these studies, the present work is aimed at exploring the effect of increased muscular tension along the trunk when performing a usual voluntary movement, the STS task. The STS task is considered as a very common daily activity (Burdett et al., 1985; Riley et al., 1991; Roebroeck et al., 1994), which is required for independent living (Inkster and Eng, 2004). It is defined as moving the mass center of the body upward, from a sitting to a standing position, without losing balance (Roebroeck et al., 1994). The STS involves a transition from an intrinsically stable three-point support to a dynamically stable two-point support and is considered in some respects as the most mechanically demanding functional task routinely undertaken during daily activities (Riley et al., 1991). Different strategies of kinematic and muscular patterns are possible (Doorenbosch et al., 1994; Rodrigues-de-Paula Goulart and Valls-Solé, 1999), with sagittal plane motion dominant (Shepherd and Gentile, 1994). Based on the above mentioned literature on postural chain mobility and muscular tension, it is hypothesized that higher muscular tensions along the trunk may cause the focal and postural components of the task to vary. This assumption will be explored using a biomechanical analysis of the STS task in different conditions varying muscular tension level and symmetry along the trunk.

MATERIALS AND METHODS

Participants

Twelve healthy female subjects (age: 23 ± 3 years; weight: 56 ± 9 kg; height: 163 ± 0.05 cm, body mass index, BMI: 21 ± 3 kg/m^2), free of any neurological or musculoskeletal disease took part in this study. To avoid any variation of muscular strength and spine mobility related to gender differences, we did not include male participants.

This study was carried out in accordance with the recommendations of the local "Ethics Committee for Human Movement Analysis". All subjects gave written informed consent in accordance with the Declaration of Helsinki.

Experimental Set-Up

Force Plate

A six-channel force plate (Bertec Corp., ref. 6012-15, Columbus, OH, USA), which collected the ground reaction forces and moments applied at its top surface was used to calculate the coordinates of the center of pressure (CP) along the anterior-posterior (Xp) and medial-lateral (Yp) axes, with the following formulas: Xp = My/Rz Yp = Mx/Rz (Rz is the vertical ground-reaction force; Mx and My are the moments around the anterior-posterior and medial-lateral axes, respectively).

A stool (height = 48 cm; depth = 39 cm) with four legs and a round wooden top (diameter = 30 cm) was screwed on to the force plate and used for the experiments (**Figure 1**). To keep constant the friction forces between the stool top and the surface contact of the body, all participants wore the same kind of shorts.

Pressure Sensor

A pressure sensor was placed under the left front leg of the stool to determine the "seat off" instant.

Accelerometers

Three pairs of mono-axial accelerometers (FGP sensors, ref XA1010-B, ±10 g, Les Clayes Sous Bois, France), were used to assess the local accelerations of the pelvis and trunk. Each pair was screwed on to a customized cube (length = 2 cm) with the two active axes located along the anterior-posterior and the vertical

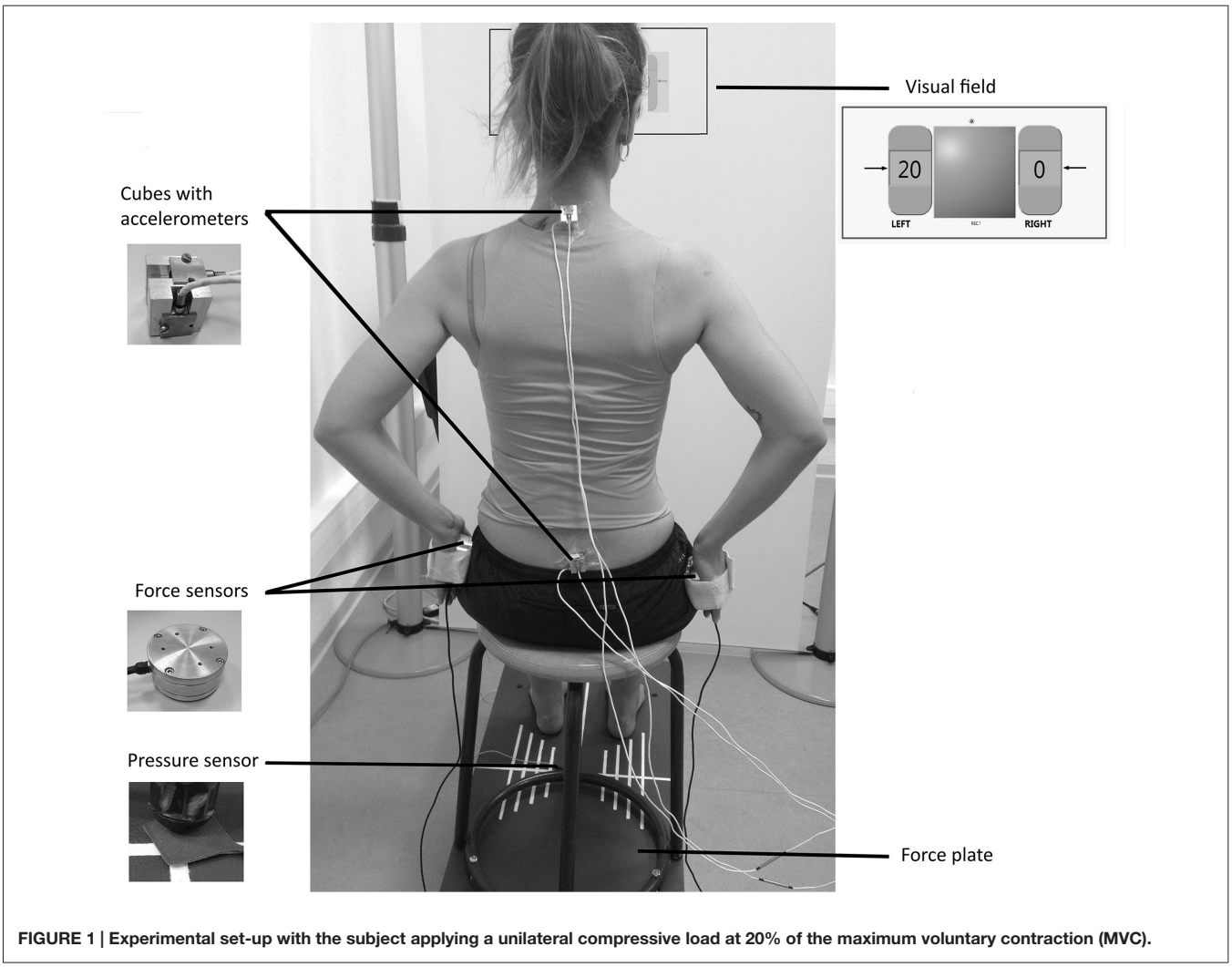

FIGURE 1 | Experimental set-up with the subject applying a unilateral compressive load at 20% of the maximum voluntary contraction (MVC).

axes. The cubes were adhered to the skin with double-sided tape at the level of the first sacral vertebra and first thoracic vertebra (**Figure 1**).

Force Sensors

Two cylindrical load cells (FN 2114 model, FGP Sensors, Les Clayes Sous Bois, France) were used to set the active muscular tension at different levels alongside the torso when performing a bimanual compressive load paradigm (**Figure 1**). They were equipped with adjustable Velcro bands designed to keep each sensor in contact with the hand palm, and preventing it from falling.

Visual Field

The subject's visual field consisted of a frontal white board, located 72 cm apart from the stool. A panel representing the tension generated on each load cell was screened on the board at the subject's eye level, using a video-projector (**Figure 1**). The signals were displayed as a percentage of the maximum voluntary contraction (MVC) in a left and a right numerical indicator representing each sensor, and designed in Labview software (National Instruments). The background color of these indicators changed from red to green when the subject reached the required value, enriching the basic feedback by a specific indication of the task to perform. The experimentation room was lit with artificial lighting to obtain constant brightness.

Data Acquisition System

Data collected by the force plate, the pressure sensor, and the load cells were sampled at 200 Hz with a 16-bit A/D converter board (model CompactDAQ with 9215 modules, National Instruments, Austin, TX, USA), controlled by a custom code written in Labview software (National Instruments).

Procedure

The participants sat on the platform with hips and knees approximately flexed to 90°, barefoot and feet apart. Adhesive tape was put around the feet outline in order to keep the same positioning for every trial. The load cells were positioned against hands palms and applied on the sides of the pelvis against the lateral surface of the trochanter major, with shoulders

abducted to 35° (**Figure 1**). Subjects were asked to focus their gaze on the numerical indicators screened on the visual field and representing the load applied on the force sensors. This bimanual compressive load paradigm, which has been extensively described in a previous study (Hamaoui and Le Bozec, 2014) was considered as a reliable tool to control the active muscular tension along each side of the torso. Using an extensive surface EMG analysis, the authors found that the main muscles of this isometric task were latissimus dorsi, pectoralis major and thoracic erector spinae, while secondary muscles were identified as lumbar erector spinae, trapezius pars ascendez and obliquus externus abdominis. The mean EMG of the main muscles was reported to increase with the compressive load level, with a negligible activity toward the non-active side in unilateral loads.

Two 3-s trials in bilateral maximum compressive load were first performed to determine the MVC. Subjects had next to achieve the STS transfer while performing a compressive load in seven conditions varying the load level (0%, 20% and 40% of the MVC) and side (left, right, bilateral). It must be noted that for a compressive load at 0% (no force applied) the experimental instructions were the same for left, right and bilateral loads, and only one condition was considered. For each condition, the participants had to reach the requested compressive load parameters before starting the STS transfer and to keep them constant during the task, using the feedback screened on the visual field. This way, the variations of the muscular pattern that may be associated with the task completion were minimized.

The "STS" paradigm consisted in rising from the stool to reach the standing position as fast as possible, in response to a "Go" signal. A training period was used to familiarize the subjects with the paradigm before recording. Six 3-s runs were performed in every condition, with six additional runs in 0% for subsequent statistical analysis. The rest period was 30 s between runs and 1 min between series.

The order of the experimental condition was randomly assigned to avoid any order effect.

Data Analysis

A careful visual inspection of CP curves along the anterior-posterior and medial-lateral axes was first performed for qualitative assessment (general time-course, curve shape). It was followed by a quantitative analysis of the APAs and FM of the STS. These two distinct phases were considered to be separated by the seat-off instant, for which the curve of the pressure sensor starts its fall towards zero. Three parameters were calculated from CP signals along the anterior- posterior axis:

- Duration of APAs (*dAPAs*): delay between the instant of seat-off and the first inflexion of the CP curve.
- Magnitude of APAs (ΔXp): difference between the maximum and the minimum values of CP during the APAs phase.
- Duration of the focal movement (*dFM*): delay between the seat-off instant and the stabilization of the CP curve (beginning of the plateau region).

Data from the accelerometers were used to ensure that the head and trunk were kept still before the « Go » signal, and to discard trials in which the participants anticipated the instructions of the experimenter.

All parameters were calculated using a customized program written in MatLab software (The MathWorks, Inc., Natick, MA, USA).

Statistical analysis was performed using the Statistical Package for Social Sciences (SPSS) software V22 (Chicago, IL, USA). Normality of data distribution and the condition of sphericity were first checked using Shapiro-Wilk and Mauchly tests, respectively. A two-way repeated measures analysis of variance (ANOVA) was conducted for each dependent variable, with compressive load intensity (0%, 20% and 40% of the MVC) and laterality (bilateral, unilateral) as within-subjects factors. Values for the unilateral level were calculated from the mean between the left and right trials, as this study did not focus on specific left and right variations that might have resulted from handedness. When statistical significance was reached for compressive load intensity, the ANOVA was followed by a within-subjects analysis of contrasts (difference contrast) to compare the three levels of the independent variable. The level of statistical significance was set at $p < 0.05$.

RESULTS

Qualitative Assessment of CP Curves

The CP time course along the anterior-posterior axis revealed a typical shape which always starts with an almost linear backward displacement (beginning of the APAs), followed by a forward displacement with a steeper slope, and which ends with a less regular stabilization phase preceding the plateau (end of the FM; **Figure 2**). This pattern, which is consistent with data displayed in previous experiments (e.g., Schenkman et al., 1990; Diakhaté et al., 2013) was reproducible across subjects and conditions.

No such typical trace was found along the medial-lateral axis, with a high variability of CP displacements during APAs and FM. In addition, the scale of the signal was about ten times lower than along the anterior-posterior axis, and no specific lateral slope was found in relation to the side of the compressive load (left or right) in unilateral conditions.

Quantitative Assessment of APAs and Focal Movement

The ANOVA revealed that increased compressive load level was associated with a longer duration of the APAs, with a significant main effect ($p < 0.05$). Subsequent contrast analysis showed a significant variation between a compressive load at 40% (comp40) and at the two other levels, namely 0% (comp0) and 20% (comp20), but no substantial difference between comp0 and comp20 conditions (**Table 1**, **Figure 3**). However APAs magnitude (ΔXp) and focal movement duration (dFM) were not sensitive to the level of the applied load (**Table 1**, **Figure 4**). These results were visible in CP traces, which exhibited longer APAs duration for comp40 and relative to comp20 and comp0,

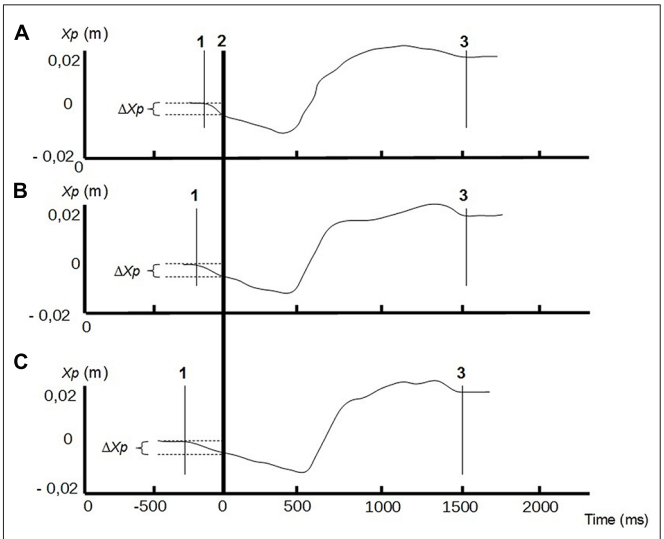

FIGURE 2 | Center of pressure (CP) traces along the anterior-posterior axis (Xp) of a representative subject, in different conditions of bilateral compressive load: no compression (A) compressive load at 20% of the MVC **(B)**, compressive load at 40% of the MVC **(C)**. Line 1: CP onset; line 2: instant of « seat-off »; line 3: CP stabilization. Anticipatory postural adjustments (APAs) phase is between lines 1 and 2, and focal phase between lines 2 and 3. ΔXp represents the amplitude of the APAs.

whereas APAs magnitude and FM duration remained stable (**Figure 2**).

Compared to bilateral loads, unilateral loads resulted in smaller mean duration of APAs and longer mean duration of FM, but with no significant variation (**Figures 3**, **5**, **Table 1**).

DISCUSSION

Increased Muscular Tension Along the Torso Induces a Reorganization of the APAs

According to the analysis of dAPAs, higher muscular tension along the trunk resulted in longer APAs, with significant variations when the compressive load reached 40% of the MVC (comp40 relative to comp20 and comp0). This variation may be interpreted as a reorganization of the motor pattern, aimed at compensating for the lower capacity to generate counter-disturbing movements due to higher active muscular tension. It has already been assumed that postural chain muscular stiffening may slow down the counter-perturbing movements necessary to keep the body stable, and make them less efficient (Hamaoui et al., 2007). In a more conceptual point of view, it was also suggested that active muscular stiffening along the torso, when it exceeds a given level, is likely to alter the posturo-kinetic capacity (PKC; Hamaoui et al., 2011), which is defined as the ability to develop a counter-perturbation to the posture perturbation induced by segmental movement (Bouisset and Le Bozec, 1999). This reorganization of the APAs, which become longer but retains a similar magnitude, can be considered as efficient enough to keep constant the performance of the FM, as no variation was observed for FM duration. Longer APAs would allow more time to generate the inertia forces, which are necessary to balance the disturbing effect of the FM when the time comes, as hypothesized by Bouisset and Zattara (1981). With respect to the STS, it may favor the generation of the early propulsive impulse in the sagittal plane, which is an essential requirement of the task (Pai et al., 1994).

This variation of APAs duration has already been described in a previous study using the paradigm of shoulder flexion at maximum velocity, in different conditions varying the support base surface (Zattara and Bouisset, 1992). The authors showed that restricted support base surface induced longer APAs, which were in this case associated with a decrease of FM performance. Therefore, it can be hypothesized that the restriction of the PKC induced by increased muscular tension along the trunk in the present study, was relatively moderate and likely to be compensated for a reorganization of the APAs. This adaptability of the APAs has been described since the early works, with a variation of their duration and magnitude according to additional inertia loads (Bouisset and Zattara, 1981, 1983), support base configuration (Zattara and Bouisset, 1992; Lino and Bouisset, 1994; Yiou et al., 2007), and pelvic mobility (Le Bozec and Bouisset, 2004; Diakhaté et al., 2013).

TABLE 1 | Anticipatory postural adjustments (APAs) and focal movement (FM) parameters as a function of compressive load parameters.

		COMP 0	COMP 20	COMP 40	*p(Comp main)*	*p(Comp 20/ Comp 0)*	*p(Comp 40/ previous)*	*p(Lat main)*
dAPAs (ms)	BILAT	98 ± 46	106 ± 50	123 ± 69	0.042	NS	0.048	NS
	UNILAT	99 ± 42	99 ± 44	107 ± 57				
ΔXP (m)	BILAT	0.043 ± 0.024	0.041 ± 0.020	0.044 ± 0.020	NS	NS	NS	NS
	UNILAT	0.046 ± 0.024	0.041 ± 0.018	0.040 ± 0.021				
dFM (ms)	BILAT	1693 ± 161	1641 ± 218	1593 ± 196	NS	NS	NS	NS
	UNILAT	1694 ± 190	1662 ± 222	1608 ± 150				

Mean ± SD of APAs duration (dAPAs, in ms), APAs magnitude (ΔXp, in m) and focal movement duration (dFM, in ms) are presented in bilateral (BILAT) and unilateral (UNILAT) compressive loads, at 0% (COMP 0), 20% (COMP 20) and 40% (COMP 40) of the maximum voluntary contraction (MVC). Results of statistical analysis display the main effect of the analysis of variance (ANOVA) for compressive load intensity (Comp main) and laterality (Lat main), and the contrast analysis for compressive load intensity (Comp 20 and Comp 40 relative to previous levels). NS: non significant.

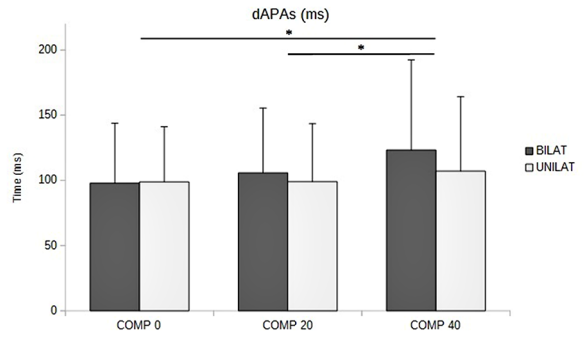

FIGURE 3 | Duration of APAs (dAPAs, in ms) as a function of the compressive load: means and standard deviations (error bars) are presented in unilateral (UNILAT) and bilateral (BILAT) compressive load, at 0% (COMP 0), 20% (COMP 20) and 40% (COMP 40) of the MVC. $*p < 0.05$.

Unilateral and Bilateral Compressive Loads Did Not Impair the Focal Component of the STS

In contrast with previous studies describing lower body balance in case of increased trunk muscular tension in seated (Hamaoui et al., 2007) or standing (Hamaoui et al., 2011) postures, no variation of FM duration, and thus of performance, was observed in the present experiment. This difference might be attributed to the high levels of motor muscles activity (Rodrigues-de-Paula Goulart and Valls-Solé, 1999) and range of motion (Roebroeck et al., 1994) associated with the STS task, as compared to the low levels required for postural maintenance. Indeed, joint movements have been reported to be less than 1° while standing (Hodges et al., 2002), with a postural activity below 10% of the MVC (Okada, 1973). This low activity might be sensitive to postural muscles tensions, even limited by the maximum compressive load at 40% of the MVC. In contrast, the very dynamic displacements of the articulated chain required for the STS task, may overcome the slowing down effect induced by the compressive load paradigm.

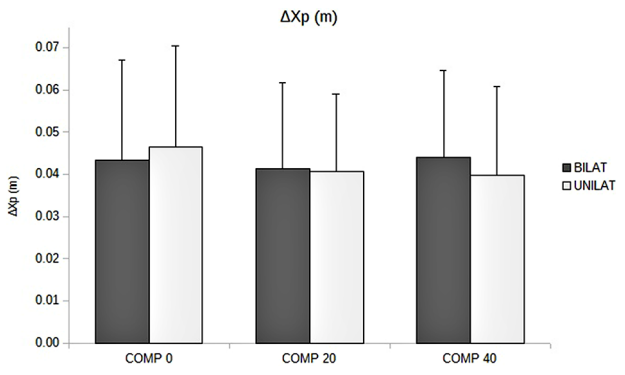

FIGURE 4 | Amplitude of APAs (△Xp, in m) as a function of the compressive load: means and standard deviations (error bars) are presented in unilateral (UNILAT) and bilateral (BILAT) compressive loads, at 0% (COMP 0), 20% (COMP 20) and 40% (COMP 40) of the MVC.

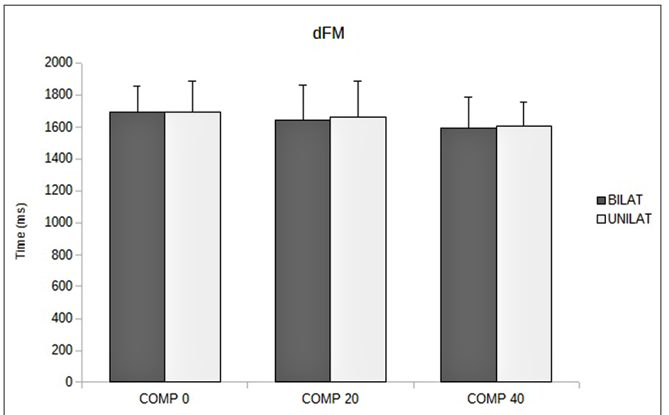

FIGURE 5 | Duration of focal movement (dFM, in ms) as a function of the compressive load: means and standard deviations (error bars) are presented in unilateral (UNILAT) and bilateral (BILAT) compressive loads, at 0% (COMP 0), 20% (COMP 20) and 40% (COMP 40) of the MVC.

Still in contrast with a study carried out during postural maintenance (Hamaoui and Le Bozec, 2014), the performance did not appear lower for unilateral loads, with similar FM duration between unilateral and bilateral conditions. Likewise, APAs duration and magnitude did not present any significant variation between the two conditions, suggesting a similar PKC. This result might first be explained by a lesser net muscular activity along the whole trunk in unilateral conditions, as the load is only applied on one side. It can also be assumed that the inherently sagittal characteristics of the STS kinematics and kinetics (Shepherd and Gentile, 1994), attested in this study by the absence of a typical CP along the medial lateral axis, may limit its sensitivity to a left-right asymmetry of muscular tension. Finally, it can also be hypothesized that the CNS has integrated the asymmetry of postural muscles activity, which was set before the « Go » signal, in the programming of the task, and tuned the postural adjustments accordingly. All these hypotheses need further experiments to be tested and refined.

Increased Muscular Tension in a Clinical Context May Require a Reorganization of the STS Motor Program

As increased active muscular tension is a very frequent symptom in various pathologies of the musculo-skeletal (muscular spasms in sports medicine or in degenerative diseases of the joints) and central nervous (hemiplegia, Parkinson's disease) systems, the results from this study are worth being interpreted in a clinical perspective. It can first be assumed that a pathological increase of trunk muscular tension, when it exceeds a given level, may require an adaptation of the APAs pattern in order to keep the same level of performance in the STS task. It can also be considered that a limited asymmetry of trunk muscular tension may induce a negligible effect on the STS task performance. However, as increased tension was experimentally induced on

healthy participants in this study, it is necessary to take into account the possible interaction with other symptoms in a pathological context, which may lead to more prominent effects. This might be the case in Parkinson's disease or stroke, which are both associated with other deficits and have proved to impair STS task performance (Inkster and Eng, 2004; Boukadida et al., 2015). Therefore, treating pathological muscular tensions, by means of drugs or physiotherapy, might reduce the necessity for APAs reprogramming and favor STS performance in some pathologies.

Limitation

There were some methodological limitations of the study which need to be acknowledged. First, we used a model of increased muscular tension based on voluntary contractions performed in healthy subjects, which intrinsically differ from pathological variations related to deficits of the nervous or musculo-skeletal systems. Second, the STS task was performed at maximum velocity in young adults, whereas slower movements are frequently observed in a pathological population, with possible variations of the focal and postural components of the task. Third, we only used participants with a normal BMI, whereas the STS task requires the generation of high propulsive forces that may lead to different strategies in subjects presenting high BMI. For these reasons, future experiments are needed to confirm our hypotheses in a more realistic context, including different pathologies and classes of participants.

CONCLUSION

The findings of this study support the view that experimentally increased muscular tension along the trunk requires an adaptation of the APAs, which become longer, to maintain the same level of performance in the STS. This effect, which might be more prominent in a clinical context where it is bound be associated with other symptoms, may have some implications in treatment strategies intended to improve functional autonomy.

AUTHOR CONTRIBUTIONS

AH contributed with project creation, data analysis, and drafted the manuscript. CA-R contributed with project creation, data collection and data analysis. AH and CA-R discussed the results and revised the manuscript.

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The handling Editor currently co-hosts a Research Topic with one of the authors AH, and confirms the absence of any other collaborations. He states that the process met the standards of a fair and objective review.

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frontiers in Human Neuroscience

ORIGINAL RESEARCH
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Influence of Cervical Spine Mobility on the Focal and Postural Components of the Sit-to-Stand Task

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The aim of this study was to determine the influence of cervical spine mobility on the focal and postural components of the sit-to-stand transition, which represent the preparatory and execution phases of the task, respectively. Sixteen asymptomatic female participants (22 ± 3 years, 163 ± 0,06 cm, 57,5 ± 5 kg), free of any neurological or musculoskeletal disorders, performed six trials of the sit-to-stand task at maximum speed, in four experimental conditions varying the mobility of the cervical spine by means of three different splints. A six-channel force plate, which collected the reaction forces and moments applied at its top surface, was used to calculate the center of pressure displacements along the anterior-posterior and medial-lateral axes. The local accelerations of the head, spine, and pelvis, were assessed by three pairs of accelerometers, oriented along the vertical and anterior-posterior axes. Restriction of cervical spine mobility resulted in an increased duration of the focal movement, associated with longer and larger postural adjustments. These results suggest that restricted cervical spine mobility impairs the posturo-kinetic capacity during the sit-to-stand task, leading to a lower motor performance and a reorganization of the anticipatory postural adjustments. In a clinical context, it might be assumed that preserving the articular free play of the cervical spine might be useful to favor STS performance and autonomy.

Keywords: sit-to-stand, postural adjustments, focal movement, posturo-kinetic capacity, cervical spine, mobility

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INTRODUCTION

The transition from sitting to standing, commonly named "sit-to-stand (STS)" is a very common daily task. In a study performed on eight wives of physicians and one man, McLeod et al. (1975) found that the STS task is performed four times an hour from 7 am to 10 pm. These results were refined by Dall and Kerr (2010) with an extended study on 140 participants, reporting an average of 60 STS movements per day and 3 per hour.

The STS task implies a rapid transition from a stable seated posture that offers a large contact area between the body and the supporting surfaces, to a less stable standing posture associated with a shorter base of sustentation, a higher location center of gravity and an extended articulated chain to stabilize. The standing posture is frequently a starting point for gait initiation, which involves a complex biomechanical process (Brenière and Do, 1991) preceding the rhythmic pattern of gait. Therefore, the ability to perform the STS movement is instrumental to autonomy, and many studies have been designed to unveil the kinematics and kinetics underlying this self-perturbing task (Burdett et al., 1985; Nuzik et al., 1986; Kralj et al., 1990; Schenkman et al., 1990; Riley et al., 1991; Coghlin and McFadyen, 1994; Roebroeck et al., 1994).

Most authors have divided the STS into two (Nuzik et al., 1986; Rodrigues-de-Paula Goulart and Valls-Solé, 1999), three (Schenkman et al., 1990; Coghlin and McFadyen, 1994; Roebroeck et al., 1994), or four (Kralj et al., 1990) different phases based on kinematics and kinetics data.

When considering the STS within the frame of the posturo-kinetic capacity concept (Bouisset and Zattara, 1983), a distinction should be made between a preparation phase, which corresponds to the anticipatory postural adjustments (APAs), and an execution phase during which the focal movement (FM) is performed. APAs allow for a better performance through a compensation of the disturbing forces associated with the FM (Bouisset and Zattara, 1981) or the generation of propulsive forces (Brenière and Do, 1991), and require postural chain mobility (Bouisset and Le Bozec, 1999). Lower articular free play of the lumbar pelvic area was associated with a reduction of the motor performance in several paradigms such as the pointing task (Lino and Bouisset, 1994), the pushing ramp effort (Le Bozec and Bouisset, 2004) or the STS task (Diakhaté et al., 2013).

However, there is a paucity of information regarding the role of the cervical spine, especially regarding the STS movement. In many kinematic studies of STS, total body movement is represented by a three-segment linkage (trunk-thigh-shank) pivoting about the foot (Shepherd and Gentile, 1994), and the influence of cervical spine mobility is taken into account only in a few experiments. In an earlier study, Jones and Hanson (1970) presented the trajectories of the head during the STS movement, traced from successive frames of motion picture. They constructed triangles from markers placed over the sternum, the seventh cervical vertebra and the head, exhibiting a cervical flexion during the first half of the trajectory. In a video-based kinematic analysis of the STS task, Nuzik et al. (1986) reported an average neck flexion of 8° during the first 35% of the movement cycle, followed by an extension phase. In an electromyographic study of the STS task, Rodrigues-de-Paula Goulart and Valls-Solé (1999) reported an activity of neck motor muscles (trapezius, sternocleidomastoideus) before and after the seat-off instant. Taken all together, these findings lead us to hypothesize that cervical mobility is involved in the preparatory

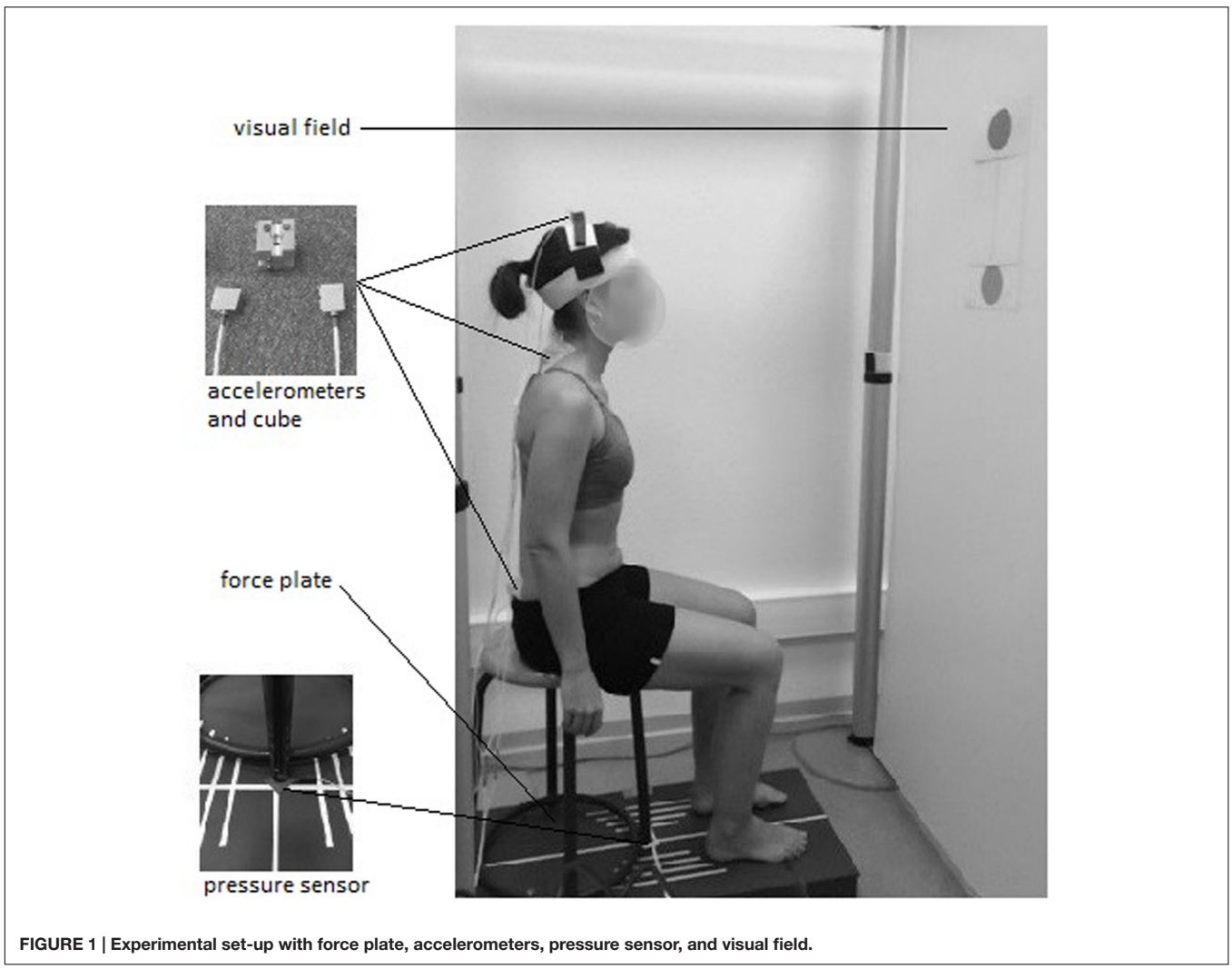

FIGURE 1 | Experimental set-up with force plate, accelerometers, pressure sensor, and visual field.

and in the execution phases of the STS movement, and that a loss of cervical mobility is likely to impair both of them. In a neurophysiological point of view, it must also be noted that the cervical spine controls the orientation of the head, which is a frame of reference for action since it contains the visual and the vestibular systems (Pozzo et al., 1990). The main goal of this study was to assess the effect of cervical mobility restriction on the APAs and on the FM for the STS task. To this aim, biomechanical parameters were analyzed in different conditions varying cervical spine range of motion by means of three different collars.

MATERIALS AND METHODS

Participants

Thirteen asymptomatic female participants (age: 23 ± 3 years; weight: 56 ± 9 kg; height: 163 ± 0,05 cm, BMI: 21 ± 3 kg/m^2), free of any neurological or musculoskeletal disease participated in this study. Only female participants were included in this study to avoid any variation of cervical spine mobility that might be related to gender differences

This study was carried out in accordance with the recommendations of the local "Ethics Committee for Movement Analysis." All subjects gave written informed consent in accordance with the Declaration of Helsinki.

Experimental Set-Up

Force Plate and Stool

A six-channel force plate (Bertec Corp., ref. 6012-15, Columbus, OH, USA), which collected the ground-reaction forces and moments applied at its top surface was used to calculate the coordinates of the center of pressure (CP) along the anterior-posterior axis (Xp), with the following formula: Xp = My/Rz (My is the moment around the medial-lateral axis and Rz is the vertical ground-reaction force).

A stool (height = 48 cm; depth = 39 cm) with four legs and a round wooden top (diameter = 30 cm) was screwed on to the force plate and used for the experiments (**Figure 1**).

To keep constant the friction forces between the stool top and the surface contact of the body, all participants wore the same kind of shorts.

Accelerometers

Three pairs of mono-axial accelerometers (FGP sensors, ref XA1010-B, ± 10g, Les Clayes Sous Bois, France), were used to assess the local accelerations of the pelvis, trunk, and head. Each pair was screwed on to a customized cube (length = 2 cm) with the two active axes located along the anterior-posterior and the vertical axes. The two first cubes were adhered to the skin with double-sided tape, at the level of the first sacral vertebra and first thoracic vertebra. The third cube was placed on top of the head using a system of Velcro bands (**Figure 1**).

Visual Field

The subject's visual field consisted of a frontal white board (72 cm apart from the stool), on which two black disks (diameter = 10 cm) joined by a vertical line were placed at the subject's eye level in the seated (lower disk) and standing (upper disk) postures (**Figure 1**). The participants were requested to focus their gaze on the lower disk at the beginning of the trial, and to follow the vertical line during the ascending phase of the STS, until they reach the upper disk. This visual field was designed to avoid unwanted cervical mobility due to a fixed visual target while the body was ascending. The experimentation room was lit with artificial lighting to obtain constant brightness.

Pressure Sensor

A pressure sensor was placed under the left front leg of the stool (**Figure 1**) to determine the "seat-off" instant.

Data Acquisition System

Data for all the recording devices were collected at 200 Hz with a 16-bit A/D converter board (model CompactDAQ with 9215

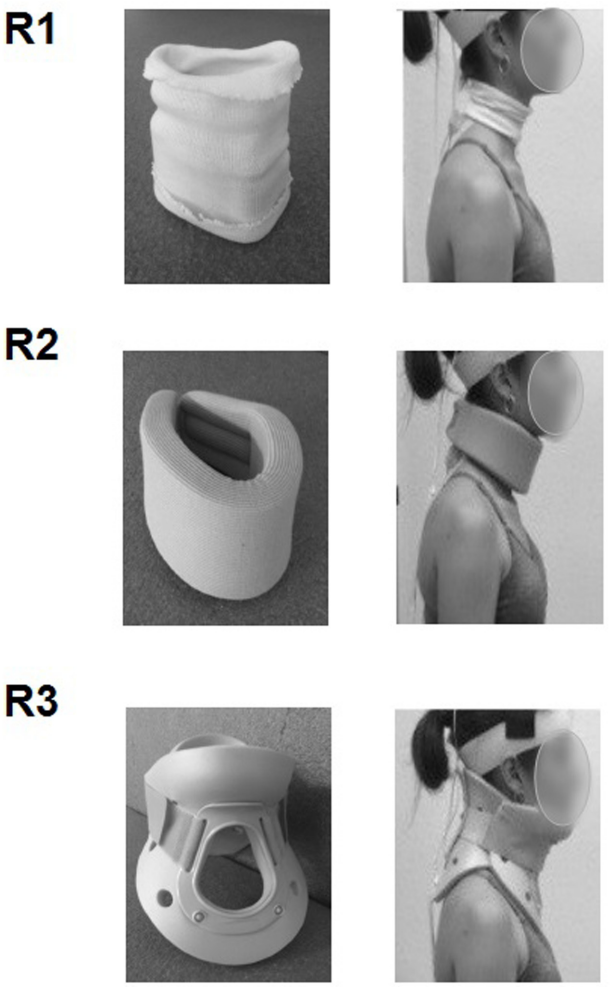

FIGURE 2 | Collars used to gradually restrict the mobility of the cervical spine: jersey tubular bandage (R1), foam cervical collar (R2), Philadelphia collar (R3).

modules, National Instruments, Austin, TX, USA), controlled by a custom code written with Labview software (National Instruments).

Cervical Collar

Three different cervical collars (**Figure 2**) were used to vary the mobility of the cervical spine passively, in accordance with the study of Hartman et al. (1975), who measured cervical spine range of motion in flexion-extension, side bending, and rotation while wearing five commonly used cervical orthoses:

- Jersey tubular bandage (Neuss, Germany): minor restriction of cervical mobility.
- Foam cervical collar (Cooper, Melun, France): medium restriction of cervical mobility.
- Philadelphia collar (Variteks, Istanbul, Turkey): major restriction of cervical mobility.

Procedure

The participants sat on the stool fixed on the platform with their upper limbs relaxed along their trunk, hips, and knees flexed to approximately 90°, barefoot and feet apart. Adhesive tape was put around the feet outline in order to keep the same positioning for every trial.

The subjects had to perform the "STS" task, which consisted in rising from the stool to reach the standing position as fast as possible, in response to a "Go" signal.

The STS was performed in four experimental conditions varying the mobility of the cervical area using the three above-mentioned collars: R0, no collar; R1, jersey tubular bandage; R2, foam cervical collar; R3, Philadelphia collar.

A training period was used to familiarize the subjects with the paradigm before recording.

Ten 3-s runs were performed in every condition, with a rest period of 30 s between runs and of 1 min between series.

The order of the experimental conditions was randomly assigned to avoid any order effect.

Data Analysis

Three parameters were calculated to characterize the APAs and the FM of the STS task along the anterior-posterior axis. These two distinct phases of the task were considered to be separated by the seat-off instant, for which the curve of the pressure sensor begins its fall toward zero (**Figure 3**).

- Duration of anticipatory postural adjustments (*dAPAs*): delay between the instant of seat-off and the first inflection of the CP curve.
- Amplitude of APAs (ΔXp): difference between the maximum and the minimum CP values during the APAs phase.

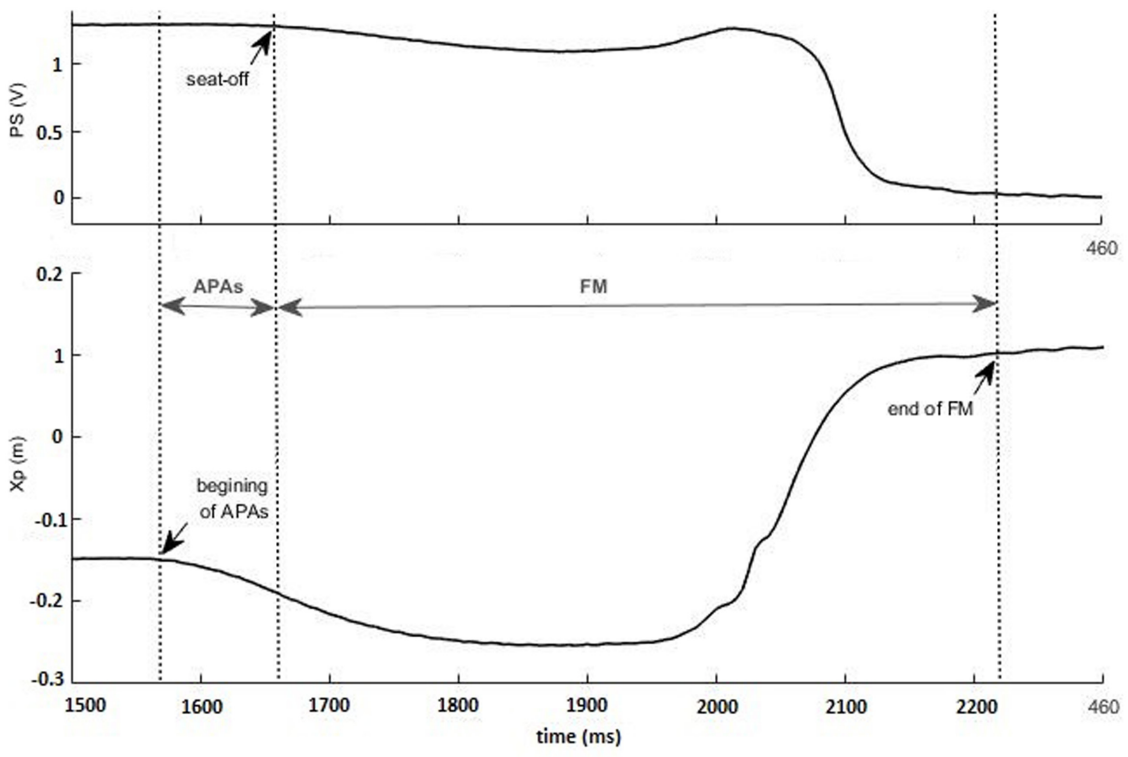

FIGURE 3 | Identification of the anticipatory postural adjustments (APAs) and of the focal movement (FM) phases, using pressure sensor (PS, in V) and anterior-posterior center of pressure (CP) (Xp, in m) traces: the beginning of the APAs and the end of the FM are identified in CP trace, whereas the seat-off is indicated in PS trace. The recording was taken in a representative subject wearing a Philadelphia collar.

- Duration of the focal movement (*dFM*): delay between the seat-off instant and the stabilization of the CP curve (beginning of the plateau region).

The different events (beginning of the APAs, seat-off, end of the FM) were based on the visual inspection of the curves, performed by a fully trained experimenter.

Data from the accelerometers were used to ensure that the head and trunk were kept still before the "Go" signal, and to discard trials in which the participants anticipated the instructions of the experimenter. The accelerometric signals were not used to separate the focal and the postural components of the task, because in complex movements such as the STS, some parts of the bony chain might be involved in both phases, with no clear distinction between the focal and the postural chains.

All parameters were calculated using a customized program written in MatLab software (The MathWorks, Inc., Natick, MA, USA).

A one-way repeated measures analysis of variance (ANOVA) was conducted for each dependent variable, with cervical mobility as a within-subjects factor. When statistical significance was reached, the ANOVA was followed by a within-subjects

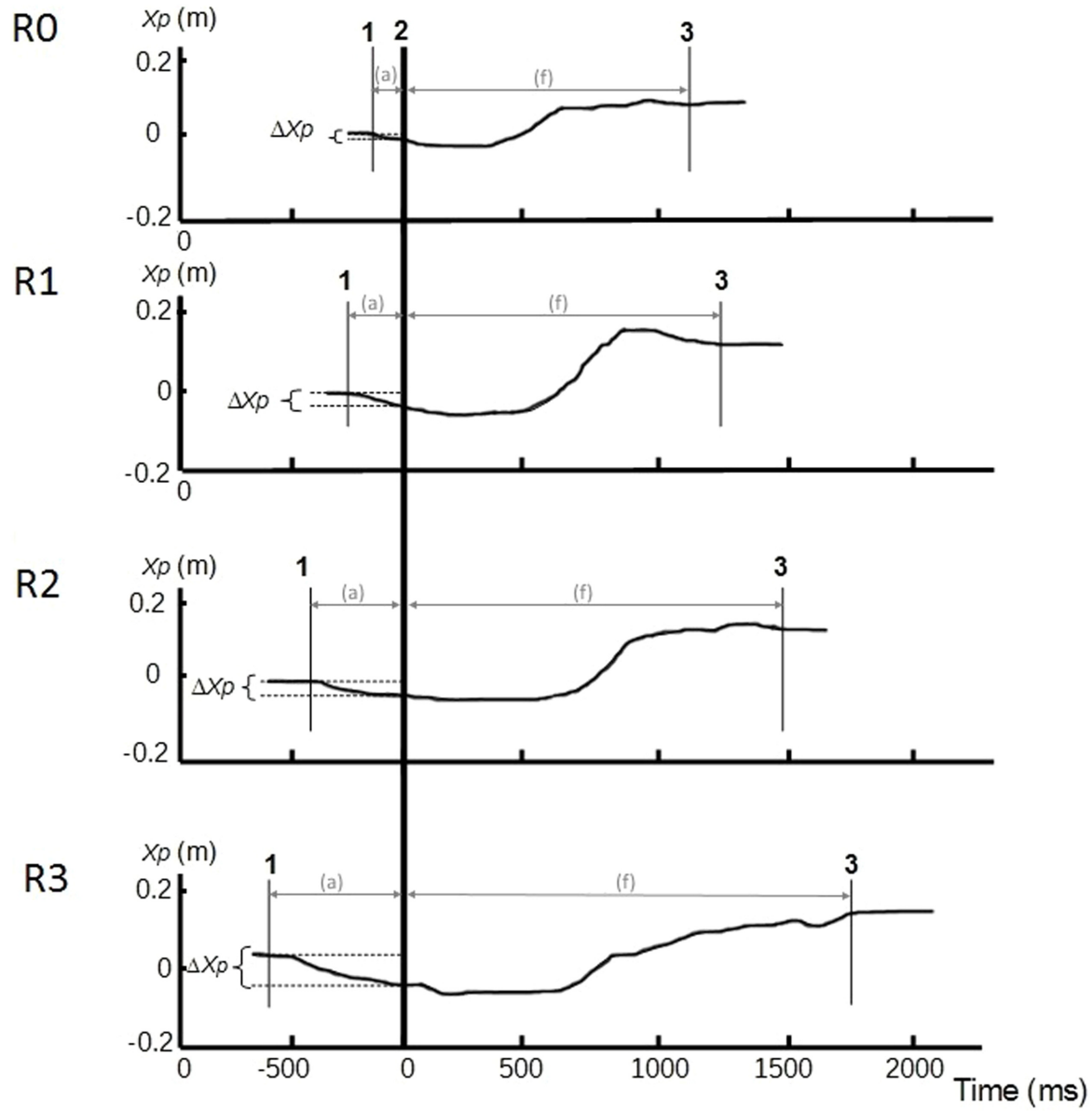

FIGURE 4 | Center of pressure traces along the anterior-posterior axis (Xp, in m) in different conditions of cervical spine mobility: no restriction (R0), jersey tubular bandage (R1), foam cervical collar (R2), Philadelphia collar (R3). Recordings were taken in a representative subject. Line 1: CP onset; line 2: instant of "seat-off"; line 3: CP stabilization. APAs (a) phase is between lines 1 and 2, and focal phase (f) between lines 2 and 3. ΔXp represents the amplitude of the APAs.

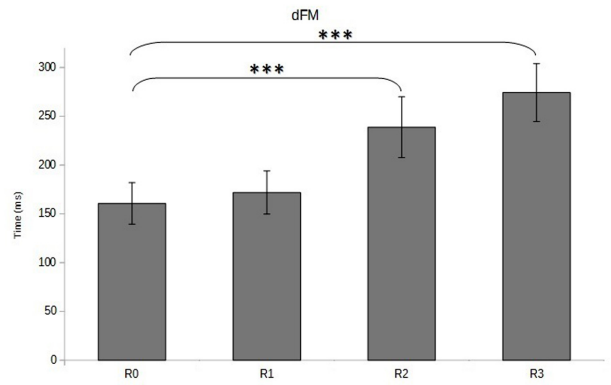

FIGURE 5 | Duration of focal movement (dFM, in ms) as a function of cervical spine mobility. Means and standard deviations are presented in four different conditions varying cervical spine mobility using cervical orthoses: no restriction (R0), jersey tubular bandage (R1, minor restriction), foam cervical collar (R2, medium restriction), Philadelphia collar (R3, major restriction). ***$p < 0.001$.

TABLE 1 | Anticipatory postural adjustments (APAs) and focal mouvement (FM) parameters as a function of cervical spine mobility.

	dAPA (ms)	*Δ Xp (m)*	*dFM (ms)*
RO	14.41 ± 8.04	0.029 ± 0.012	195.3 ± 35.06
R1	15.76 ± 4.16	0.037 ± 0.019	191.42 ± 31.92
R2	22.38 ± 4.51	0.051 ± 0.023	241.66 ± 42.97
R3	27.77 ± 6.83	0.059 ± 0.022	268.29 ± 40.63
Overall effect	$p < 0.01$	$p < 0.001$	$p < 0.001$
p(R0/R1)	*NS*	*NS*	*NS*
p(R0/R2)	$p < 0.05$	$p < 0.01$	$p < 0.001$
p(R0/R3)	$p < 0.001$	$p < 0.001$	$p < 0.001$

Mean ± SD of APAs duration (dAPAs), APAs amplitude (ΔXp), and focal movement duration (dMF) are presented in the different conditions varying cervical spine mobility: jersey tubular bandage (R1), foam cervical collar (R2), Philadelphia collar (R3).

analysis of contrasts to compare the levels of the independent variable. As we presumed a significant difference between a reference condition (R0, no collar) and the three others ones (R1, R2, and R3), we used a simple contrast which compared R0 to each category (R1, R2, and R3). All statistical analysis were performed using the Statistical Package for Social Sciences (SPSS) software V22 (Chicago, IL, USA).

RESULTS

The visual inspection of CP traces along the anterior-posterior axis showed a gradual increase of APAs duration, APAs amplitude, and FM from R0 to R3 (**Figure 4**), which was confirmed by the statistical analysis. Indeed, the ANOVA revealed that the duration of the FM increased with the restriction of cervical spine mobility induced by the three collars ($p < 0.001$ for the overall effect) with significant variations in R2 and R3 relative to R0 (**Figure 5** and **Table 1**).

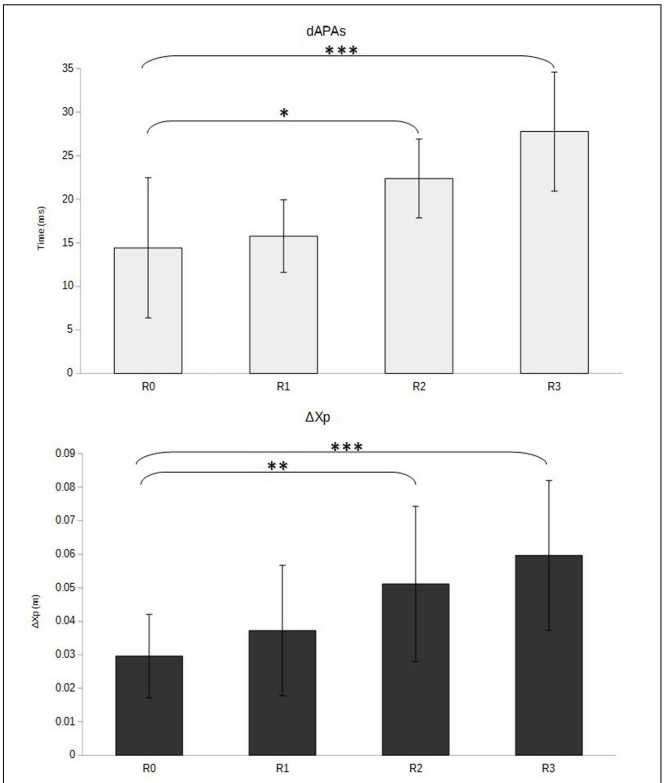

FIGURE 6 | Duration (dAPAs, in ms) and amplitude (ΔXp, in m) of anticipatory adjustments as a function of cervical spine mobility. Means and standard deviations are presented in four different conditions varying cervical spine mobility using cervical orthoses: no restriction (R0), jersey tubular bandage (R1, minor restriction), foam cervical collar (R2, medium restriction), Philadelphia collar (R3, major restriction). *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Similar variations were observed for the APAs, which presented higher duration ($p < 0.01$ for the overall effect) and magnitude ($p < 0.001$ for the overall effect) when cervical spine mobility was restricted (**Figure 5** and **Table 1**). The within-subjects contrast analysis showed significant differences between the R0 and R2 conditions ($p < 0.05$ for APAs duration and $p < 0.01$ for APAs amplitude) and between the R0 and R3 conditions ($p < 0.001$ for APAs duration and APAs amplitude) (**Figure 6**).

It must be noted that no significant variation was observed between R0 (no collar) and R1 (jersey tubular bandage) for any of the three analyzed parameters.

DISCUSSION

Cervical Spine Mobility Is a Significant Parameter in the STS Task

The statistical analysis of the biomechanical parameters revealed that the FM duration of the STS task increased stepwise with the restriction of cervical spine mobility. As the subjects were requested to perform the task as fast as possible, it can be assumed

that lower cervical spine mobility results in poorer performance for the STS task. This phenomenon could firstly be related to a lower ability to perform the FM when the articular free play of the cervical spine is restricted, in accordance with literature depicting the mobilization of this area during the focal phase of the STS. Indeed, Nuzik et al. (1986) reported a neck extension after the first 35% of the movement cycle, and Rodrigues-de-Paula Goulart and Valls-Solé (1999) showed that two motor muscles of the neck, namely trapezius and sternocleidomastoideus, present a noticeable EMG activity during the focal phase of the movement.

Secondly, the loss of cervical mobility may also impair the ability to perform efficient APAs, which represent a part of the central motor program that tends to reduce the early perturbations induced by the FM. In the paradigm of STS (Diakhaté et al., 2013) as in gait initiation (Brenière and Do, 1991), which include a shift of the center of mass (CM), APAs also contribute to the generation of the propulsive forces. It is assumed that APAs must be developed for the movement to be performed efficiently (Bouisset and Zattara, 1981). APAs involve postural chain mobility, and restricted articular free play has been shown to induce poorer performance in various paradigms, such as manual pointing or pushing (Bouisset and Le Bozec, 1999). The implication of cervical spine mobility during the anticipatory phase of the STS task is supported by existing literature, with Jones and Hanson (1970) representing a cervical flexion at the beginning of the STS trajectory in accordance with Nuzik et al. (1986). In the study by Rodrigues-de-Paula Goulart and Valls-Solé (1999), early EMG activity of the sternocleidomastoideus prior to the seat-off instant, very close to the onset of tibialis anterior that is the first muscle to be activated, has been reported. As the motor pattern of the APAs, including the motor muscles and the mobilized joints, is task specific (Bouisset and Zattara, 1981), the restriction of cervical spine mobility might not be easily compensated for. Consequently, APAs will become less efficient and require a significant increase of their amplitude and duration to counterbalance the disturbances associated with the FM, or to generate the propulsive forces. This adaptation of APAs programming is in line with a previous study exploring the effect of support base surface on the paradigm of shoulder flexion at maximum velocity while standing (Zattara and Bouisset, 1992). In this study, the authors showed that restricted support surface was associated with longer APAs and a lower performance of the FM (represented by the angular velocity peak).

Cervical Spine as a Possible Guide for STS Kinematics

Beyond its key role as a part of the postural chain whose mobility reduces the disturbance associated with the FM in the STS, the cervical spine may also have other functions due to its upper location along the bony chain and articulation with the head. The early head flexion followed by an extension (Jones and Hanson, 1970), with a similar pattern for the trunk and pelvis (Nuzik et al., 1986), might provide the head and cervical spine with a guide function for STS kinematics. This function was suggested in a series of pictures taken in the burst mode in a few trials, with head mobility apparently starting and guiding the whole body trajectory. These hypotheses require an extended EMG and kinematic study to be assessed.

This specific role of the cervical spine could also be considered from a neurophysiological point of a view, as these vertebrae determines head orientation in space, and may vary visual field, vestibular activity, and cervical proprioception, which all provide substantial input for motor control (Paulus et al., 1984; Roll et al., 1989; Cullen, 2012). In the performance of complex tasks such as jumping, it has been shown that the head is sequentially stabilized in different positions, during several successive time periods (Pozzo et al., 1990). Hence, restricted articular free play in the cervical area might also impair the sensitive and sensory flow used by the CNS to control the STS task.

APAs Are Adaptable

The analysis of CP displacements according to the seat-off instant showed that APAs duration and magnitude increased stepwise with the restriction of cervical spine mobility, suggesting that the local variations of the articular free play were integrated in the central programming of the task. This fine tuning of APAs is in line with literature demonstrating their adaptability to different biomechanical parameters, such as the size of the base of support (Yiou et al., 2007), or additional loads (Bouisset and Zattara, 1981). It may now be assumed that APAs are also adaptable to spine mobility variations.

Clinical Implications

To date, little attention has been paid to cervical spine mobility in the STS task, either in a physiological perspective or in treatment and prevention strategies. It is well know that restriction of cervical spine mobility is frequent in the elderly (Lansade et al., 2009) or in neck pain syndroms (Cagnie et al., 2007), and results from this study suggest that it may impair the ability to perform the STS task. As a consequence, preserving or extending the cervical articular free play in these cases, using rehabilitation techniques or adapted physical programs, may be useful to preserve functional autonomy. Indeed, it must be recalled that the STS, which is considered a fundamental prerequisite for daily activities (Boukadida et al., 2015), is performed in mean 60 times per day (Dall and Kerr, 2010).

Elsewhere, the prescription of cervical collars, although they may represent an efficient tool to relieve pain or to favor cervical spine recovery (Muzin et al., 2007), should take into account their negative effect on the STS task, especially for patients presenting a loss of functional autonomy.

CONCLUSION

This study has shown that passive restriction of cervical mobility results in a lower motor performance in the STS task, with an adaptation of the APAs, which become longer and larger. It is assumed that cervical spine mobility is an integral part of both the postural and the focal components of the STS

task, with potential implications in rehabilitation strategies and adapted physical activity programs.

AUTHOR CONTRIBUTIONS

AH contributed with project creation, data analysis, and drafted the manuscript. CA-R contributed with project creation, data collection, and data analysis. AH and CA-R discussed the results and revised the manuscript.

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Short-Term Effects of Thoracic Spine Manipulation on the Biomechanical Organisation of Gait Initiation: A Randomized Pilot Study

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Speed performance during gait initiation is known to be dependent on the capacity of the central nervous system to generate efficient anticipatory postural adjustments (APA). According to the posturo-kinetic capacity (PKC) concept, any factor enhancing postural chain mobility and especially spine mobility, may facilitate the development of APA and thus speed performance. "Spinal Manipulative Therapy High-Velocity, Low-Amplitude" (SMT-HVLA) is a healing technique applied to the spine which is routinely used by healthcare practitioners to improve spine mobility. As such, it may have a positive effect on the PKC and therefore facilitate gait initiation. The present study aimed to investigate the short-term effect of thoracic SMT-HVLA on spine mobility, APA and speed performance during gait initiation. Healthy young adults (n = 22) performed a series of gait initiation trials on a force plate *before* ("pre-manipulation" condition) and *after* ("post-manipulation" condition) a sham manipulation or an HVLA manipulation applied to the ninth thoracic vertebrae (T9). Participants were randomly assigned to the sham (n = 11) or the HVLA group (n = 11).The spine range of motion (ROM) was assessed in each participant immediately after the sham or HVLA manipulations using inclinometers. The results showed that the maximal thoracic flexion increased in the HVLA group after the manipulation, which was not the case in the sham group. In the HVLA group, results further showed that each of the following gait initiation variables reached a significantly lower mean value in the post-manipulation condition as compared to the pre-manipulation condition: APA duration, peak of anticipatory backward center of pressure displacement, center of gravity velocity at foot-off, mechanical efficiency of APA, peak of center of gravity velocity and step length. In contrast, for the sham group, results showed that none of the gait initiation variables significantly differed between the pre- and post-manipulation conditions. It is concluded that HVLA manipulation applied to T9 has an immediate beneficial effect on spine mobility but a detrimental effect on APA development and speed performance during gait initiation. We suggest that a neural effect induced by SMT-HVLA, possibly mediated by a transient alteration in the early sensory-motor integration, might have masked the potential mechanical benefits associated with increased spine mobility.

Keywords: anticipatory postural adjustments, gait initiation, spinal manipulation HVLA, T9 vertebrae, range of motion, posturo-kinetic capacity

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INTRODUCTION

The coordination between posture and movement is known to be a key factor in motor performance. Gait initiation, which is the transient phase between quiet standing posture and ongoing walking, is a classical model used in the literature to investigate this coordination (e.g., Mann et al., 1979; Brenière et al., 1987; Yiou et al., 2007; Honeine et al., 2016). It is composed of a postural phase preceding the swing foot-off, which corresponds to the "anticipatory postural adjustments (APA)". The postural phase is followed by an execution phase ending when the peak of forward center of gravity (COG) velocity (or speed performance) is reached (Brenière et al., 1987; Lepers and Brenière, 1995). During these APA, the forward propulsive forces required to reach the peak COG velocity are generated by an anticipatory backward center of pressure (COP) shift. The larger this shift, the greater the speed performance (Brenière et al., 1987; Lepers and Brenière, 1995). The relationship between APA and speed performance during gait initiation illustrates the biomechanical concept of "Posturo-kinetic capacity (PKC)" (Bouisset and Zattara, 1987; Bouisset and Do, 2008), according to which the motor performance of any motor task (in terms of speed, force or precision) depends on the capacity of the central nervous system to generate appropriate APA. According to this concept, any factors that would impair (or conversely enhance) APA development may impair (or enhance) the motor performance. This PKC concept was substantiated by experimental studies which investigated the relationship between postural chain mobility, APA and motor performance during various motor tasks such as isometric ramp push (Le Bozec and Bouisset, 2004), pointing (Lino et al., 1992; Teyssèdre et al., 2000), and more recently, trunk flexion (Diakhaté et al., 2013) or sit-to-stand (Diakhaté et al., 2013; Alamini-Rodrigues and Hamaoui, 2016; Hamaoui and Alamini-Rodrigues, 2017a,b). In these studies, postural chain mobility was varied by changing the seat-thigh contact (Teyssèdre et al., 2000; Le Bozec and Bouisset, 2004; Diakhaté et al., 2013), by increasing the muscular tension along the torso (Hamaoui et al., 2004, 2011; Hamaoui and Le Bozec, 2014) or by restraining the spine mobility at different levels by means of splints (Alamini-Rodrigues and Hamaoui, 2016; Hamaoui and Alamini-Rodrigues, 2017a,b). These studies showed that the restriction of the postural chain mobility, and especially the spine mobility, has a negative influence on APA and motor performance. Conversely, according to the PKC concept, enhancing the postural chain mobility should have a positive influence on these parameters. Besides this purely mechanical influence, APA associated with stepping initiation are also known to be finely tuned to the continuous proprioceptive (Ruget et al., 2010) and cutaneous inflow (Do and Gilles, 1992; Ruget et al., 2008) arising from the postural body segments. Perturbations of this sensory inflow, e.g., by reducing the plantar support or by vibrating the ankle muscles, have been shown to alter APA and motor performance.

"Spinal Manipulative Therapy High-Velocity, Low-Amplitude" (SMT-HVLA) is a healing technique applied to the spine that has been used for centuries by healthcare practitioners including Osteopaths, Chiropractors and Physiotherapists to relieve symptomatic patients from acute and chronic low back/neck pain and/or to improve spine mobility (Wiese and Callender, 2005). As such, SMT-HVLA may have the potential to improve the PKC and thus motor performance. As stressed in the literature (e.g., the review of Pickar and Bolton, 2012), a number of sustained changes in the spinal biomechanics have been thought to occur as a result of SMT-HVLA. For example, the impulsive thrust delivered during the manipulation may alter the segmental biomechanics by releasing trapped meniscoïds, releasing adhesions, or by diminishing distortion in the intervertebral disc. In addition, recent studies reported relaxation of paraspinal muscles following SMT-HVLA as revealed with decreased electromyographic (EMG) activity (DeVocht et al., 2005; Lehman, 2012). Increased spine mobility might result from such changes in the spinal biomechanics and/or EMG activity. Interestingly, this technique is nowadays widely used by healthy athletes (runners, footballers, sprinters etc.) just before a competition in order to reach their "peak performance" (Leonardi, 1994). However, it must be noted that the effect of SMT-HVLA on the articular free play is still controversial (for review see Millan et al., 2012a), with mitigated results on sports performance (Miners, 2010). Shrier et al. (2006) compared jump height and running velocity with and without pre-event SMT-HVLA in elite healthy athletes. These authors found that there was no significant effect of SMT-HVLA on the countermovement jump height and sprint times. However, they also stressed that the direction and magnitude of the observed changes were consistent with a clinically relevant performance enhancement. A similar conclusion was stated by Humphries et al. (2013) with regard to the immediate effect of lower cervical spine manipulation on handgrip strength and free-throw accuracy of asymptomatic basketball players. These authors reported a slight increase in free-throw percentage, which according to them, deserved further investigation.

Besides the potential increase in spine mobility, movement kinematics may also be potentially influenced by neurophysiological changes induced by SMT-HVLA. For example, studies on the anesthetized cat have shown that spinal manipulation induced changes in the discharge of somatosensory afferents from the paraspinal region (Pickar, 2002; Pickar and Bolton, 2012; Reed et al., 2015), including those afferents innervating muscle spindles, Golgi Tendon Organs and high threshold mechanoreceptors. There are currently no unequivocal data regarding whether SMT-HVLA activates nociceptors. In humans, changes in the sensori-motor pathways following SMT-HVLA have been reported in the literature, but with sometimes contradictory results. For example, studies using the Hoffman reflex (H-reflex) technique indicated that spinal manipulation induced a decreased motoneuronal excitability in asymptomatic subjects (Murphy et al., 1995; Dishman and Burke, 2003) and in low back pain patients (Suter et al., 2005), while Niazi et al. (2015) indicated, on the contrary, an increased excitability. Data collection and data analysis methodology of the H-reflex have been evoked by these latter authors to explain this discrepancy with the literature. At the cortical level, it seems that there exists a consensus concerning the

alteration of the sensorimotor processing and sensorimotor integration following spinal manipulation, as evidenced with the somatosensory-evoked potential technique (e.g., Haavik-Taylor and Murphy, 2007; Taylor and Murphy, 2008; Haavik Taylor and Murphy, 2010; see "Discussion" Section on this aspect).

As stressed in the literature (e.g., Pickar and Bolton, 2012), the extent to which these mechanical and neurophysiological responses to spinal manipulation reflect beneficial outcomes (e.g., pain relief or enhanced spine mobility) remains unclear. However, each of these responses has the potential to induce changes in the coordination between posture and movement, which strongly relies on both sensory inputs from the postural limbs and postural joint mobility as stressed above. The present study, therefore, aimed to investigate the short-term effect of SMT-HVLA on spine mobility, APA and speed performance during gait initiation in young healthy adults. We first hypothesized that a SMT-HVLA applied to the ninth thoracic vertebra (T9) will increase the spine range of motion and facilitate APA development in the gait initiation paradigm, which is known to involve spine mobility (e.g., Ceccato et al., 2009). Second, we also assumed that the various short-term neurological effects of this manipulation may either improve or reduce the PKC and task performance.

MATERIALS AND METHODS

Subjects

The study was a randomized investigation that included 22 right-handed young healthy adults. The non-probability convenience method was used, i.e., participants were randomly assigned to one of the two following groups using the envelope method (**Figure 1**): 11 participants (six female, five male; 28 ± 4 years [mean ± SD]; 64 ± 8 kg; 169 ± 8 cm) were assigned to the HVLA group and eleven participants (five female, six male; 29 ± 4 years; 63 ± 8 kg; 170 ± 8 cm) to the sham group. Participants were blinded to their group allocation. They had no known contraindications to spinal manipulation such as recent history of trauma, known metabolic disorders, inflammatory infectious arthropathies, or bone malignancies. None of them suffered from back pain during the experiment or have suffered in the past months. In addition, participants were all naïve about SMT-HVLA manipulation. They all gave written consent after having been informed of the nature and purpose of the experiment which was approved by local ethics committees from the CIAMS Research Unit, Equipe d'Accueil (EA) 4532. The study complied with the standards established by the Declaration of Helsinki. Our study was assigned the following trial registration number: 2017-002389-34.

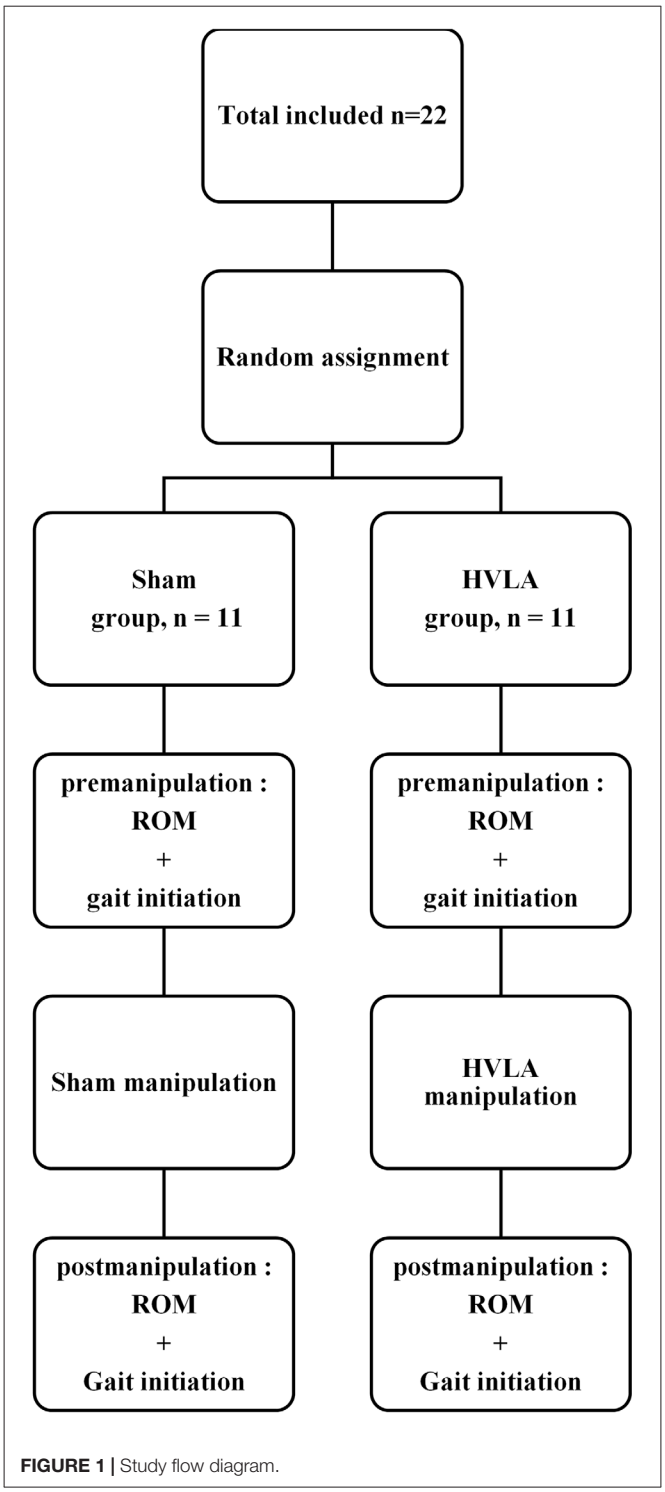

FIGURE 1 | Study flow diagram.

Experimental Task and Conditions

All experiments took place in the Biomechanics laboratory of the Paris Saclay University which is located within the Kremlin Bicêtre Hospital (Paris, France). Physical conditions (room temperature and time of the day) were common to all treatment groups (see below), and also constant before/after the manipulation.

Participants initially stood barefoot in a natural upright posture on a force plate embedded at the beginning of a 6 m walkway track. The feet were shoulder-width apart, with the arms alongside the trunk and the gaze directed forward to a small target at eye level and out of reach (2 cm diameter, 5 m

distant). The locations of the heel and big toe of each foot in the initial posture were marked with sections of adhesive tape placed on the force plate and were used as a visual reference on which participants positioned themselves under the supervision of the experimenters. From the initial posture, participants performed two series of ten gait initiation trials: one just before, and a second one immediately after a specific manipulation (pre- and post-manipulation conditions, respectively) depending on their group (HVLA or sham). All ten trials within each condition were averaged. In these two conditions, participants initiated gait at a spontaneous velocity and at their own initiative following an auditory signal delivered by the experimenter, and then continued walking straight until the end of the track. Participants initiated gait with their preferred leg in all trials. One blank trial was provided in the pre-manipulation condition (not recorded) to ensure that the instructions were well understood by the participant and that the material was operational. The rest time was approximately 10 s between trials. The Range of Motion (ROM) of the thoracic spine was assessed (see description below) for each participant in the HVLA and sham groups immediately before and after the HVLA or sham manipulations (see description below), respectively.

FIGURE 2 | Profile (left) and front (right) views of the participant's and the practitioner's initial postures in the sham and HVLA manipulations. The written informed consent was obtained from the participants depicted in the images.

HVLA and Sham Manipulations

The HVLA and sham manipulations complied with the 2016 Consensus on Interventions Reporting Criteria List for Spinal Manipulative Therapy (CIRCLE SMT; Groeneweg et al., 2017). Both manipulation procedures were performed by one of the authors of the present study, an experienced professional physiotherapist and osteopath practitioner with 10 years of clinical experience in his own practice. The practitioner is also a teacher at the Ecole Nationale de Kinésithérapie et Rééducation (France). He has received extensive training in the study protocols and was certified for both thoracic lift manipulation and sham procedure by simulating multiple study visit scenarios overseen by research team members.

SMT-HVLA was applied to the ninth thoracic vertebra (T9) since this vertebra is described as the "walking vertebra", a concept arising from the classical article of Wernham (1985). This concept is based on the fact that the T9 vertebra is the inflexion point of the curvature change of thoracic cyphosis in lumbar lordosis. This vertebra ensures the junction between the thoracic and lumbar segments, mainly in their counter-rotation movement, especially during walking. In this plane, the center of rotation between the thoracic and the pelvic belts is presumably positioned between L3 and T7 (Konz et al., 2006).

In the HVLA group, the spinous process of the ninth thoracic vertebrae (T9) of the participant was identified by the practitioner and was marked with a pen. The participant stood upright with the hands positioned on the transverse processes of the selected vertebra with palms facing the back. The practitioner stood behind him/her with the front foot positioned between the participant's feet. The practitioner circled the participant's trunk by passing his arms under his/her armpits, and his chest was in contact with the palms of the participant's hands. From this posture, he applied a single manual rapid horizontal pressure to the T9 vertebrae, followed by a single rapid vertical traction of the vertebral column. This technique corresponds to the standing thoracic "lift-off" technique. Before the manipulation, the practitioner systematically informed the participant that the sound of a cavitation was not a sign of success, and after the manipulation, that the manipulation was successful.

In the sham group, the experimental protocol was exactly the same as in the HVLA group with regard to the T9 marking, the initial/final postures, and the information given to the participant on the efficacy of the manipulation (positive verbal reinforcement). This guaranteed the blindness of participants with respect to their group allocation. Only the manipulation differed between the two groups. The manipulation used in the sham group corresponded to the "light touch methodology" validated by the North Texas Chronic Low Pain Trial (Licciardone et al., 2013). In this manipulation, the practitioner did not apply any compression or traction of the vertebral column but solely maintained the above-described posture with the participant for 10 s.

The HVLA and sham manipulations took place beside the force plate to ensure minimal time between the end of the manipulation procedure and the beginning of the first gait initiation trial of the post-manipulation condition. A brief overview of the practitioner's and the participant's postures adopted for the manipulations is provided in **Figure 2**.

Evaluation of Spine ROM

Spine ROM was evaluated before the series of gait initiation trials in the pre- and post-manipulation conditions (**Figure 1**). Two inclinometers (Bubble® Inclinometer, Fabrication Enterprises, White Plains, NY, USA) were used to evaluate spine ROM.

The reliability and accuracy of inclinometers in measuring lumbar lordosis and cervical spine flexion and extension ROM have been assessed in previous studies (Lewis and Valentine, 2010; Garmabi et al., 2012). The measurement of the spine ROM was conducted according to the standard protocol set out in the American Medical Association guide to the evaluation of permanent impairment (Doege and Houston, 1993; Cocchiarela and Andersson, 2001). The spinous process of the first and last thoracic vertebrae (T1 and T12) and the second sacral vertebrae (S2) of the participant were identified by the experimenter and marked with a pen while the participant stood upright. The inclinometers were then placed on these marks two by two (T1 and T12 or T12 and S2) and were calibrated to zero in this position. The participant was then instructed to perform maximum trunk flexion and extension with legs stretched. Each movement was repeated two times with the inclinometer positioned at T1/T12 then at T12/S2 (**Figure 3**). The mean ROM value obtained in these two trials was computed. For each movement direction, trunk inclination was computed as the difference between the values provided by the two inclinometers (thoracic flexion/extension: T1/T12; lumbar flexion/extension: T12/S2). The thoraco-lumbar flexion and extension were calculated from the sum of the thoracic and lumbar values in flexion and extension, respectively.

Materials

External forces and moments applied to the participants were recorded from a force plate (600 × 1200 mm, AMTI, Watertown, MA, USA). Before analysis, the force-plate signals were filtered using a low-pass Butterworth filter with a 10 Hz cutoff frequency (Caderby et al., 2017). Biomechanical data were sampled at 500 Hz and stored on a hard disk for off-line analysis. Data acquisition and stimulus display were controlled by a custom-made program written in Matlab^{TM} (R2009b, The MathWorks Inc., Natick, MA, USA). Only the postural dynamics along the anteroposterior axis were considered in the present study as we were mainly interested in the speed performance of gait initiation. Instantaneous COG acceleration was obtained with the ratio [ground reaction forces/subject's mass] following Newton's second law ($\Sigma F = m\gamma$, where ΣF, the sum of external forces applied to the whole body; m, body mass; γ, COG acceleration). The COG velocity was obtained through simple integration of the COG acceleration trace. The instantaneous COP displacement (xP) was computed using the formula:

$$xP = \frac{-My + Fx \times dz}{Fz}$$

where My, Fx, Fz are the moment around the mediolateral axis, the anteroposterior and vertical ground reaction forces, respectively; *dz* is the distance between the surface of the force plate and its origin, located at the center of the force plate.

Swing toe-off (TO) and foot-contact (FC) instants were detected with force plate data (Caderby et al., 2013) and with foot switches (Force Sensing Resistor, 1 cm^2 surface, Biometrics, France) affixed under the heel and big toe of the swing foot.

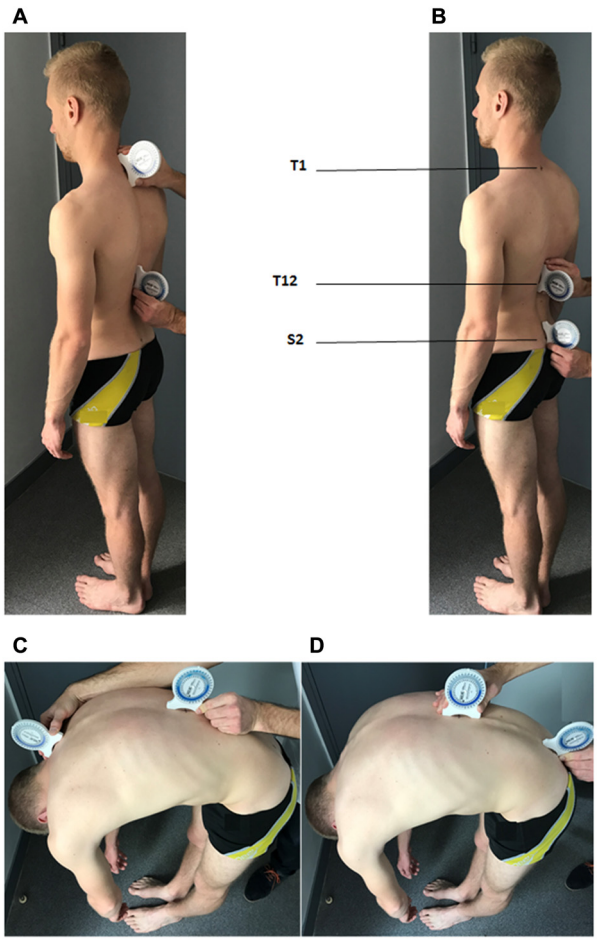

FIGURE 3 | Positioning of the two inclinometers for the evaluation of the spine range of motion. **(A)** Inclinometers are positioned over the spinous process of the first and last thoracic vertebrae (T1 and T12, respectively) and are calibrated in this position for the evaluation of the maximal thoracic flexion **(C)**. **(B)** Inclinometers are positioned over T12 and the spinous process of the second sacral vertebrae (S2) and are calibrated in this position for the evaluation of the maximal lumbar flexion **(D)**. The written informed consent was obtained from the participants depicted in the images.

The "biomechanical traces" (see **Figure 4**) will refer to the COP displacement and COG velocity traces obtained from the force plate recordings.

Gait Initiation Variables

Data acquisition was triggered 200 ms prior to the auditory signal, which allowed *post hoc* calculation of the COP position in the initial posture. The anteroposterior component of the COP initial position was computed as the mean COP value obtained during these 200 ms. APA duration corresponded to the time between the onset rise of the COP trace to the time of swing TO (e.g., Yiou et al., 2011; Delafontaine et al., 2015). The APA onset was detected when the COP trace deviated 2.5 standard deviations from its baseline value (e.g., Caderby et al., 2017). APA amplitude was estimated with

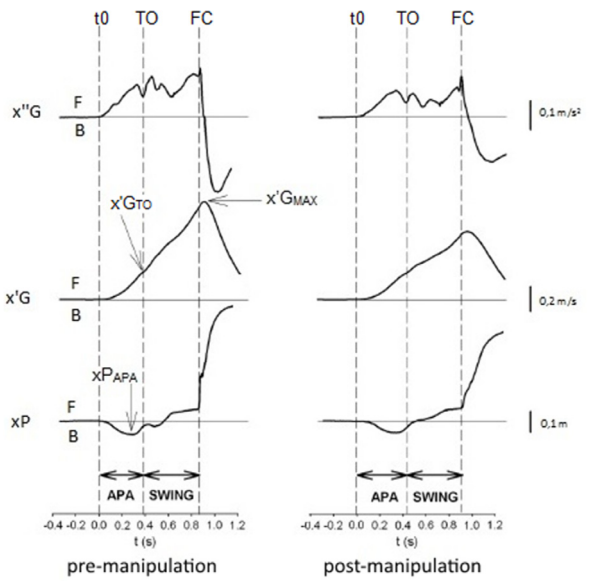

FIGURE 4 | Biomechanical profiles of gait initiation in the pre- and post-manipulation conditions in one representative participant of the HVLA group. x″G, x′G, xP: anteroposterior center of gravity (COG) acceleration, COG velocity, and center of pressure (COP) displacement, respectively. t0, TOT, foot-contact (FC): onset rise of x″G trace, swing toe-off (TO) and swing FC. Anticipatory postural adjustments (APA), SWING: APA and swing phase. $x'G_{MAX}$, $x'G_{TOT}$, xP_{APA}: peak of COG velocity, COG velocity at TO, peak of anticipatory backward COP displacement. F: forward displacement, velocity or acceleration, B: backward displacement, velocity or acceleration.

the forward COG velocity at the TO time and with the maximal backward COP displacement during APA (**Figure 4**). Swing phase duration corresponded to the time between swing TO and swing FC. Step motor performance (speed performance) was quantified with the maximal COG velocity. Step length corresponded to distance between the peak backward COP position obtained during the APA and the COP position at the time of the rear TO (Yiou et al., 2016). Finally, the mechanical efficiency of the APA was quantified with the ratio [COG velocity at TO/APA duration] (Yiou et al., 2011). It is assumed that the greater this ratio, the greater the mechanical efficiency.

The experimenter who analyzed the data and performed the ROM measures (pre and post treatment) was different from the practitioner and was blinded to the treatment group so as to ensure absence of expectation bias and optimize the reliability of the test procedure.

Statistics

Mean values and standard deviations of ROM and gait initiation variables were computed in each condition for all subjects. The normality of data was checked using the Kolmogorov-Smirnov test and the homogeneity of variances was checked using the Bartlett test. A 2 × 2 mixed-model analysis of variance (ANOVA) was used, with GROUP (HVLA vs. sham) as the between-subject factor and CONDITION (pre-manipulation vs. post-manipulation) as the within-subject factor. For each ANOVA, the hypothesis of interest was the 2-way-interaction (GROUP × CONDITION). Significant outcomes were followed up with the Tukey *post hoc* test. In addition, the participants' anthropometrical characteristics were compared between groups using independent Student's *t*-tests for continuous data, and chi-square tests of independence were used for categorical data to evaluate the adequacy of the randomization. The level of statistical significance was set at alpha = 0.05. Data analysis was performed using Statistica 12, statsoft®.

RESULTS

Anthropometrical Characteristics of Participants

Participants were randomly assigned to the sham or HVLA groups. Their anthropometrical characteristics are reported in **Table 1**. Statistical analysis showed that the two groups were homogenous in terms of mean age, gender, height and weight.

Comparison of Spine ROM between Groups and Conditions

The results showed that there was no significant main effect of GROUP, CONDITION or GROUP × CONDITION interaction on any of the spine ROM values, except on the thoracic flexion. For this variable, there was a significant main effect of GROUP ($F_{(1,21)} = 4.53$, $p < 0.05$), CONDITION ($F_{(1,21)} = 15.73$, $p < 0.01$) and GROUP × CONDITION interaction ($F_{(1,21)} = 14.55$, $p < 0.01$). For the HVLA group, the *post hoc* analysis further indicated that this variable was significantly larger in the post-manipulation condition (mean value: 24 ± 12°) than in the pre-manipulation condition (20 ± 12°) ($p < 0.05$). In contrast, for the sham group, it was not significantly different. Finally, it is noteworthy that there was no significant difference in any of the spine ROM values (including the thoracic flexion) between the HVLA and the sham group in the pre-manipulation condition. The spine mobility was therefore equivalent between the two groups before the manipulation.

Description of Typical Biomechanical Traces Obtained during Gait Initiation

The time-course of the biomechanical traces obtained during gait initiation was globally similar in the pre- and the post-manipulation condition for both the HVLA and sham groups. As classically reported in the literature, the swing TO was

TABLE 1 | Anthropometrical characteristics of participants.

	HVLA group (n = 11)	Sham group (n = 11)	P Value
Age (years)	28 ± 4	29 ± 4	0.633† NS
Gender	Females 6 Males 5	Females 5 Males 6	0.670‡ NS
Height (cm)	169 ± 8	170 ± 8	0.913† NS
Weight (kg)	64 ± 8	63 ± 8	0.815† NS

Values given are means ± 1 standard deviation, except for gender; †Independent samples t test; ‡Chi-square test. NS: non-significant difference.

systematically preceded by dynamic phenomena corresponding to APA (**Figure 4**). These APA included the backward COP displacement along with the forward COG acceleration. The COG velocity increased progressively until it reached a maximum value a few milliseconds after the time of swing FC.

Comparison of Gait Initiation Variables between Groups and Conditions

The results showed that there was a significant main effect of GROUP on every gait initiation variables investigated in this study, i.e., APA duration ($F_{(1,21)}$ = 6.25, $p < 0.01$), peak of anticipatory backward COP displacement ($F_{(1,21)}$ = 19.07, $p < 0.001$), COG velocity at TO ($F_{(1,21)}$ = 6.92, $p < 0.01$), mechanical efficiency of APA ($F_{(1,21)}$ = 10.05, $p < 0.01$), peak COG velocity ($F_{(1,21)}$ = 19.75, $p < 0.001$), step length ($F_{(1,21)}$ = 11.81, $p < 0.001$) and swing phase duration ($F_{(1,21)}$ = 5.87, $p < 0.01$). In addition, there was a significant main effect of CONDITION on each of the following variables: APA duration ($F_{(1,21)}$ = 3.95, $p < 0.05$), peak of anticipatory backward COP displacement ($F_{(1,21)}$ = 19.73, $p < 0.001$), COG velocity at TO ($F_{(1,21)}$ = 12.40, $p < 0.001$), mechanical efficiency of APA ($F_{(1,21)}$ = 9.39, $p < 0.01$), peak COG velocity ($F_{(1,21)}$ = 12.04, $p < 0.001$) step length ($F_{(1,21)}$ = 22.22, $p < 0.001$) and swing phase duration ($F_{(1,21)}$ = 2.39, $p < 0.05$). Finally, there was a significant GROUP X CONDITION interaction on each of the following variables: APA duration ($F_{(1,21)}$ = 2.92, $p < 0.05$), peak of anticipatory backward COP displacement ($F_{(1,21)}$ = 11.92, $p < 0.01$), COG velocity at TO ($F_{(1,21)}$ = 4.22, $p < 0.05$), mechanical efficiency of APA ($F_{(1,21)}$ = 8.51, $p < 0.01$), peak COG velocity ($F_{(1,21)}$ = = 3.27, $p < 0.05$), step length ($F_{(1,21)}$ = 9.66, $p < 0.01$) and swing phase duration ($F_{(1,21)}$ = 6.29, $p < 0.05$).

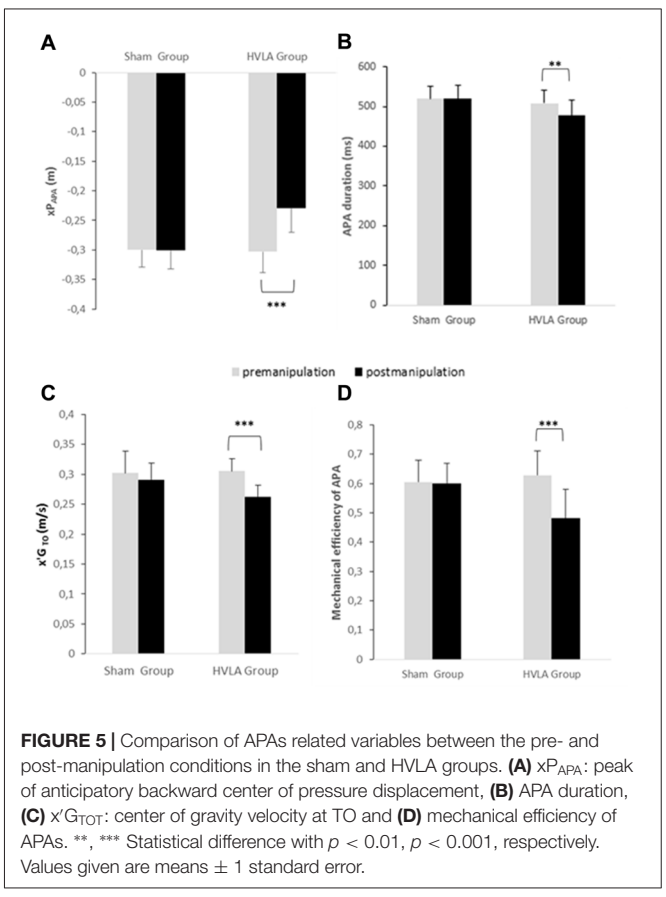

FIGURE 5 | Comparison of APAs related variables between the pre- and post-manipulation conditions in the sham and HVLA groups. **(A)** xP_{APA}: peak of anticipatory backward center of pressure displacement, **(B)** APA duration, **(C)** $x'G_{TOT}$: center of gravity velocity at TO and **(D)** mechanical efficiency of APAs. **, *** Statistical difference with $p < 0.01$, $p < 0.001$, respectively. Values given are means ± 1 standard error.

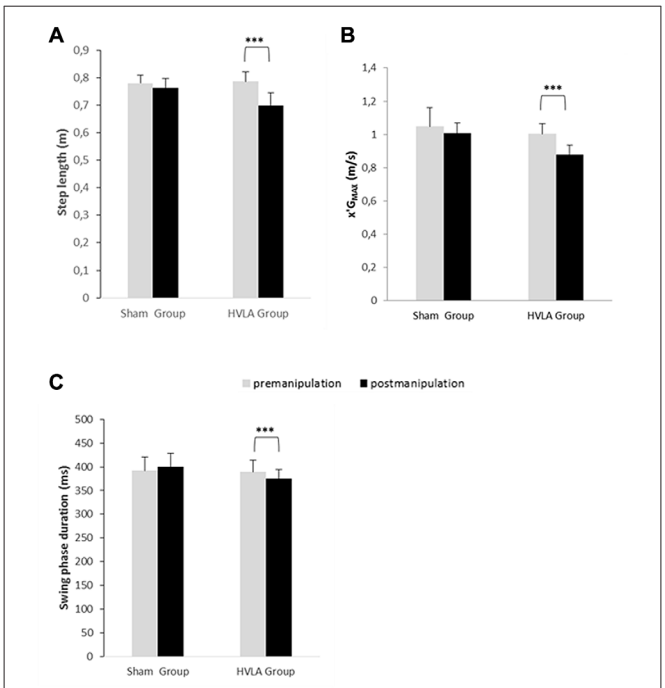

FIGURE 6 | Comparison of swing phase-related parameters of gait initiation between the pre- and post-manipulation conditions in the sham and HVLA groups. **(A)** Step length, **(B)** $x'G_{MAX}$: peak center of gravity velocity and **(C)** swing phase duration. *** Statistical difference with $p < 0.01$, $p < 0.001$, respectively. Values given are means ± 1 standard error.

The *post hoc* analysis further indicated that, for the HVLA group, each of the gait initiation variables investigated in this study was significantly lower in the post-manipulation condition than in the pre-manipulation condition (see **Figures 5**, **6** for details on the *post hoc* analysis). In contrast, regarding the sham group, none of these variables significantly differed between the pre- and post-manipulation condition. Finally, it is noteworthy that none of the gait initiation variables significantly differed between the sham and the HVLA groups in the pre-manipulation condition. The two groups were therefore homogeneous with respect to these variables before the manipulation.

DISCUSSION

This study investigated the effect of SMT-HVLA manipulation applied to T9 on spine ROM and on the biomechanical organisation of gait initiation. Participants purposely performed series of gait initiation trials before and after sham or SMT-HVLA manipulations. Spine ROM and classical biomechanical gait initiation parameters were compared in the pre- and post-manipulation conditions.

The results showed that the spine ROM, and especially the maximal thoracic flexion, was larger post-manipulation than pre-manipulation in the HVLA group, which was not the case in the sham group. The mean increase was 20%. The HVLA manipulation applied to T9 had, therefore, a beneficial effect on spine mobility, even in a group composed of young adults with no known spine pathologies. A similar result was found in the sole study to date that tested the effect of thoracic HVLA manipulation on spine ROM (Schiller, 2001). However, this study only examined right and left thoracic lateral flexion using a goniometer (BROM 2), and the population tested included patients with thoracic back pain. To our knowledge, the other studies focusing on thoracic HVLA measured the cervical ROM, and reported small or no beneficial effects (González-Iglesias et al., 2009; Suvarnnato et al., 2013). These negligible variations have led us to exclude the cervical section from spine ROM measurement.

SMT-HVLA has been shown to have a beneficial effect on spine-related pain, both clinically and in experimentally-induced pain (for reviews see Millan et al., 2012a,b). However, it remains unclear from the literature if it has an immediate noticeable biomechanical effect on spinal motion that can be measured in terms of an increased ROM (Millan et al., 2012a). One of the main goals of healthcare practitioners applying SMT-HVLA manipulation is to increase spine ROM, e.g., in athletes before competition or in patients with spine stiffness. A recent review on this aspect emphasized that some studies found spinal manipulation to have limited effect on the ROM, while others found it had none (Millan et al., 2012a). These mitigated effects could probably stem from many factors such as the different tools used in research and in clinical practice to measure ROM (single/double/triple inclinometers, goniometers, a rangiometer, tape measures, visual estimation, spine motion analyzer, etc.), the direction, duration and force applied to the participant's spine, the expertise of the practitioner etc. The present study shows that analogical inclinometers may be used to detect an increased spine ROM following thoracic SMT-HVLA.

Postural mobility, and especially spine mobility, is known to be a key factor of the PKC (Bouisset and Zattara, 1987; Bouisset and Do, 2008). According to the PKC concept, any factor that may enhance (or conversely, alter) this capacity would favor (or hinder) the motor performance and postural stability. This concept has been substantiated by many recent experimental studies which manipulated spine mobility using various means, e.g., by the application of splints at different levels of the spine (Alamini-Rodrigues and Hamaoui, 2016), by experimentally-induced trunk muscular tension (Hamaoui et al., 2004, 2011; Hamaoui and Le Bozec, 2014), or by changing the contact surface between the thighs and seat in the sitting posture (Lino et al., 1992; Teyssèdre et al., 2000; Le Bozec and Bouisset, 2004; Diakhaté et al., 2013). It has been shown that constraining spine mobility may disturb postural equilibrium when maintaining erect posture as revealed by measuring the COP. In dynamical tasks, such as sit-to-stand (Diakhaté et al., 2013; Alamini-Rodrigues and Hamaoui, 2016), maximal isometric ramp push (Le Bozec and Bouisset, 2004), arm pointing (Lino et al., 1992; Teyssèdre et al., 2000) or trunk flexion (Diakhaté et al., 2013) from the sitting posture, facilitating spine mobility has been shown to favor APA development and thus motor performance. Based on the results of these studies—and given that spine mobility is known to be highly solicited during locomotion and gait initiation (e.g., Thorstensson et al., 1984; Ceccato et al., 2009; Cusin et al., 2017), APA development and motor performance could have been expected to be facilitated following SMT-HVLA. It is also noteworthy that T9 is described as the "walking vertebra", a concept arising from the classical article of Wernham (1985). This concept is based on the fact that the T9 vertebra is the inflexion point of the curvature change of thoracic cyphosis in lumbar lordosis. This vertebra ensures the junction of the thoracic and lumbar segments, mainly in their counter-rotation movement, especially while walking. As such, the T9 HVLA manipulation is commonly used by healthcare practitioners in patients with locomotor deficiencies. However, its impact on the locomotor function has to date never been evaluated in systematic studies. In contrast to our expectations, APA amplitude and duration decreased following manipulation in the HVLA group, by 24% and 6%, respectively. This was not the case in the sham group, which shows that this result could not be ascribed to a placebo effect. Not only were the APA parameters reduced, but their efficiency (computed as the ratio [COG velocity at foot-off/APA duration]) was reduced (by 23% as compared to the pre-manipulation condition). In other words, the capacity of the postural system to generate forward propulsive forces during the limited duration of APA was less efficient post-manipulation. As a consequence of the lower initial (foot-off) COG velocity, the peak COG velocity (speed performance) and step length both reached lower values post-manipulation in the HVLA group (compared to the pre-manipulation condition, the decrease was 14%, 12% and 11%, respectively). This finding was expected since it is well-known that the two latter step parameters are positively correlated with the amplitude of APA, i.e., the higher the peak anticipatory backward COP shift is, the higher the speed performance and step lengths are (Brenière et al., 1987). Because there was no change in APA parameters post-manipulation in the sham group, step length and speed performance remained the same as in the pre-manipulation condition. Because in the present study, spine mobility was increased following the HVLA manipulation, which is known to be a factor of improved motor performance, the question arises as to why APA development and speed performance were impaired instead of being improved.

Besides its mechanical effect on spine mobility (for reviews see Pickar, 2002; Millan et al., 2012a), SMT-HVLA is known to induce transient changes in the sensorimotor pathways and structures involved in the coordination between posture and movement. As stressed in the "Introduction" Section, studies using the H-reflex technique to investigate the effect of SMT-HVLA on motoneuronal excitability reported controversial findings, i.e., both an increased (Niazi et al., 2015) and a decreased excitability (Murphy et al., 1995; Dishman and Burke, 2003; Suter et al., 2005) have been found. It seems however

that there exists a consensus concerning the effects of spinal manipulation on the sensorimotor processing and integration at the cortical level, as evidenced with the somatosensory evoked potential technique (SEP). Specifically, recent studies reported an alteration of the amplitude of the cortical SEP peaks N20 and N30 following SMT-HVLA (Haavik and Murphy, 2012; Lelic et al., 2016). The N20 peak is known to represent the arrival of the afferent volley at the primary somatosensory cortex (Desmedt and Cheron, 1980; Nuwer et al., 1994; Mauguière, 1999), while later peaks such as the N30 SEP peak are thought to reflect early sensory-motor integration (Rossi et al., 2003; regarding the possible generators of this peak, see Haavik and Murphy, 2012; Lelic et al., 2016). In addition, studies in the anesthetized cat have shown that spinal manipulation induced changes in the discharge of mechanoreceptors from the paraspinal region, especially group Ia spindle afferents (Pickar, 2002; Reed et al., 2015). The extent to which the cortical and afferent responses to spinal manipulation reflect beneficial outcomes (e.g., pain relief), remains largely unclear in the literature; however, what is clear, is that these responses have the potential to induce changes in the coordination between posture and movement, which is known to strongly rely on proprioceptive inputs from the postural limbs, and even more importantly, on how the CNS processes, interprets and transforms this afferent information into motor commands (Paulus and Brumagne, 2008; Haavik and Murphy, 2012). Lelic et al. (2016) recently speculated that since spinal manipulation is known to reduce pain and improve function in clinical trials (Botelho and Andrade, 2012; Mieritz et al., 2014; Schneider et al., 2015), the observed reduction of the N30 amplitude following SMT-HVLA may reflect a beneficial change. However, it should be noted (as the authors did) that reduced N30 SEP peak amplitudes have also been found in the literature in pathological populations such as Parkinson's disease (Cheron et al., 1994; Kang and Ma, 2016), known to have deficits in APA production during both voluntary lower (e.g., Delval et al., 2014) and upper limb tasks (e.g., Bazalgette et al., 1987). Kang and Ma (2016) even reported that frontal N30 status indicated the motor severity of Parkinson's disease. During gait initiation, disturbances in Parkinson's disease include reduced APA and abnormal APA timing (Delval et al., 2014). During arm elevation, postural movements are known to be less anticipatory in Parkinson's patients than in controls (Bazalgette et al., 1987). In the present study, APA were also less anticipatory, had a smaller amplitude and were less efficient in the HVLA group following manipulation than prior to manipulation. Globally taken, the results from the literature may thus suggest that a reduction of the N30 amplitude after HVLA manipulation may reflect a transitory alteration in the cortical integration of sensory-motor information, and may thus reflect a negative change. If so, such alteration has the potential to affect motor coordination during locomotor tasks such as gait initiation. In other words, we propose that a neural effect, possibly mediated by a transient alteration in the early sensory-motor integration following SMT-HVLA could be one of the mechanisms responsible for the present results. This neural effect may have masked the potential mechanical benefits associated with increased spine mobility.

STUDY LIMITATIONS

There are some limitations to the present study that should be pointed out. First, this study only focused on a biomechanical investigation. It is clear that studies linking the changes in motor behavior observed in the present study, to the changes of activity in the neural structures and pathways reported in the literature should be carried out to further substantiate the data interpretation. This is why we used the term "pilot" in the title of this article. Second, it should be emphasized that only short-term effects were investigated. It is not excluded that thoracic HVLA manipulation may have a long-term beneficial effect on APA and speed performance. Third, the biomechanical responses described in this study were obtained from young healthy participants and may not be generalizable to other populations, including patients with spinal pain. Finally, it is known that a manipulation is rarely specific to only the adjustment site (Ross et al., 2004). This non-specificity is amplified by the technique used in this article as it is an indirect technique. There is no direct contact of the practitioner with the chosen vertebra since the compressive force is indirectly transmitted by the hand of the patient between his own vertebrae and the thorax of the practitioner. We point out that the role of T9 vertebra and the interest of its manipulation is based solely on empirical knowledge although these notions are still taught in physiotherapy and osteopathy schools. Currently, some studies suggest that the center of rotation of the thoracic zone in the horizontal plane corresponds to a very wide area (T7–L3; Konz et al., 2006).

CONCLUSION

The present results showed that thoracic HVLA manipulation in young healthy participants has an immediate beneficial effect on spine mobility but a detrimental effect on APA development and speed performance during gait initiation. It thus seems that HVLA manipulation should be considered with caution by participants who seek an immediate increase of speed performance during locomotor tasks.

AUTHOR CONTRIBUTIONS

SD and EY designed the study; collected, analyzed and interpreted the data; drafted and revised the manuscript; gave final approval. AH and AD interpreted the data; drafted and revised the manuscript.

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Recovery from Multiple APAs Delays Gait Initiation in Parkinson's Disease

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Background: Freezing of gait in Parkinson's disease (PD) has been linked with deficits in inhibitory control, but causal mechanisms are not established. Freezing at gait initiation (start hesitation) is often accompanied by multiple anticipatory postural adjustments (APAs). If inhibition deficits contribute to freezing by interfering with ability to inhibit initial weight shifts in the wrong direction, then PD subjects should experience more episodes of multiple APAs than healthy controls (HCs) do. If inhibition deficits contribute to freezing by interfering with ability to release a previously inhibited step following multiple APAs, then step onset following multiple APAs should be delayed more in people with PD than in HCs.

Methods: Older adults with PD and HC subjects rapidly initiated stepping in response to a light cue in blocks of simple (SRT) and choice (CRT) conditions. We recorded kinematics and ground reaction forces, and we administered the Stroop task to assess inhibitory control.

Results: Multiple APAs were more common in CRT than SRT conditions but were equally common in HC and PD subjects. Step onsets were delayed in both conditions and further delayed in trials with multiple APAs, except for HC subjects in SRT trials. Poor Stroop performance correlated with many multiple APAs, late step onset, and rearward position of center of mass (COM) at cue presentation. Forward motion of the COM during the APA was higher in trials with multiple APAs than in trials with single APAs, especially in CRT trials and in PD subjects *without* self-reported freezing.

Conclusion: Start hesitation is not caused by multiple APAs *per se*, but may be associated with difficulty recovering from multiple APAs, due to difficulty releasing a previously inhibited step.

Keywords: Parkinson's disease, anticipatory postural adjustment, freezing of gait, start hesitation, inhibition, inhibitory control, gait initiation, voluntary stepping

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INTRODUCTION

People with Parkinson's disease (PD) commonly experience a gait problem known as *start hesitation*, a brief episode of freezing of gait in which step initiation is involuntarily delayed (Nutt et al., 2011). While the precise causes of start hesitation (and the wider category of gait freezing) are not yet known, several intriguing clues exist. For instance, start hesitation is often accompanied by trembling of the knees and multiple lateral weight shifts, termed anticipatory postural adjustments, or *APAs* (Jacobs et al., 2009). The dissociation between APA onset and step onset in these cases led

to the proposal that freezing may be caused by decoupling between the postural preparation and the step (Jacobs et al., 2009). Freezing of gait has also been associated with cognitive deficits in the domain of executive function, especially inhibitory control (Amboni et al., 2008; Vandenbossche et al., 2011; Cohen et al., 2014). We postulate that posture-step decoupling and inhibitory deficits may play a joint role in the etiology of start hesitation.

Previous work investigating start hesitation in PD demonstrated multiple APAs in protective stepping but did not elicit substantial numbers of multiple APAs in voluntary stepping (Jacobs et al., 2009). In everyday life, however, start hesitation is particularly problematic during voluntary stepping; the accepted definition of freezing, "brief, episodic absence or marked reduction of forward progression of the feet despite the intention to walk" (Nutt et al., 2011), implies the thwarting of a voluntary act. Therefore, the present study makes use of a protocol known to elicit multiple APAs in voluntary stepping in healthy adults (Cohen et al., 2011).

To initiate a step, it is necessary to select a stepping leg and shift the weight off the stepping leg onto the stance leg. Shifting the weight off of the intended stepping leg is achieved by first briefly *increasing* vertical ground reaction force under the stepping foot, in order to push off (Brenière et al., 1987). Because the needed initial weight shift is toward the stepping foot (in the opposite direction from the goal), inhibition may be required to avoid shifting the weight in the wrong direction when attempting to step. Therefore, inhibitory control may be challenged experimentally by forcing subjects to make rapid choices about which foot to step with. In a previous study, we asked healthy older subjects to perform a stepping task in a choice reaction time (CRT) condition, which presented a foot selection challenge, as well as a simple reaction time (SRT) condition, in which the stepping foot was known in advance (Cohen et al., 2011). We found that in the CRT condition only, healthy older adults made initial weight shift errors, leading to multiple APAs in 25% of trials. The presence of multiple APAs resulted in statistically significant step onset delays of about 130 ms. Furthermore, the proportion of trials with weight shift errors was strongly correlated with the time to complete the conflict condition of the Stroop task, a typical measure of inhibitory control. Thus, a possible mechanism by which inhibitory deficits could contribute to freezing of gait is by making foot selection more difficult, leading to multiple APAs and start hesitation. However, questions remain as to whether and how the multiple APAs elicited by CRT stepping in healthy older adults are related to start hesitation in subjects with PD.

Parkinson's disease impairs frontostriatal circuitry, which is important for selection and inhibition of actions (Mostofsky and Simmonds, 2008). Individuals with PD who freeze have significantly reduced structural and functional connectivity in the right hemisphere inhibitory circuit between the SMA and STN compared to individuals with PD who do not freeze (Fling et al., 2013, 2014). Furthermore, freezing of gait is specifically associated with deficits in cognitive inhibitory control and conflict resolution (Amboni et al., 2008; Vandenbossche et al., 2011; Cohen et al., 2014) and especially with difficulty releasing inhibition (Cohen et al., 2014). We investigated two (non-exclusive) ways that deficits in inhibitory control could interact with multiple APAs and lead to posture-step decoupling and start hesitation. One possible way that inhibitory deficits could contribute to start hesitation is if individuals with PD who experience freezing of gait are particularly *predisposed* to multiple APAs, due to problems selecting the correct stepping leg initially. Another possibility is that individuals with PD who freeze might have a particularly difficult time *recovering* from multiple APAs, due to difficulty releasing inhibition.

The primary purpose of the present study was to examine the prevalence and influence of multiple APAs on step onset in adults with PD who did and did not report freezing, compared with healthy older adults, and to relate these findings to differences in inhibitory control. A secondary purpose of the study was to examine the kinematics of step onset associated with multiple APAs. Freezing of gait is strongly associated with fall risk (e.g., Bloem et al., 2004; Delval et al., 2014b). If, during a delayed step onset, the center of mass (COM) continues to move forward in adults with PD, this could predispose these individuals to falls.

Subjects performed a cued step initiation task in which trials were presented with (SRT) or without (CRT) foreknowledge of the stepping foot. To assess start hesitation, we measured kinematics and forces under subjects' feet; we then identified trials with multiple APAs and looked at onset times of weight shifts and first steps, as well as body position. Our hypotheses were as follows: (1) If inhibition is important for step initiation, we predicted that poor performance on the Stroop task would correlate with high prevalence of multiple APAs and delayed step onset. (2) If difficulty selecting the stepping leg (and inhibiting shifting weight in the wrong direction) contributes to start hesitation, we predicted that PD subjects who freeze would demonstrate a larger proportion of multiple APAs (especially in the CRT condition) relative to subjects who do not freeze. (3) If difficulty recovering from a multiple APA (and releasing inhibition of the step) contributes to start hesitation, we predicted that multiple APAs would lead to a larger step onset delay in PD subjects (especially those who freeze) than in subjects without PD. (4) We also predicted that the COM would travel forward farther during multiple APAs in subjects with PD (especially in those who tend to freeze) than in subjects without PD.

MATERIALS AND METHODS

Subjects

Twenty-five adults with idiopathic PD in a practical (14-h) OFF state participated in the study. Twelve self-identified as experiencing freezing of gait, and 13 did not. These subjects were compared with 12 previously studied healthy comparison (HC) subjects without PD (Cohen et al., 2011). None of the subjects had orthopedic problems or identified neurological disorders other than PD. All had normal or corrected-to-normal vision and hearing. See **Table 1** for details. The experiment was conducted in accordance with the Declaration of Helsinki and its later amendments. All procedures were carried out with adequate understanding and written consent by the subjects involved and

TABLE 1 | Demographic attributes of participants in healthy control (HC), non-freezing Parkinson's (NF), and Parkinson's with freezing (FR) groups; mean (SD); UPDRS, Unified Parkinson's Disease Rating Scale (Fahn and Elton, 1987).

	HC	*NF*	*FR*
Age	66.9 (6.6)	66.6 (5.9)	67.7 (8.9)
Number Men/Women	11/2	10/3	10/2
UPDRS III total	–	32.2 (7.7)	43.0 (14.0)
UPDRS: bradykinesia	–	15.0 (5.4)	19.9 (5.4)
UPDRS: PIGD	–	2.6 (2.2)	5.2 (3.4)
UPDRS: rigidity	–	8.0 (5.2)	8.9 (3.7)
Disease duration (Years)	–	6.2 (3.6)	10.0 (9.0)
H&Y (Hoehn and Yahr, 1967)	–	2.2 (0.4)	3.0 (0.8)

with the ethical approval of the institutional review board at Oregon Health and Science University.

Design and Protocol

The task was to initiate walking as quickly as possible in response to a cue, taking three steps before stopping. Subjects completed 2 blocks of 20 trials in a counterbalanced repeated measures design, with and without foreknowledge of stepping foot. Subjects began each trial looking straight ahead, with their body weight evenly balanced across two separate force platforms. Their feet were placed at a self-chosen comfortable width for walking, marked with tape so that every trial would begin from the same foot position. Before each trial, the experimenter monitored the force on each force plate on a computer screen and, when necessary, instructed the subject to shift to the left or right to achieve a balanced weight distribution (with no more than 51% of weight on either foot). An eight-camera motion-capture system (Motion Analysis System, Santa Rosa, CA, USA) gathered position data from passive reflective markers on each subject's trunk, head, and limbs, sampled at 60 Hz. Markers were placed bilaterally on the calcaneus, fifth metatarsal, lateral malleolus, lateral condyle, trochanter, acromial extremity of the clavicle, proximal and distal ends of the ulna, tragus, and supraorbital foramen of the subject, and on the force plate for reference.

The "go" cue was a point of light that appeared on a low wall about 4 m in front of the subjects, approximately 30 cm either to the left or right of the subject's midline. A vertical line of tape halfway between the locations of the target lights ensured that subjects could distinguish which side the light was on **Figure 1** shows the setup. Subjects were instructed to initiate stepping with whichever foot was indicated by the light, to respond quickly, and to take three steps before stopping. The light cue appeared 2200 ms after the start of the trial and remained on for 600 ms. Data collection lasted 4000 ms. In the block with foreknowledge of the stepping foot (SRT trials), subjects were informed in advance that the light cue would always appear on the same side as their dominant foot. In the block without foreknowledge (CRT trials), subjects were informed that the cue could appear on either side. In half of these trials the cue appeared on the left, and in half it appeared on the right, in pseudo-random order.

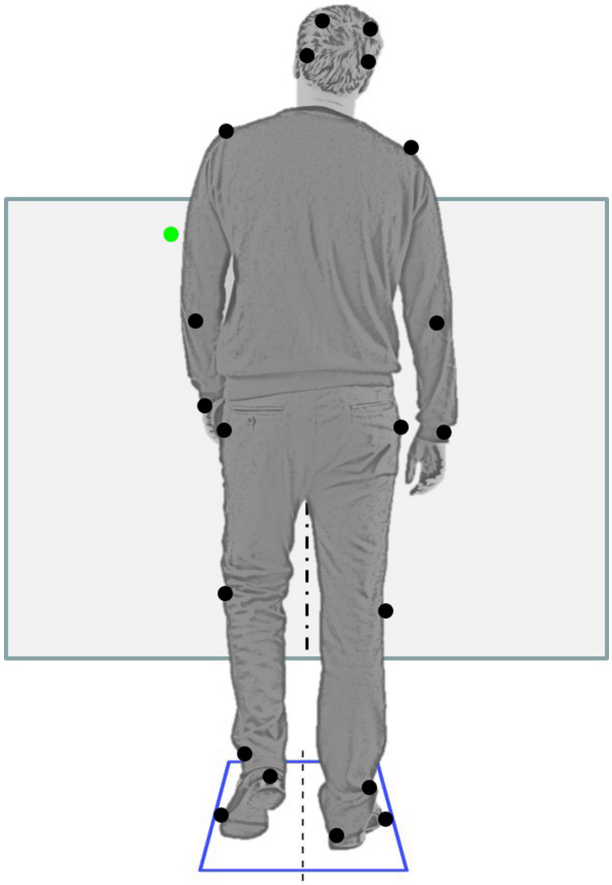

FIGURE 1 | Setup: rear view of a subject beginning to step. The subject's feet are on two separate force plates. Black dots show the placement of reflective markers on bony landmarks and force platform (top two markers are actually above eyebrows). The subject faces a low wall 4 m away. A green laser pointer light appears either on the left (shown) or on the right. The subject steps with the foot on the same side as the light. Figure modified from an image by Konstantin Kamenetskiy © 1234RF.com.

Data Analysis

Our main dependent measures were the onset times of the first APA and the first step as a function of group (HC, PD without freezing, PD with freezing), trial type (SRT, CRT), and presence or absence of multiple APAs. The first APA onset was defined as the time when the difference in vertical force under the two feet increased by 5% of body weight. The step onset was defined as the time when vertical force under either foot decreased to zero. Post-processing was performed in Matlab (R2014a, The Mathworks Inc, Natick, MA, USA). We also examined APA duration, defined as (time of step onset – time of APA onset).

Variables of secondary interest were the relative location of the COM in the anteroposterior (A/P) axis at cue and step onset, the peak velocity of stepping foot, and the first step length. To determine whole body COM, we computed the weighted average of the position of each body segment (Vaughan et al., 1992) based on measurements of the length, width, and circumference of 26 body segments, and self-reported heights and weights for each

subject (Chandler et al., 1975). Peak velocity and step length were computed from a reflective marker on the foot. Finally, we looked at correlations between APA/step measures and score on the Stroop task. **Figure 2** shows the vertical force under the stepping foot and the A/P position of the COM for three exemplar trials from a single PD subject with freezing: a normal step with a single weight shift, a trial with two weight shifts, and a trial with more than two weight shifts.

To assess inhibitory function, we had subjects complete the Stroop color-word task (Stroop, 1935). This task measures how well subjects can inhibit a well-learned response to a common stimulus (reading words) in order to respond to another aspect of the stimulus (color names). The task includes three conditions: color naming, reading, and conflict. The conditions are tested in blocks, in fixed order. For each condition, subjects viewed a page containing 100 stimuli (4 columns of 25 items). Words were written in 20-point Times New Roman font, and the page was placed at a comfortable reading distance in front of the subject. Subjects were to respond verbally to each stimulus in order, pointing to each item as they responded to it, to facilitate the experimenter's monitoring of errors. For the color naming condition, the stimuli were blocks of black, red, blue, purple, and green, arranged in random order. For the reading condition, the stimuli were words naming the colors previously presented, printed in black ink and arranged in random order. For the conflict condition, stimuli were the same words as those in the second condition, printed in the same colors as those in the first condition, with words and colors randomly paired. For this condition, subjects were required to ignore the words and name the ink colors. Before every condition, a few practice trials were conducted to assure that subjects understood the task and were able to correctly read the words and name the colors. The Stroop interference score was computed as (time + errors in conflict condition – time in reading condition).

Before analyzing the data, we removed trials in which subjects (1) drifted laterally so that one side had >52.5% of the weight during the baseline period, (2) initiated an APA before the light cue, (3) stepped with the wrong foot, or (4) did not step within the 6 s window of data collection, as well as (5) trials during which the equipment did not properly record. Statistics were computed with R (R Development Core Team, 2014), with an alpha of 0.05 for all tests. We first conducted 2 × 3 ANOVAs on each dependent variable, with foreknowledge of stepping foot (SRT vs. CRT) and group (HC vs. PD with freezing vs. PD without freezing) as the factors. Because we were comparing three groups, we followed significant ANOVA results on the group factor with Tukey *post hoc* comparisons.

For a more in-depth analysis, we then further divided the trials by presence or absence of multiple APAs and performed three-way ANOVAs. Because these included the effect of multiple APAs as a factor, we did not have equal numbers of trials in each cell. Therefore, we used a linear mixed model approach in which data from each trial were entered individually into each model using subject as a random effect. This approach accounts for different numbers of trials in different cells (Stroup, 2012). *Post hoc* comparisons were computed using the "phia" (*post hoc* interaction analysis) package in R, with Bonferroni corrections applied to the *p*-values. Finally, we computed the correlations between Stroop score and step characteristics.

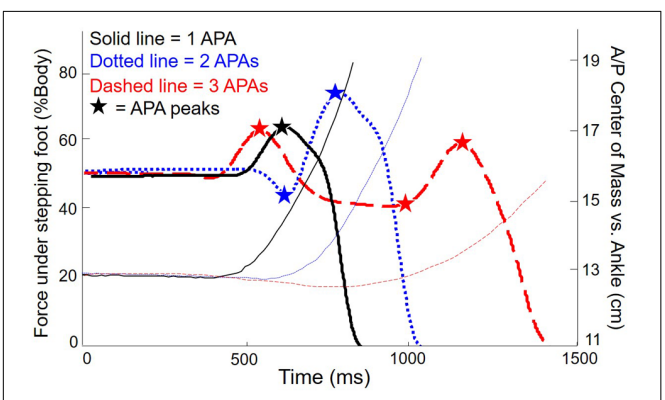

FIGURE 2 | Force and anteroposterior (A/P) center of mass (COM) for three exemplary trials from one subject with PD. Thick lines: vertical force under stepping foot. Thin lines: COM with respect to ankles (baseline shifted to emphasize forward motion of COM). Solid lines: single APA. Dotted lines: two APAs. Dashed lines: three APAs.

RESULTS

Two-Way ANOVAs

After cleaning the data as described above, we were left with 1205 trials for analyses (an average of 32.6 per subject). **Figure 3** shows the proportion of trials with multiple APAs, as a function of group and condition. Multiple APAs were four times more prevalent in the CRT condition (∼20%) than in the SRT condition (∼5%),

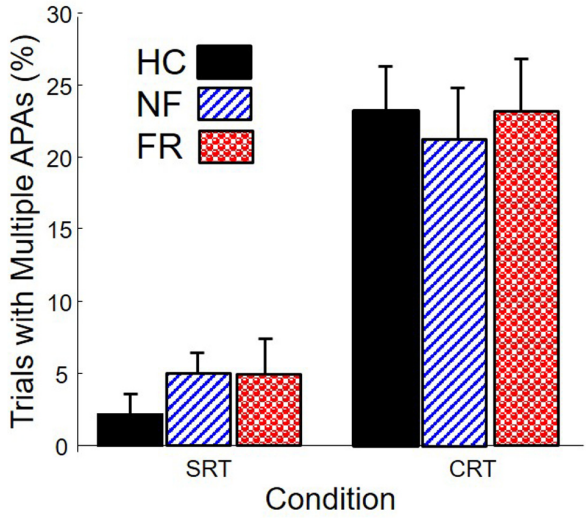

FIGURE 3 | Percentage of trials with multiple APAs in healthy control subjects (HC), PD subjects without freezing (NF), and PD subjects with freezing (FR), in simple reaction time (SRT) and choice reaction time (CRT) stepping.

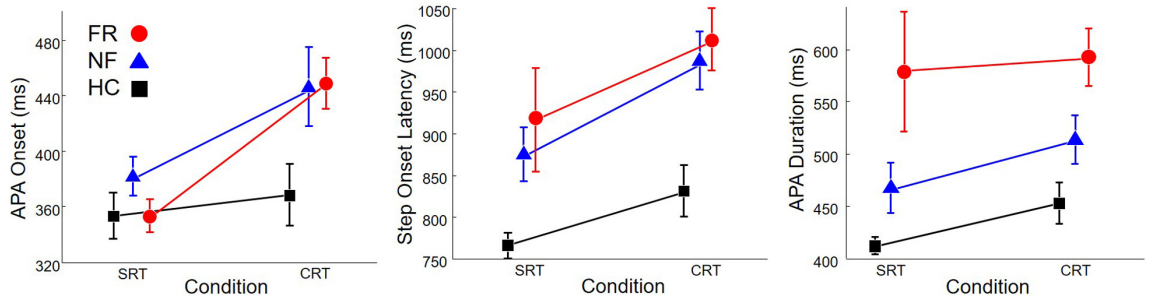

FIGURE 4 | Onset of anticipatory postural adjustment (APA; Left), step onset (Middle), and APA duration (Right) in healthy control subjects (HC, Squares), PD subjects without freezing (NF, Triangles), and PD subjects with freezing (FR, Circles), in SRT and CRT stepping. Note that the scale on the *y*-axis is different in each sub-figure.

$F(1,68) = 45.2, p < 0.0001$. Surprisingly, there were no differences in prevalence of multiple APAs among the groups.

Onset times of the first APA and first step, as well as APA duration, are shown in **Figure 4**. APA onset was 88 ms earlier in SRT trials than in CRT trials (left plot), $F(1,68) = 12.8, p < 0.0001$. There was also a significant effect of group, $F(2,68) = 3.9$, $p = 0.02$. *Post hoc* comparison indicated that PD subjects without freezing initiated APAs later than HC subjects.

In addition, step onset (middle plot) was 91 ms earlier in SRT trials than in CRT trials, $F(1,68) = 7.6$, $p = 0.008$, and was also affected by group, $F(2,68) = 11.5$, $p < 0.0001$. *Post hoc* comparison indicated that HC subjects stepped 155 ms earlier than PD subjects without freezing and 183 ms earlier than PD subjects with freezing.

Anticipatory postural adjustment duration (right plot) was not affected by trial type but was affected by group, $F(2,68) = 10.1$, $p = 0.0001$. APA duration in HC subjects was 101 ms shorter than in PD subjects without freezing and 146 ms shorter than in PD subjects with freezing.

Three-Way Mixed Model ANOVAs

To determine the influence of multiple APAs on step preparation, we analyzed the outcome variables with trials divided according to whether or not there were multiple APAs. The primary results can be seen in **Figure 5**, and the statistics are shown in **Table 2**. The top row shows initial APA onsets. There was a main effect of the presence of multiple APAs, with initial APAs occurring, on average, 70 ms earlier in trials with multiple APAs than in trials with single APAs. There was also an interaction between group and trial type, with *post hoc* tests revealing that trial type had less influence on APA initiation in HC subjects (51 ms) than in PD subjects with freezing (136 ms).

The effect of multiple APAs on step onset time depended on the group and trial type, as seen in the middle row of **Figure 5**. Multiple APAs caused a step onset delay in PD subjects with freezing (134 ms) and in PD subjects without freezing (153 ms) but not in HC subjects. There were also interactions between group and trial type and between trial type and presence of multiple APAs that are best understood by examining the three-way interaction: multiple APAs delayed step onset in both trial types for PD subjects, but only in CRT trials for HC subjects.

Anticipatory postural adjustment durations, shown in the bottom row of **Figure 5**, were longer in PD subjects with freezing (613 ms) and in PD subjects without freezing (604 ms) than in HC subjects (449 ms). Multiple APAs lengthened APA duration an average of 174 ms; the effect was larger in PD subjects with freezing (199 ms) and in PD subjects without freezing (220 ms) than in HC subjects (102 ms). There was also a three-way interaction: the effect of multiple APAs on APA duration was smallest in HC subjects in SRT trials.

Most of the multiple weight shifts we observed were actually *dual* weight shifts, in which the initial weight shift was in the wrong direction and was followed by a single corrective weight shift. Occasionally, subjects exhibited *more than two* APAs before a step. This pattern only occurred in six subjects (one HC, two PD without freezing, and three PD with freezing), so there were not enough trials with more than two APAs to perform a statistical analysis on these trials separately. Instead, we examined their influence by removing them from the data and reanalyzing it (see **Table 3**). The reanalysis did not substantially alter the results.

Kinematic data are presented in **Figure 6**. The left plot shows the length the initial step as a function of group, trial type, and presence or absence of multiple APAs. Only group had an effect, $F(2,34) = 12.4$, $p < 0.0001$: initial steps of PD subjects with freezing were 16 cm shorter than those of PD subjects without freezing and 21 cm shorter than those of HC subjects, but there was no difference between non-freezing PD subjects and healthy controls, and no significant effect of condition or number of APAs. Peak velocity (not pictured) was 0.98 correlated with peak velocity and showed the same effect of group, $F(2,34) = 15.6$, $p < 0.0001$. *Post hoc* tests indicated that PD subjects with freezing stepped at approximately 90 cm/s, which was 52 cm/s more slowly than PD subjects without freezing and 78 cm/s more slowly than HC subjects, but there was no other difference.

At the time of the "go" cue, the anteroposterior location of the COM relative to the ankles averaged 7.7 cm and was not affected by group, trial type, or presence or absence of multiple APAs. The center and right plots of **Figure 6** show the amount of forward motion of the COM between the time of the "go" cue and the step onset. There was an interaction between group and presence/absence of multiple APAs, $F(2,1144) = 8.0$, $p = 0.0004$, with multiple APAs leading to the largest increase in forward

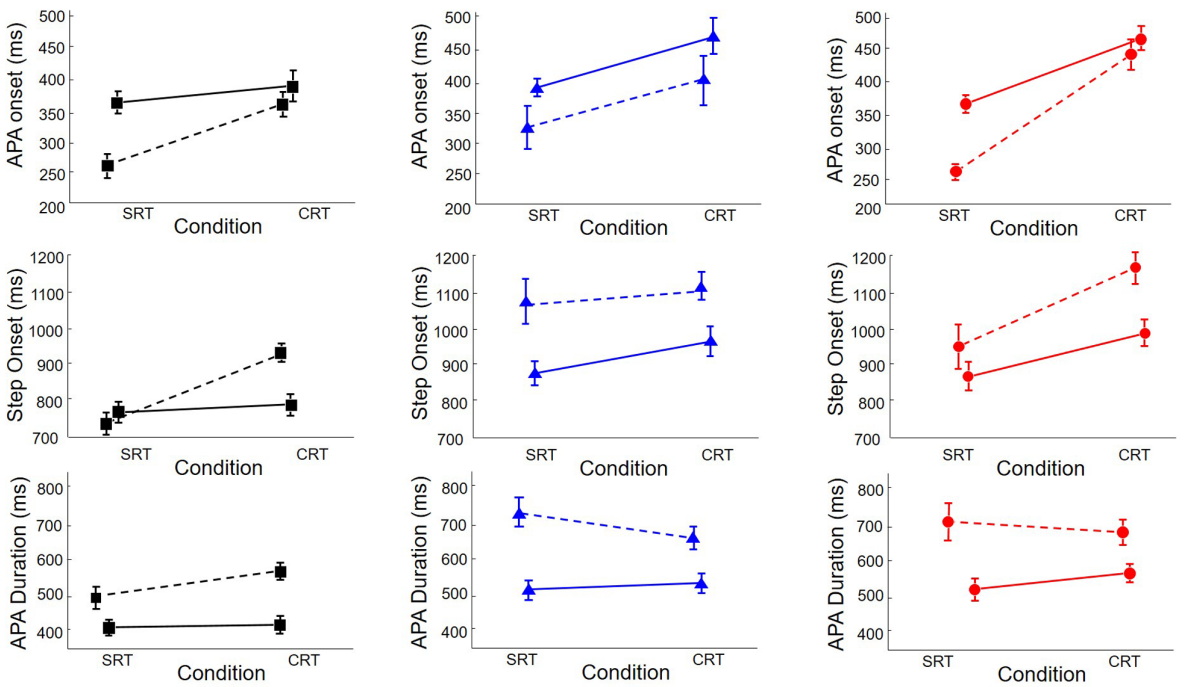

FIGURE 5 | Onset of APA (Top), step onset (Middle), and APA duration (Bottom) in healthy control subjects (HC, Squares, Left), PD subjects without freezing (NF, Triangles, Middle), and PD subjects with freezing (FR, Circles, Right), in SRT and CRT stepping, divided according to whether there was only a single APA (solid lines) or multiple APAs (dashed lines).

TABLE 2 | Anticipatory postural adjustment (APA) and step onset latencies as a function of group, condition, and single vs. multiple APAs; df, degrees of freedom.

	APA onset latency			Step onset latency			APA duration		
	df	F	p	df	F	p	df	F	p
Group	2,34	0.6	0.56	2,34	3.1	0.06	2,34	4.1	**0.03**
Condition	1,1159	2.8	0.09	1,1159	2.8	0.10	1,1159	0.4	0.54
Single vs. Multiple APAs	1,1159	9.9	**0.002**	1,1159	1.0	0.31	1,1159	4.3	**0.04**
Group × Condition	2,1159	9.1	**0.0001**	2,1159	10.0	**0.0001**	2,1159	2.0	0.13
Group × Multiple APAs	2,1159	0.6	0.52	2,1159	7.1	**0.0008**	2,1159	12.6	**<0.0001**
Condition × Multiple APAs	1,1159	2.7	0.10	1,1159	8.4	**0.004**	1,1159	6.5	**0.01**
Group × Condition × Multiple APAs	2,1159	2.1	0.12	2,1159	4.4	**0.01**	2,1159	6.2	**0.002**

Bolded p values are < 0.05.

TABLE 3 | Anticipatory postural adjustment and step onset latencies as a function of group, condition, and single vs. dual APA; df, degrees of freedom.

	APA onset latency			Step Onset Latency			APA Duration		
	df	F	p	df	F	p	df	F	p
Group	2,34	0.6	0.57	2,34	3.2	0.06	2,34	4.3	**0.02**
Condition	1,1151	2.8	0.09	1,1151	3.0	0.08	1,1151	0.4	0.50
Single APA vs. Dual APA	1,1151	9.4	**0.002**	1,1151	2.0	0.16	1,1151	2.6	0.10
Group × Condition	1,1151	9.2	**0.0001**	1,1151	10.9	**<0.0001**	1,1151	2.5	0.08
Group × Dual APA	1,1151	0.8	0.45	1,1151	8.2	**0.0003**	1,1151	16.6	**<0.0001**
Condition × Dual APA	1,1151	2.5	0.12	1,1151	9.7	**0.002**	1,1151	9.4	**0.002**
Group × Condition × Dual APA	1,1151	1.8	0.17	1,1151	5.4	**0.005**	1,1151	10.2	**<0.0001**

Bolded p values are < 0.05.

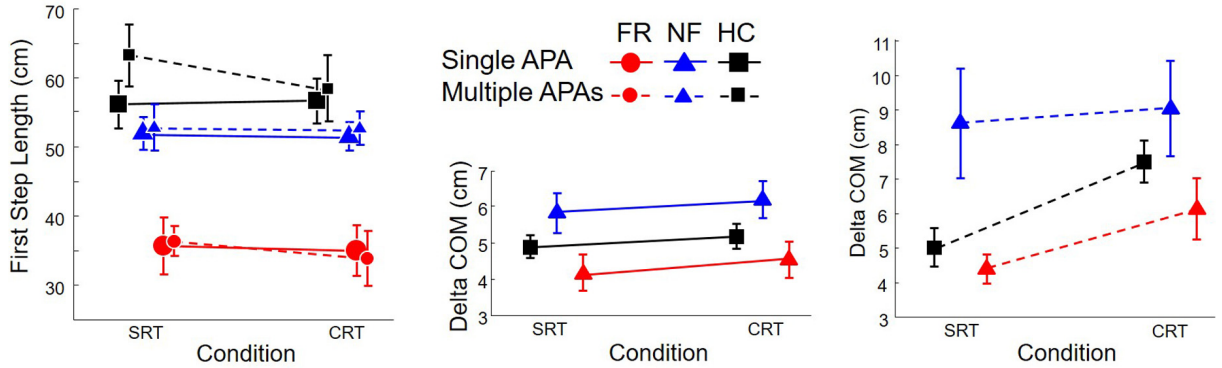

FIGURE 6 | Kinematics for healthy control subjects (HC, Squares), PD subjects without freezing (NF, Triangles), and PD subjects with freezing (FR, Circles), in SRT and CRT stepping. Left: length of first step. Middle and Right: Forward motion of the COM from the time of the "go" cue to the time of step onset. Solid lines: trials with single APAs. Dashed lines: trials with multiple APAs.

motion in PD subjects without freezing (28 mm), to a lesser increase of forward motion in HC subjects (13 mm), and to no significant change in forward motion of COM in PD subjects with freezing. There was also an interaction between trial type and presence/absence of multiple APAs, $F(1,1144) = 12.0$, $p = 0.0005$, with multiple APAs increasing forward motion more in CRT trials (21 mm) than SRT trials (10 mm). A three-way interaction, $F(2,1144) = 3.2$, $p = 0.04$, reflected the large forward lean of PD subjects without freezing during SRT trials.

Correlations between Stroop score and APA/step measures are shown in **Figure 7** and **Table 4**. High values for Stroop score indicate poor inhibitory control. There was no overall difference in Stroop score between PD subjects with and without self-reported freezing of gait. Poor Stroop performance correlated with high proportion of trials with multiple APAs, with slow step onset latency and APA duration, and with COM farther back at the time when the cue appeared. Stroop scores were not related to APA onset, step velocity, or forward motion of the COM during

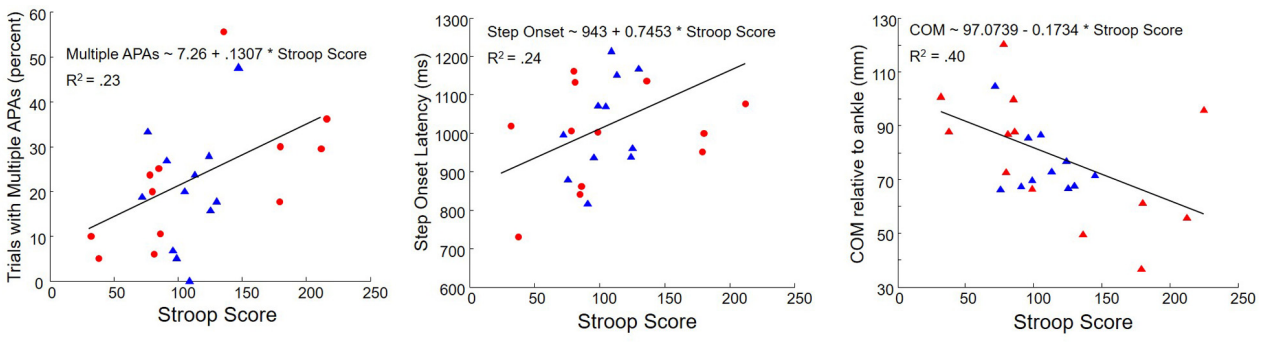

FIGURE 7 | Correlations between Stroop Score and percent trials with multiple APAs (Left), step onset latency (Middle), and COM at cue presentation (Right) in subjects with PD. Triangles: subjects without freezing. Circles: subjects with freezing.

TABLE 4 | Pearson's correlation coefficient (and two-tailed *p*-value) for main outcome variables (PD subjects only).

	Multiple APAs	APA onset latency	Step onset latency	Peak velocity	COM at Cue	Change in COM	UPDRS
Stroop score	**0.48 (0.02)**	0.24 (0.26)	**0.49 (0.02)**	−0.33 (0.12)	**−0.63 (0.001)**	−0.18 (0.40)	0.34 (0.10)
Multiple APAs	–	0.06 (0.76)	0.13 (0.52)	−0.36 (0.08)	−0.33 (0.10)	−0.29 (0.16)	0.01 (0.95)
APA onset	–	–	**0.65 (0.005)**	−0.12 (0.56)	−0.17 (0.45)	−0.16 (0.45)	0.08 (0.71)
Step onset	–	–	–	−0.18 (0.38)	−0.15 (0.48)	0.14 (0.51)	**0.60 (0.001)**
Peak velocity	–	–	–	–	0.26 (0.21)	**0.69 (0.001)**	−0.31 (0.12)
COM at cue	–	–	–	–	–	0.28 (0.18)	−0.01 (0.95)
Change in COM	–	–	–	–	–	–	0.08 (0.68)

Bolded p values are < 0.05.

the APA. The proportion of trials with multiple APAs was not related to any other measured aspect of step initiation.

DISCUSSION

This study investigated the relationships among inhibition, foot selection, multiple APAs, and start hesitation in voluntary stepping. Previous results indicated that when protective steps are evoked by postural perturbations, multiple APAs are more common in PD subjects who tend to freeze than in HC subjects (Jacobs et al., 2009). Previous findings also indicated that challenging foot selection leads to a substantial increase in the prevalence of multiple APAs during voluntary step initiation in healthy older adults (Cohen et al., 2011). The experiment described here built on both of those studies by introducing challenging foot selection during voluntary step initiation in subjects with PD. To manipulate foot selection difficulty, we compared step initiation during SRT and CRT conditions. To assess inhibitory control, we measured performance on a Stroop task.

We found some overall differences among the groups that were consistent with the literature: HC subjects had the earliest APA onsets, and PD subjects had the latest step onsets and the longest APA durations. These differences were in the range of 150 ms. In addition, PD subjects with freezing took the shortest initial steps, with the lowest peak velocity. The step length difference between PD subjects with and without freezing was 16 cm, which is a substantial 30% reduction. The difference in peak velocity of the stepping foot was proportional to the difference in step length. These findings are consistent with previous findings, e.g. (Gantchev et al., 1996).

The CRT manipulation was successful at increasing the prevalence of multiple APAs before stepping: multiple APAs were four times more likely in CRT trials than in SRT trials. CRT trials also led to a small (less than 100 ms) delay in onset of the first APA and the first step, relative to the SRT trials. Trial type did not affect APA duration, peak stepping velocity, or step length. In addition (and contrary to our prediction), multiple APAs were no more likely in PD subjects than in HC subjects, nor in PD subjects with a self-reported freezing tendency than in PD subjects without self-reported freezing. This result suggests that the observed link among inhibition deficits, multiple APAs, and freezing is probably *not* due to a greater tendency in people with freezing to initially shift their weight in the wrong direction before stepping. It also emphasizes the fact that although multiple APAs are linked to start hesitation, they are not one and the same thing.

Multiple APAs were associated with early APA onsets in all subjects; however, they were followed by delayed step onsets only in PD subjects, with APA durations increasing about 140 ms. This result is consistent with the idea that PD leads to a reduced ability to release inhibition of the step when the APA has been initiated (Boulinguez et al., 2009; Cohen et al., 2014). The resulting decoupling between the APA and the step could lead to start hesitation (Jacobs et al., 2009; Delval et al., 2014a; Lin et al., 2016). This line of thinking is supported by recent neuroimaging evidence that freezing episodes are associated with functional decoupling between the cognitive control network and the basal ganglia network (Shine et al., 2013) and is in general agreement with a recent review suggesting that freezing of gait is likely due to a combination of cognitive and decoupling factors (Nieuwboer and Giladi, 2013). However, the power of this argument is weakened by our finding that step onset delays following multiple APAs were not larger in PD subjects with freezing than in PD subjects without freezing. Furthermore, PD subjects were more affected than HC subjects by multiple APAs *only* when the stepping foot was known in advance (SRT condition). This relative deficit for PD subjects in SRT trials could indicate a failure to fully benefit from advance knowledge of the stepping foot, which would make sense given the well-established deficit of subjects with PD in automatic movement preparation (Bloxham et al., 1984; Wu and Hallett, 2005; Cameron et al., 2010).

One motivation for studying start hesitation in PD is its association with fall risk (e.g., Bloem et al., 2004; Delval et al., 2014b). If, during a delayed step onset, the COM continued to move forward, this could pose a threat to balance. For all groups of subjects in the present study, the COM moved farther forward during trials with multiple APAs than during trials with single APAs, especially in CRT trials. However, despite the markedly later step onset latencies in subjects with PD and freezing compared to other groups during multiple-APA trials, and contrary to our prediction, the forward travel of the COM was actually affected *less* by multiple APAs in the self-reported freezing group than in the other subject groups. It may be that people with PD who are aware that they might freeze develop compensatory strategies, such as not leaning forward when initiating gait. It is also possible that difficulty shifting weight forward is a primary element of the dysfunction in people who freeze. In support of the latter alternative, the amount of forward weight shift during step preparation was strongly correlated with the subsequent peak velocity of the step. This explanation is also consistent with (Brenière et al., 1987).

We predicted that subjects who performed poorly in the Stroop task would also show a high prevalence of multiple APAs and delayed step onset; this prediction was supported. This result is consistent with previous findings that inhibitory deficits are associated with self-reported freezing severity (Amboni et al., 2008; Vandenbossche et al., 2011; Cohen et al., 2014) and with clinician-rated severity (Cohen et al., 2014). As described above, we propose that inhibition deficits in PD may also play a *causal* role in start hesitation and freezing, by contributing to the decoupling of the APA and the step.

Interestingly, poor Stroop performance was also associated with a tendency to stand with the COM relatively far back while waiting for the cue to appear. This is not an artifact of severity, as UPDRS was related only with step onset latency and not with Stroop or COM. There is a well-known relationship between attentional control and the steadiness or stability of COM during standing balance, e.g. (Woollacott and Shumway-Cook, 2002).

However, few studies have examined the relationship between cognitive factors and postural alignment or standing position, c.f. (Cohen et al., 2016). This relationship may bear further investigation.

This study had several limitations. First, although we examined voluntary stepping (not protective stepping), subjects were provided with a "go" cue. External cues are thought to assist step preparation in people with PD (Delval et al., 2014a), and the basal ganglia are thought to be more critical for self-initiated, rather than externally triggered, voluntary movements (Boecker et al., 2008; Toyomura et al., 2012). Therefore, future studies of step initiation and freezing should eliminate the external cue. Second, although our interest is in freezing of gait and start hesitation, we didn't actually measure freezing episodes. Instead, our primary outcome was latency of step onset, which might reflect a tendency to freeze but is not the same thing. Finally, it should be noted that the PD subjects with self-reported freezing were, on average, more severely affected by the disease than the PD subjects without freezing; thus, the results that we describe as differences between PD subjects with and without self-reported freezing may also be described as differences between PD subjects with greater or lesser disease severity. However, our main interest here was in understanding the phenomenon of delayed stepping and what is associated with it, rather than with distinguishing a subtype of PD, especially given ongoing questions about whether a freezing subtype of PD even exists (Nieuwboer and Giladi, 2013).

In sum, this study provides evidence that start hesitation in PD is associated not with a greater tendency to produce multiple APAs before stepping, but with difficulty recovering when multiple APAs occur. The results are consistent with the proposal that inhibition deficits – especially difficulty releasing inhibition – play a causal role in start hesitation and freezing in PD, by contributing to the decoupling of the APA from the step.

AUTHOR CONTRIBUTIONS

RC participated in study design, data collection, data analysis, and results interpretation, and wrote the manuscript. JN participated in study design and results interpretation, and gave feedback on the manuscript. FH participated in study design and results interpretation, and gave feedback on the manuscript. All authors approved the final version of the manuscript to be published and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Elderly Fallers Enhance Dynamic Stability Through Anticipatory Postural Adjustments during a Choice Stepping Reaction Time

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In the case of disequilibrium, the capacity to step quickly is critical to avoid falling in elderly. This capacity can be simply assessed through the choice stepping reaction time test (CSRT), where elderly fallers (F) take longer to step than elderly non-fallers (NF). However, the reasons why elderly F elongate their stepping time remain unclear. The purpose of this study is to assess the characteristics of anticipated postural adjustments (APA) that elderly F develop in a stepping context and their consequences on the dynamic stability. Forty-four community-dwelling elderly subjects (20 F and 24 NF) performed a CSRT where kinematics and ground reaction forces were collected. Variables were analyzed using two-way repeated measures ANOVAs. Results for F compared to NF showed that stepping time is elongated, due to a longer APA phase. During APA, they seem to use two distinct balance strategies, depending on the axis: in the anteroposterior direction, we measured a smaller backward movement and slower peak velocity of the center of pressure (CoP); in the mediolateral direction, the CoP movement was similar in amplitude and peak velocity between groups but lasted longer. The biomechanical consequence of both strategies was an increased margin of stability (MoS) at foot-off, in the respective direction. By elongating their APA, elderly F use a safer balance strategy that prioritizes dynamic stability conditions instead of the objective of the task. Such a choice in balance strategy probably comes from muscular limitations and/or a higher fear of falling and paradoxically indicates an increased risk of fall.

Keywords: balance, fall, elderly, anticipatory postural adjustments, dynamic stability, step initiation

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INTRODUCTION

Falling is a common and unexpected event that is a concerning health problem for the elderly population (World Health Organisation, 2008). Normal aging increases the risk of fall (Rubenstein, 2006), because of a reduced capacity to use the different resources involved in the control of balance (Horak, 2006). The physical consequences of a fall are more severe than for a young person (van Dieën and Pijnappels, 2008) and falls induce psychological issues, notably by increasing the fear of falling (FoF; Maki et al., 1991). As such, falls currently represent a large and increasing health cost for societies (Stevens et al., 2006; World Health Organisation, 2008). Early identification of

community-dwelling elderly that are at risk of fall is a priority, in order to: (1) prevent them from the loss of different capacities leading to dependency and frailty; and (2) reduce the health costs of falls.

In community-dwelling elderly, "most falls occur as a result of an inability to react appropriately [to the imbalance] and produce an effective compensatory response" (Brauer et al., 2002). A natural, effective and privileged reaction to recover when balance is compromised is taking a step (Rogers et al., 1996; Maki and McIlroy, 1997). The choice stepping reaction time test (CSRT; Lord and Fitzpatrick, 2001) is a simple test to assess the capacity of a person to rapidly trigger and execute a step. The subject has to step as quickly as possible on one of several targets placed in front or around her/him. The time to reach the targets is an effective way to assess the risk of fall in elderly, as several studies showed that elderly fallers (F) have significantly longer performances compared to non-fallers (NF; Lord and Fitzpatrick, 2001; Melzer et al., 2007; St George et al., 2007; Ejupi et al., 2014). Moreover, the time to perform the CSRT appears to be a good predictor for the future risk of fall (Pijnappels et al., 2010). However, the reasons why the CSRT predicts this risk are not well established. In particular, it has been shown in simple (one leg, one target) stepping reaction time (RT) condition that elderly F are able to move their foot as fast as NF (White et al., 2002; Melzer et al., 2007). So the difference is probably made before, i.e., during the mechanisms that precede the step.

A voluntary step initiation is a self-perturbation of balance, with a modification of the base of support (BoS) and a transition from a static to a dynamic situation. To keep balance, coordinated muscular activations preceding the voluntary focal movement, namely anticipatory postural adjustments (APA), are performed (for a review see Bouisset and Do, 2008). They are part of the motor command elaborated by the central nervous system (CNS; Massion, 1992; Aruin and Latash, 1995; Brunt et al., 1999, 2005). In step (or gait) initiation, their functional role is to put the whole-body center of mass (CoM_{WB}) in motion: (1) in the desired direction; and (2) toward the future stance foot (Winter, 1995). This strategy reduces the subject's mediolateral instability during the forthcoming single support phase (Jian et al., 1993; Patla et al., 1993; Lyon and Day, 1997), where the BoS is reduced to only one foot. The motor program of this strategy has been well described, with coordinated ankle and hip muscles activations and inhibitions (Crenna and Frigo, 1991; Brunt et al., 1999). This coordination creates joint torques that move the center of pressure (CoP) backward and laterally (Brenière et al., 1987; Jian et al., 1993; Winter, 1995; Lyon and Day, 1997). Then, the movement of the subject's CoM_{WB} is principally driven by gravity effects during the swing phase (SP; Lepers and Brenière, 1995; Lyon and Day, 1997).

If APA are a very automatized postural control process, they are not invariant. They are adapted by the CNS to the external context, depending on the own resources of the subject (Patla et al., 1993; McIlroy and Maki, 1999; Luchies et al., 2002; Zettel et al., 2002; Yiou et al., 2012). In the context of a simple step initiation without a specific target, the studies that were interested in step preparation phases showed that elderly have APA elongated in time and reduced in amplitude compared to young adults (Halliday et al., 1998; Polcyn et al., 1998; Luchies et al., 2002). In the context of a CSRT, similar results have been found for elderly compared to young (Patla et al., 1993; Luchies et al., 2002) and for elderly F compared to NF, under normal (Lord and Fitzpatrick, 2001; St George et al., 2007) and dual-task conditions (Melzer et al., 2007; St George et al., 2007; Uemura et al., 2012a). Moreover, liftoff time is increased in CSRT compared to a simple RT test, increasing the landing time of the stepping foot (Luchies et al., 2002). So, the adaptable APA phase seems to be the major reason why the landing step timing is increased in elderly, and particularly in F, during a CSRT.

Why are APA elongated in time in elderly F? First, it is reported in the literature that a high FoF is associated to APA elongated in time and reduced in amplitude (Maki et al., 1991; Adkin et al., 2000; Yiou et al., 2011; Uemura et al., 2012b) and elderly F have an increased FoF compared to NF (Lajoie and Gallagher, 2004). The FoF has been shown to reduce the attentional resources available (Gage et al., 2003) and movement reinvestment (Huffman et al., 2009). So, elderly F probably have reduced attentional resources available. Moreover, normal aging reduces cognitive capacities. A reduced cognitive capacity is correlated to a longer stepping performance in elderly F during the CSRT (Lord and Fitzpatrick, 2001; Pijnappels et al., 2010; Schoene et al., 2015). The APA phase is also lengthened in elderly F during the CSRT, under dual-task paradigm (Melzer et al., 2007; St George et al., 2007; Sturnieks et al., 2008). This is probably because they need more attentional resources than NF during postural tasks under dual-task (Brauer et al., 2002; Woollacott and Shumway-Cook, 2002). Finally, elongated stepping performance is related to reduced proprioception (Pijnappels et al., 2010) and both sensorial and muscular capacity (Lord and Fitzpatrick, 2001). The muscular capacity of the lower limb is affected in elderly F, particularly around the hips (Johnson et al., 2004; Inacio et al., 2014; Morcelli et al., 2016).

Few studies have focused on the mechanics of the APA and its consequences on the stability, in a population of elderly F during a CSRT. We only found three studies talking about stability in the interpretation of their results in the conditions of step initiation. Patla et al. (1993) showed that elderly have a longer weight transfer time than young adults during CSRT, which resulted in a slower stepping response. Notably, in case of lateral steps, they found that elderly need more time because they choose to load their swing leg first, which is a sub-optimal strategy. They interpreted it as a "safer" strategy that helps elderly to increase their balance conditions. Later, Luchies et al. (2002) observed a slower weight transfer and a larger percentage of weight on the stance foot for elderly compared to young adults, in both simple step initiation and CSRT. They also used the term "safer" to describe the stepping strategy used by elderly. Unfortunately, the population of these two studies did not include elderly F. In the context of an induced step under dual-task condition the elderly—and even more for those who experienced a fall—reduce their secondary task performance (Brauer et al., 2002). They would do so to focus most of the available resources on the postural control, and by extension to increase the stability.

According to their results there could be a prioritization of a more "stable" balance strategy in elderly and particularly in elderly F. This would be observed because their CNS has better integrated than NF that falling engages the physical integrity. Nevertheless, there still is a lack in the literature of a precise biomechanical analysis of the dynamic stability for a group of elderly F during a CSRT.

To sum-up, elderly F are slower to step than NF under both normal and dual-task conditions of CSRT. As already observed in stepping tasks, a hypothesis would be that it comes from a lengthened APA phase, in an attempt to maximize their stability. The aim of this study is to investigate the characteristics of the APA for both F and NF community-dwelling elderly subjects, in normal CSRT conditions (i.e., without a secondary task). We expect that APA will be longer for F compared to NF, as a result of a strategy that elderly F use to increase their conditions for dynamic stability.

MATERIALS AND METHODS

Population

Forty-four healthy subjects participated in this study. They were divided in two groups: elderly F and elderly NF. Subjects were retrospectively categorized as F if they experienced at least a fall in the past year. A fall was defined as "an event, following an imbalance, which results in a person coming to rest inadvertently to a lower level, involving an impact, consecutive to the balance recovery actions failure and not a result of a major intrinsic event or overwhelming hazard". This definition was chosen based on previous literature (Tinetti et al., 1988; Hauer et al., 2006; Segev-Jacubovski et al., 2011). Headcounts and anthropometrical data of the two groups are summarized in **Table 1**.

All subjects were included if they: (1) were aged 70 or more; (2) performed at least 25 on the Mini Mental State Examination (MMSE); and (3) had no neurological, musculoskeletal or sensorial (vision and cutaneous sensation) disorders, after a medical inspection. Forty-four healthy elderly adults participated in the study. Their mean age, mass and height were 75 years (ranging from 70 to 82), 66 kg (45 to 95) and 1.62 m (1.50 to 1.95), respectively. All subjects provided written informed consent to the experiment as conformed to the Declaration of Helsinki and was approved by the ethics committee Comité de Protection des Personnes Lyon Sud Est III.

TABLE 1 | Mean (standard deviation) anthropometrical and MMSE data relative to the participants.

	Elderly F	Elderly NF
Number of subjects	20	24
Number of women	15	14
Right-shooters	16	20
Age *[years]*	76.0 (3.9)	74.2 (3.9)
Age range *[years]*	70–82	70–82
Height *[m]*	1.61 (0.10)	1.64 (0.09)
Weight *[kg]*	68.6 (12.2)	65.3 (11.9)
BMI *[kg.m^{-2}]*	26.5 (3.7)	24.2 (3.5)
MMSE *[score]*	28.7 (1.4)	28.9 (1.0)

No statistical difference (using a T-test) was seen between the two groups. BMI, Body Mass Index; MMSE, Mini Mental State Examination.

Protocol

Each subject performed a CSRT. Subjects initially stood quietly, in a comfortable position, with arms along the body, eyes open and feet on two force platforms (60 cm × 40 cm, Bertec®, OH, USA). The positions of the feet was freely chosen by the subject and marked on the ground in order to repeat trials from the same initial posture. Four large targets (squared panels, 10 cm × 10 cm) were positioned on the ground at 40% of the subject's lower limb length (LLL; see **Figure 1**). This distance was comfortable for the subject. The LLL was measured vertically, between the femoral trochanter center (Van Sint Jan, 2007) and the ground. Two targets were placed strictly anterior to the right and left foot (Central). The two others were placed 30° on each lateral side (Lateral). A light-emitting diode (LED) was placed in front of each target. LEDs were initially turned off. Instructions given to the subjects were: "as soon as one of the LED gets illuminated, step with the ipsilateral foot (i.e., left foot for the two left targets, right foot for the two right targets) on the corresponding target, as quickly as possible". Each subject performed four trials on each target, randomly presented. To enhance the unpredictability of the imperative signal, the duration between the subjects said he/she was "ready" and the illumination of the LED was randomly chosen between 1 and 10 s.

Subjects were equipped with 39 reflective markers located on anatomical landmarks (Van Sint Jan, 2007) and recorded by eight cameras (Eagle 1.3 Mpx, Motion Analysis®, Santa Rosa, CA, USA) at 100 Hz sample frequency. Markers trajectories were filtered at 6 Hz with a Butterworth filter. The whole-body center of mass (CoM_{WB}) trajectory was calculated using these markers trajectories and a segmental method (Dumas et al., 2007, 2015). Ground reaction forces (GRFs) were recorded at a sampling frequency of 1000 Hz with four force platforms, to integrate both the starting and landing areas (see **Figure 1**). The CoP was then estimated from the GRF measured by the force platforms at the same frequency. The CoP was estimated only when the resultant vertical force was higher than a threshold fixed at 20 N. No additional filtering was performed.

Data Analysis

Step Phases Duration

All signals (markers' positions, GRFs and LEDs' voltage) were recorded on the same data acquisition card (National Instruments USB 6218) and synchronized. They were further time shifted so that the beginning of the trial (T0) corresponded to the LED's lightning (given by a raise in the LED's voltage). Three particular instants were then defined relative to T0, based on the vertical components of the GRFs (see **Figure 2**):

- *Beginning of loading* (BL) which corresponds to the beginning of APA is the instant where the force under the swing leg increases more than two standard deviations of a reference

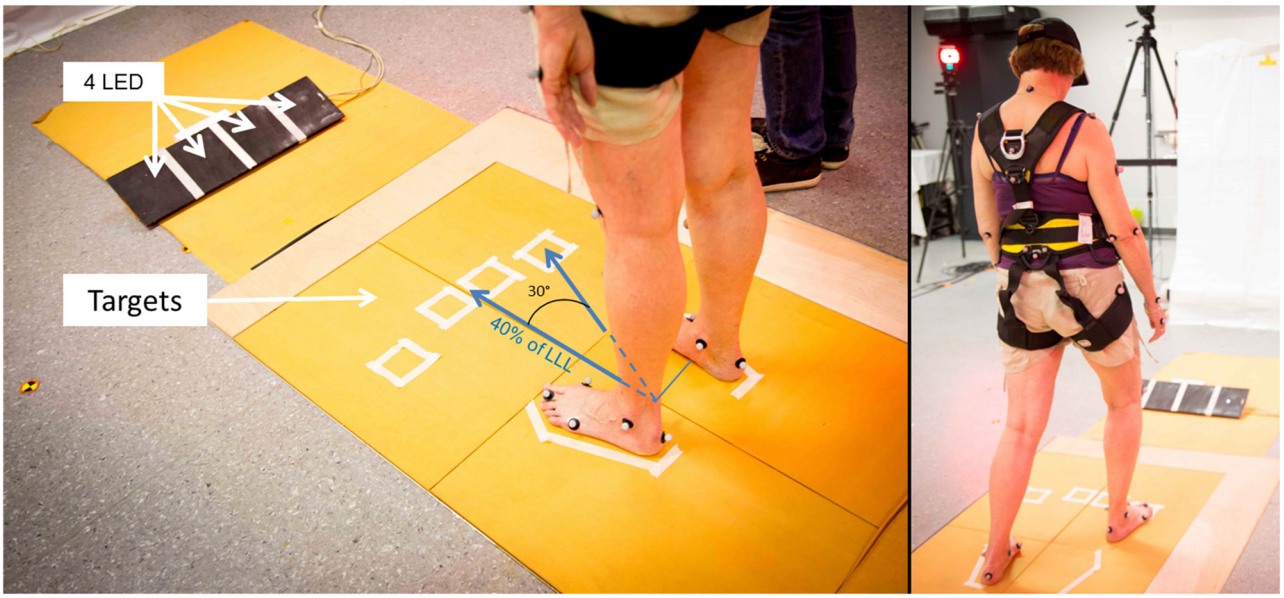

FIGURE 1 | Experimental set up for the choice stepping reaction time test (CSRT). Initial position of the subject, targets and board with light-emitting diode (LED) are shown on the left. Distance from the middle of the ankles and center of each target was 40% of the subject's lower limb length (LLL). On the right, the same subject in the final position, after the lightning of the "Lateral-Right" target.

period calculated between the beginning of the recording and T0;
- *Foot-Off* (FO) is the first instant where the swing leg force is inferior to 2.5% of the subject's body weight;
- *Foot Landing* (FL) is the first instant where the swing leg force is superior to 2.5% of the subject's body weight after FO.

Then, the three temporal phases were identified: the RT between T0 and BL, the anticipated postural adjustments (APA) between BL and FO and the SP between FO and FL.

APA and Swing Phases Analysis

Specific variables were extracted and analyzed during the APA and the SP phases. First, we measured the presence of an APA error. An APA error was considered when the lateral trajectory of the CoP first moved toward the stance foot side—instead of the swing foot side—more than two standard deviations of the reference period measured between 0 and T0. Then, we were interested in the two subphases of APA used during forward step initiation (see **Figure 3**): a "loading" subphase where the CoP moves backward and toward the swing foot, leading the CoM_{WB} to be put in motion forward and toward the stance foot; and an "unloading" subphase, during which the swing foot is unloaded, leading the CoP to move laterally under the stance foot (Jian et al., 1993). The beginning of the unloading subphase (BU)—corresponding the end of the loading subphase—was identified as the time when the vertical force under the swing leg was maximal (see **Figure 2**). The unloading subphase ended with the APA at FO. During the two APA subphases, the CoP displacements were characterized using the six following variables:

- CoP_B: the maximal excursion of the CoP backward along the AP axis during the loading subphase;
- CoP_L: the maximal excursion of the CoP along the ML axis toward the swing foot during the loading subphase;
- CoP_U: the amplitude of the CoP displacement along the ML axis during the unloading subphase;
- $VCoP_B$: the peak of the AP component of the velocity of the CoP during the loading subphase;
- $VCoP_L$: the peak of the ML component of the velocity of the CoP during the loading subphase;
- CoM_U : the peak of the ML component of the velocity of the CoP during the unloading subphase;

The CoP velocity was obtained by the first time derivative of the CoP trajectory, with a 2nd order lowpass digital Butterworth filter and a cutoff frequency of 20 Hz. Finally, during the SP, we analyzed the horizontal tangential velocity of the swing foot, using the first derivative of the ankle center trajectory given by the middle of the two malleolus markers. The horizontal distance traveled by the CoM_{WB} between T0 and FL was also calculated.

Dynamic Stability: XCoM and MoS Analysis

The position of the XCoM in the horizontal plane was computed with the following equation (Hof et al., 2005):

$$XCoM = \left(CoM_{WB} + \frac{1}{\omega_0} Co\dot{M}_{WB}\right) \cdot e_{proj} \qquad \omega_0 = \sqrt{\frac{g}{h}} \quad (1)$$

$Co\dot{M}_{WB}$ is the vector of the CoM_{WB}'s velocity, obtained by numerical derivation and filtering. g is the gravitational constant and h the distance along the vertical axis between the ankle

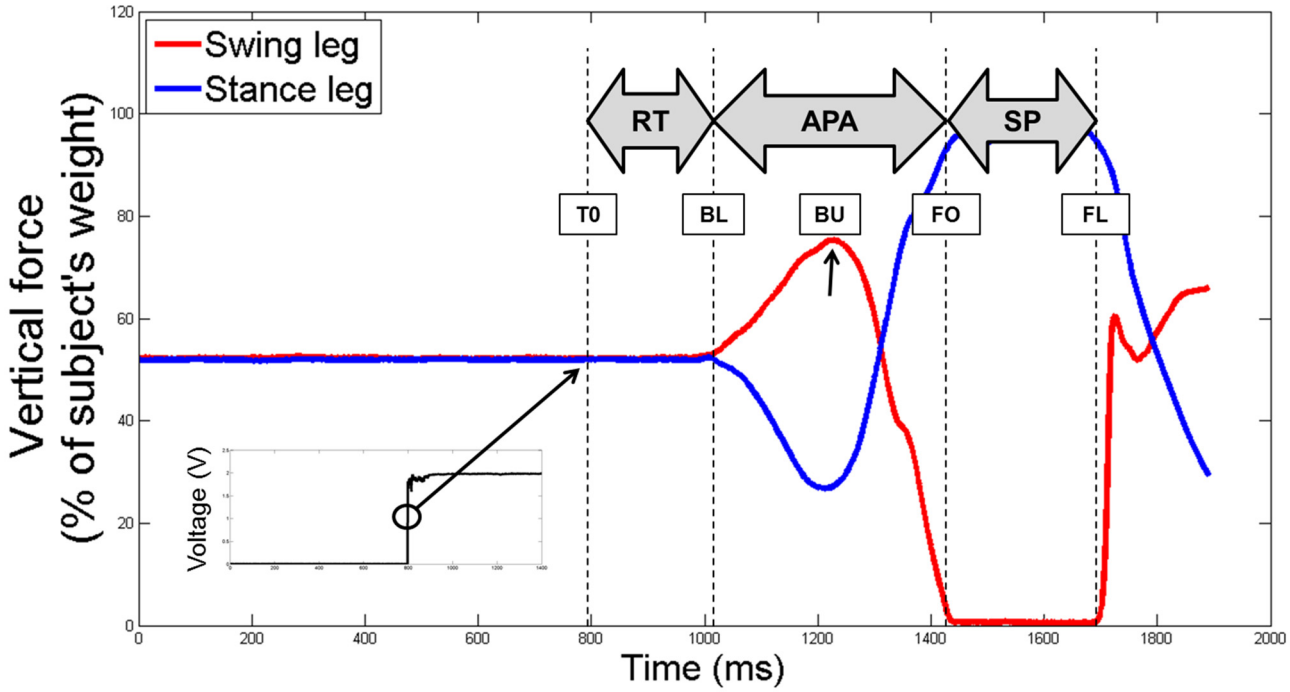

FIGURE 2 | An example of the raw vertical component of the ground reaction forces (GRFs) under the swing (in red) and stance (in blue) legs of a non-faller subject, before being time shifted. The four particular instants identified (T0, BL, FO and FL) are reported with dotted lines. The beginning of the unloading is also reported with a black arrow (BU). The black squared signal in the bottom left shows the voltage signal of the LED, used to determine the T0. Abbreviations used: T0, first instant lighting the LED; BL, beginning of loading; BU, beginning of unloading; FO, foot off; FL, foot landing; RT, reaction time phase; APA, anticipated postural adjustments; SP, swing phase.

and CoM_{WB}'s position in static initial posture. The vector e_{proj} projects the results in the horizontal plane of the laboratory coordinate system.

The dynamic stability was quantified at FO using the minimal distance between the positions of the XCoM and the edges of the stance foot, along both the AP and ML directions of the stance foot (see **Figure 3**). These variables, further referred as MoS_{AP} and MoS_{ML}, could be seen as the margin of stability (MoS; Hof et al., 2005) in these two directions. AP and ML directions of the stance foot were first defined as the lines passing through the markers positioned on calcaneus and 3rd toe and through the markers positioned on 1st and 5th metatarsal heads, respectively (dotted blue lines on **Figure 3**). The advantage of this method is that it takes into account the horizontal orientation of the foot. The anterior and medial edges of the BoS were then obtained by translating these lines to pass through the 1st metatarsal head marker and the 3rd toe marker, respectively (solid blue lines in **Figure 3**). Note that recent articles suggested the use of a functional BoS, i.e., a proportion of the initial BoS, instead of the mechanical BoS to correctly analyze the MoS values (Vallée et al., 2015; Hof and Curtze, 2016). However, the correct proportions to be used are still debated and using the mechanical or functional BoS will not change the meaning and interpretation of our results. At FO the BoS is the stance foot. MoS_{AP} and MoS_{ML} were calculated as the perpendicular distances between XCoM and the BoS edges (see **Figure 3**) and normalized by the BoS length (distance between the calcaneus and 3rd toe markers) and width (distance between the 1st and 5th metatarsal markers of the stance foot), respectively. For interpretation, the higher (and positive) these values, the higher the stability. Note that the XCoM being most of the time medial to the ML BoS edge (as it is shown on **Figure 3**), MoS_{ML} is quasi-systematically negative. It means that the subject is in condition of instability and, not surprisingly, that a static stable standing posture can only be reached by placing the swing foot laterally to the stance foot.

Statistics and Graphic Representations

The steps on the left side were reflected about the laboratory AP axis to the steps on the right side. *T*-tests performed on the total duration comparing left and right target for both Central and Lateral conditions inside each group revealed probabilities to be different superior to 0.50 (for example in NF, $p = 0.85$ for Central and $p = 0.64$ for Lateral). So, right and left trials were combined in the two targets: Central and Lateral.

A first analysis on the frequency of APA error was performed with a χ^2 test. Next, the normality of the distribution in the other variables was evaluated with a Shapiro-Wilk test. All of them were reported normal, so we tested them with two-way repeated measures ANOVA. The factors tested are the independent factor "Group" (F or NF) and the repeated factor "Target" (Central or Lateral). When an interaction was found, *post hoc T*-tests with

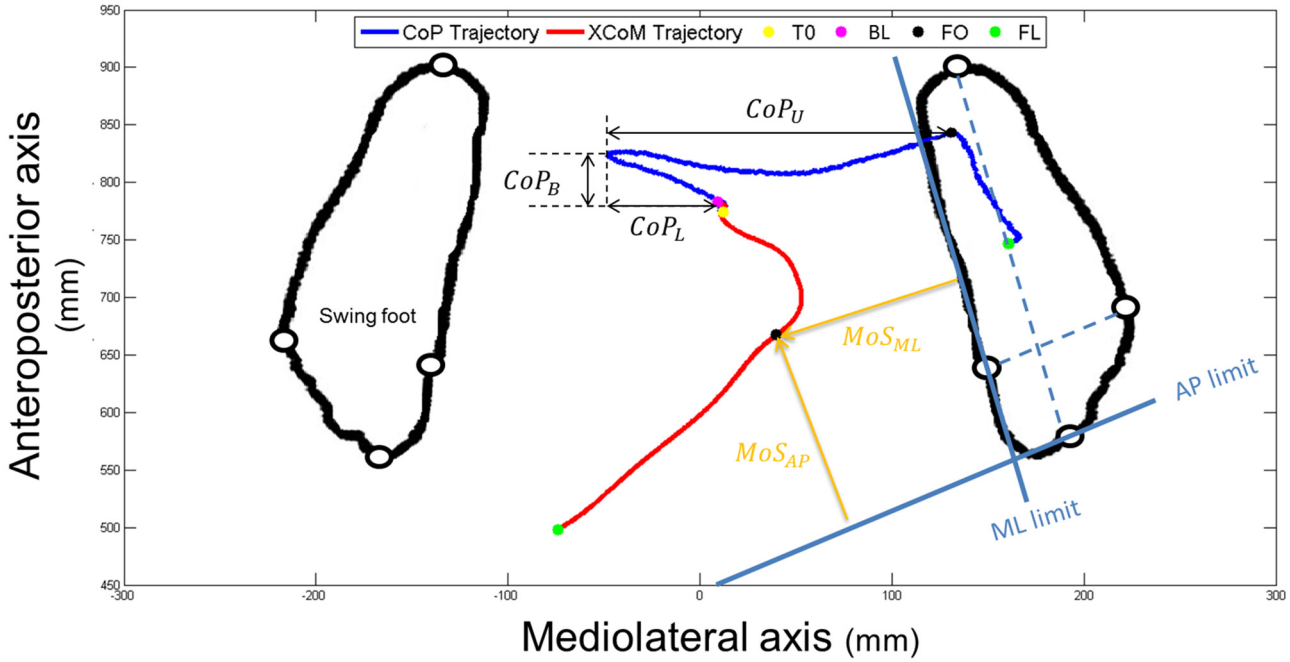

FIGURE 3 | An example of the horizontal center of pressure (CoP; in dark blue) and XCoM (in red) trajectories of a non-faller subject during the CSRT, seen from the top. Particular instants identified (T0, BL, FO and FL) are reported with colored points on CoP trajectory. Only FO and FL are reported on both trajectories. Foot markers are represented with white disks circled in black. Amplitudes of the CoP displacements are represented with black double arrows (CoP_B = backward; CoP_L = loading and CoP_U = unloading). The horizontal foot orientation is represented with dotted light blue lines that are then translated to the edges of the stance foot (solid light blue lines). Margin of stability (MoS) sizes at FO are represented with orange arrows. AP, anteroposterior; ML, mediolateral.

the Bonferroni correction were performed. We did all statistical tests using the R® software and a $p < 0.05$ was considered for a statistical difference.

For clarity, we choose to represent on the graphs the results for the two groups on each target even if an interaction was absent. In this case only the main factor effects of the ANOVA are reported. If an interaction was present, the results of the *post hoc* test are added to the main factor results coming from the ANOVA.

RESULTS

Seven hundred and four trials were collected. Twenty-Seven were instantly removed for the following reasons: subjects stepped with the wrong foot (19) or problems with forceplates data recordings appeared (signal partly or totally absent, 8). The 677 trials left were analyzed to detect the presence of APA errors. APA errors were observed in 21.6% (146) of the trials. Results of APA errors were 22.7% and 20.6% for F and 24.9% and 21.4% for NF in Central and Lateral targets, respectively. For both targets, there were no statistical difference between F and NF: $\chi^2 = 0.02$, $p = 0.89$ and $\chi^2 = 0.03$, $p = 0.87$ for Central and Lateral, respectively.

As no difference was seen between F and NF, we chose to analyze only the 78.4% left of the collected trials. So, the following results concern only the 531 "correct" trials of the initial 677.

In those trials, the results of the ANOVA tests have been summed up in **Table 2**.

A significant effect of the factor "Group" was found on the total step duration. F compared to NF needed 1131 ± 231 ms vs. 997 ± 175 ms in Central and 1019 ± 161 ms vs. 870 ± 117 ms in Lateral, to execute a quick step during the CSRT (see **Figure 4**, top). This observation was independent from the target, although no significant differences between F and NF were observed on the CoM_{WB} displacement (see **Figure 5**, top). Indeed, for F compared to NF, the CoM_{WB} horizontal displacement was 12.5 ± 4.0% vs. 13.3 ± 4.0% of the subject's height for Central and 10.2 ± 2.6% vs. 12.1 ± 3.0% of the subject's height for Lateral. We also found an effect of the factor "Target", indicating that the total step duration was significantly increased in Central compared to Lateral targets.

The analysis of each step phase duration (**Figure 4**, bottom) showed that APA was the only phase significantly elongated in elderly F compared to NF (534 ± 150 ms vs. 457 ± 139 ms in Central and 441 ± 98 ms vs. 357 ± 84 ms and in Lateral). As for the total step duration, this result was independent from the target and the mean values measured on Central targets were significantly higher than on Lateral targets.

The mean values measured on the RT phase duration for F compared to NF were 261 ± 61 ms vs. 272 ± 82 ms in Central and 249 ± 57 ms vs. 247 ± 55 ms in Lateral. Analysis of this phase reported neither effect of the factors "Group" nor "Target" (see **Table 2**).

For the SP duration and swing foot velocity, a significant effect of the factor "Target" was found, whereas the effect of the factor

TABLE 2 | Recapitulation of the results using two-way repeated measures ANOVA performed for all the variables in this study.

		Group		Target		Interaction	
		F	p	F	p	F	p
Durations							
	Total	9.86	**<0.01**	105.39	**<0.001**	<0.01	0.97
	Reaction time	2.34	0.13	0.25	0.62	2.01	0.16
	APA phase	13.01	**<0.001**	102.04	**<0.001**	0.10	0.75
	Swing phase	2.79	0.10	20.71	**<0.001**	0.49	0.49
	Loading subphase	5.98	**0.02**	54.80	**<0.001**	1.73	0.19
	Unloading subphase	6.84	**0.01**	34.59	**<0.001**	0.06	0.81
CoP amplitude							
	CoP_B	4.88	**0.03**	1.81	0.18	0.24	0.63
	CoP_L	0.49	0.49	37.57	**<0.001**	0.04	0.83
	CoP_U	1.60	0.31	26.84	**<0.001**	2.29	0.14
CoP velocity							
	$VCoP_B$	11.31	**0.02**	0.38	0.54	0.02	0.88
	$VCoP_L$	0.94	0.34	8.37	**<0.01**	0.44	0.51
	$VCoP_U$	2.17	0.15	3.52	0.07	2.80	0.10
MoS sizes							
	MoS_{AP}	4.64	**0.04**	7.93	**<0.01**	0.48	0.49
	MoS_{ML}	2.45	0.13	385.11	**<0.001**	5.48	**0.02**
Swing phase							
	Foot velocity	2.21	0.15	24.00	**<0.001**	0.01	0.94
CoM_{WB} displacement		0.31	0.58	75.09	**<0.001**	0.53	0.47

F and p from the ANOVA are provided. p inferior to 0.05 are indicated in bold.

"Group" revealed trends (see **Table 2**, **Figures 4**, **5**). Those trends indicated that the mean values for SP duration are always longer for F compared to NF (336 ± 111 vs. 290 ± 87 ms in Central and 305 ± 79 vs. 265 ± 73 ms in Lateral), and that the mean values for swing foot velocity were always smaller in F than in NF (0.16 ± 0.04 vs. 0.18 ± 0.04 $m.s^{-1}$ in Central and 0.15 ± 0.4 vs. 0.17 ± 0.4 $m.s^{-1}$ in Lateral).

In order to illustrate the APA mechanisms and their consequences on stability, the CoP and XCoM trajectories were plotted between T0 and FO. Results for Lateral targets are provided in **Figure 6**. Similar patterns were observed for Central targets. For clarity, all trajectories have been normalized on zero. Only for the representation, the BL instant has been averaged between the two groups. This figure highlights the differences in APA between F and NF and their consequences on the stability. First, as previously mentioned, we observed that the APA duration was elongated in F. Indeed, FO arose around 100 ms later in F than in NF. Also, the plot of the CoP displacement along the ML axis illustrates well the two APA subphases (bottom left in **Figure 6**): the "loading" is when the CoP move to the swing-foot side while the "unloading" is when the CoP moves to the stance-foot side. The duration of these two subphases (see **Figure 7**) were significantly increased for F compared to NF: 254 ± 45 ms vs. 237 ± 45 ms in Central and 220 ± 30 ms vs. 183 ± 26 ms in Lateral to complete the loading subphase; 263 ± 47 ms vs. 217 ± 52 ms in Central and 227 ± 35 ms vs. 173 ± 24 ms in Lateral to complete the unloading subphase.

Two different CoP displacement strategies were observed in the AP and ML directions, respectively (see **Figure 6**, left panels). Both resulted in a similar effect on the stability (see **Figure 6**, right panels): an increased stability in the AP direction and a less important instability (the XCoM is mostly external to the BoS at FO) in the ML direction, for the elderly F compared to NF (see **Figures 8**, **9**).

- In the AP direction F moved their CoP less backward than NF: 9 ± 3.8% vs. 13.4 ± 5.5% of the BoS length in Central and 9.8 ± 3.9 vs. 14.7 ± 5.7% of the BoS length in Lateral. They also moved their CoP slower than NF: 0.21 ± 0.07 $m.s^{-1}$ vs. 0.32 ± 0.12 $m.s^{-1}$ in Central and 0.21 ± 0.07 $m.s^{-1}$ vs. 0.34 ± 0.11 $m.s^{-1}$ in Lateral. Consecutively, this strategy resulted in a smaller forward displacement of the XCoM (see **Figure 6**) and a significantly increased MoS_{AP} (23.2 ± 7.7% vs. 14.1 ± 11.5% of the BoS length in Central and 24.6 ± 6.6% vs. 16.6 ± 9.2% in Lateral).
- In the ML direction there were no significant differences between F and NF in the amplitude of CoP displacements. For F compared to NF, we measured mean CoP displacements of 16.0 ± 5.6% vs. 17.2 ± 5.7% of the initial BoS width in Central and of 14.4 ± 4.4% vs. 14.0 ± 5.0% of the initial BoS width in Lateral during the loading subphase. During the unloading subphase, the amplitude of this displacement was 32.7 ± 8.1% vs. 32.8 ± 7.5% of the initial BoS width in Central and 30.6 ± 6.7% vs. 29.6 ± 7.4% in Lateral. We also did not found any significant differences between F and NF for the CoP velocity peaks ($VCoP_L$ and $VCoP_U$). For F compared to NF, the mean $VCoP_L$ measured were 0.46 ± 0.21 $m.s^{-1}$ vs. 0.50 ± 0.31 $m.s^{-1}$ in Central and 0.39 ± 0.13 $m.s^{-1}$ vs. 0.42 ± 0.16 $m.s^{-1}$ in Lateral. We found however a significant effect of the factor "Target" ($p < 0.01$), with mean values measured on Central targets significantly higher than those on Lateral. $VCoP_U$ was 1.21 ± 0.37 $m.s^{-1}$ vs. 1.45 ± 0.64 $m.s^{-1}$ in

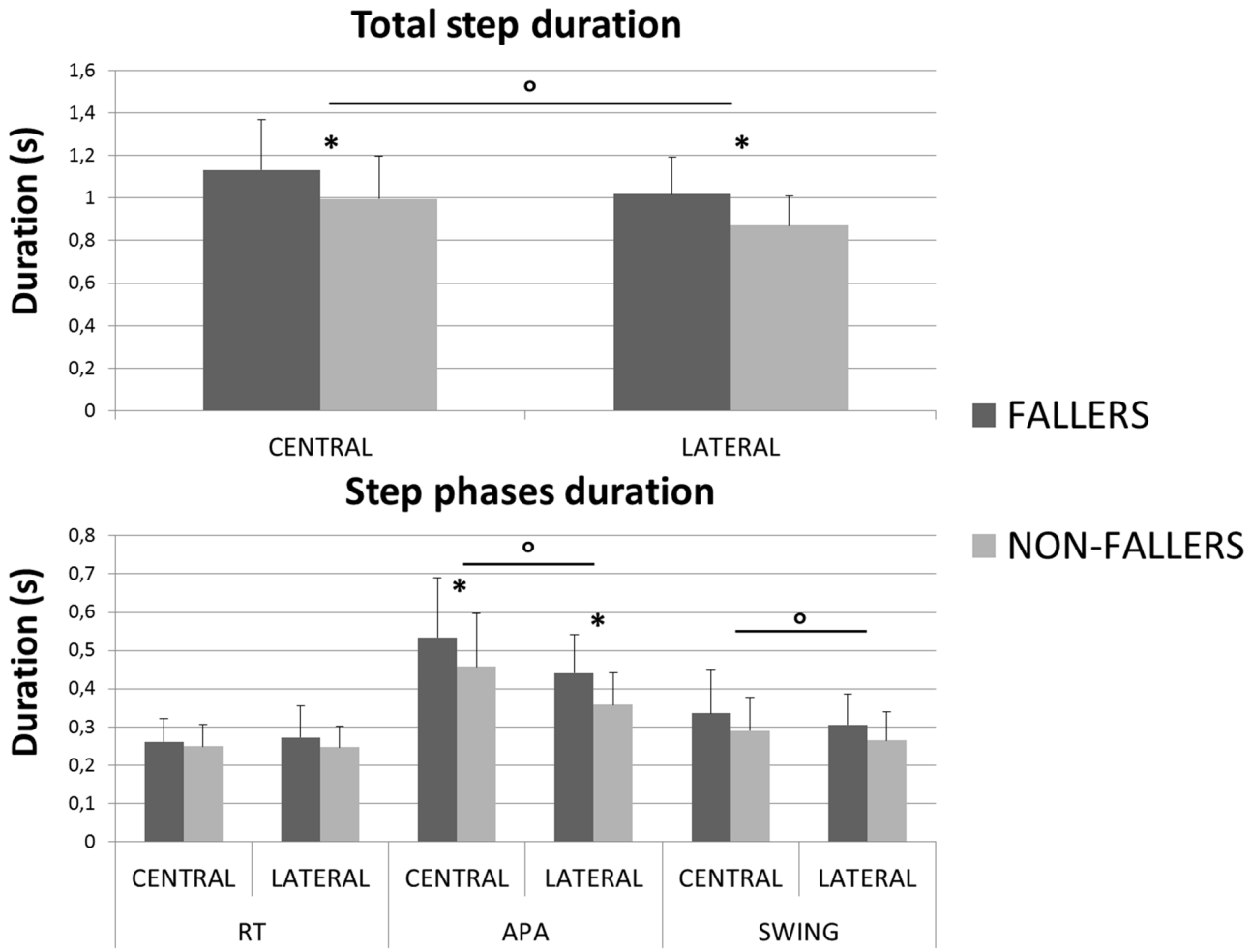

FIGURE 4 | Mean durations (with standard deviations) measured for both groups and targets during the CSRT. On top are presented results for the total step duration. On the bottom are presented results for the three steps phases (RT, APA and Swing). *Indicates a significant effect of the main factor "Group". °Indicates a significant effect of the main factor "Target".

Central and 1.31 ± 0.43 m.s^{-1} vs. 1.46 ± 0.50 m.s^{-1} in Lateral, for F compared to NF. Nonetheless, longer APA duration for F tended to induce a larger lateral displacement of the XCoM at FO (see **Figure 6**). Whether the MoS_{ML} was not significantly different between F and NF (-9.6 ± 19.8% vs. -24.2 ± 27.1% of the stance-foot BoS width in Central and -40.0 ± 20.6 vs. -60.0 ± 29.4% of the stance-foot BoS width in Lateral), the significant interaction Group * Target (see **Table 2**) showed that this result depended on the Target. Independent analysis of each target revealed that F had a significantly larger MoS_{ML} than NF only for the Lateral targets ($p < 0.01$ after Bonferroni correction).

DISCUSSION

Step and Step Phases Durations

As previously in the literature (Lord and Fitzpatrick, 2001; St George et al., 2007), we found that elderly F need more time to perform a CSRT under normal conditions (i.e., no secondary task). This result confirms that this test is relevant to identify community-dwelling elderly that are at risk of fall, with a simple measurement (the total duration of the step) conceivable outside of the laboratory (clinical environment, home, etc.) (Lord and Fitzpatrick, 2001; Schoene et al., 2011; Ejupi et al., 2014). The total mean durations obtained in our study are shorter than in Lord and Fitzpatrick (2001) study: 1075 ms vs. 1322 ms for F and 933 ms vs. 1168 ms for NF. This difference could be explained by the fact that we removed the trials with APA errors from analysis. Interestingly, the mean difference between the two groups is similar in both studies (∼150 ms). So, the total step duration difference between F and NF does not seem to be influenced by the presence of APA errors. Despite the fact that they need more time to step, elderly F made similar steps (see results in **Figure 5**) and as many APA errors as NF. This last result may seem contradictory with those from the previous studies (St George et al., 2007; Sparto et al., 2014) who found that subjects who make more APA errors are mostly the subjects

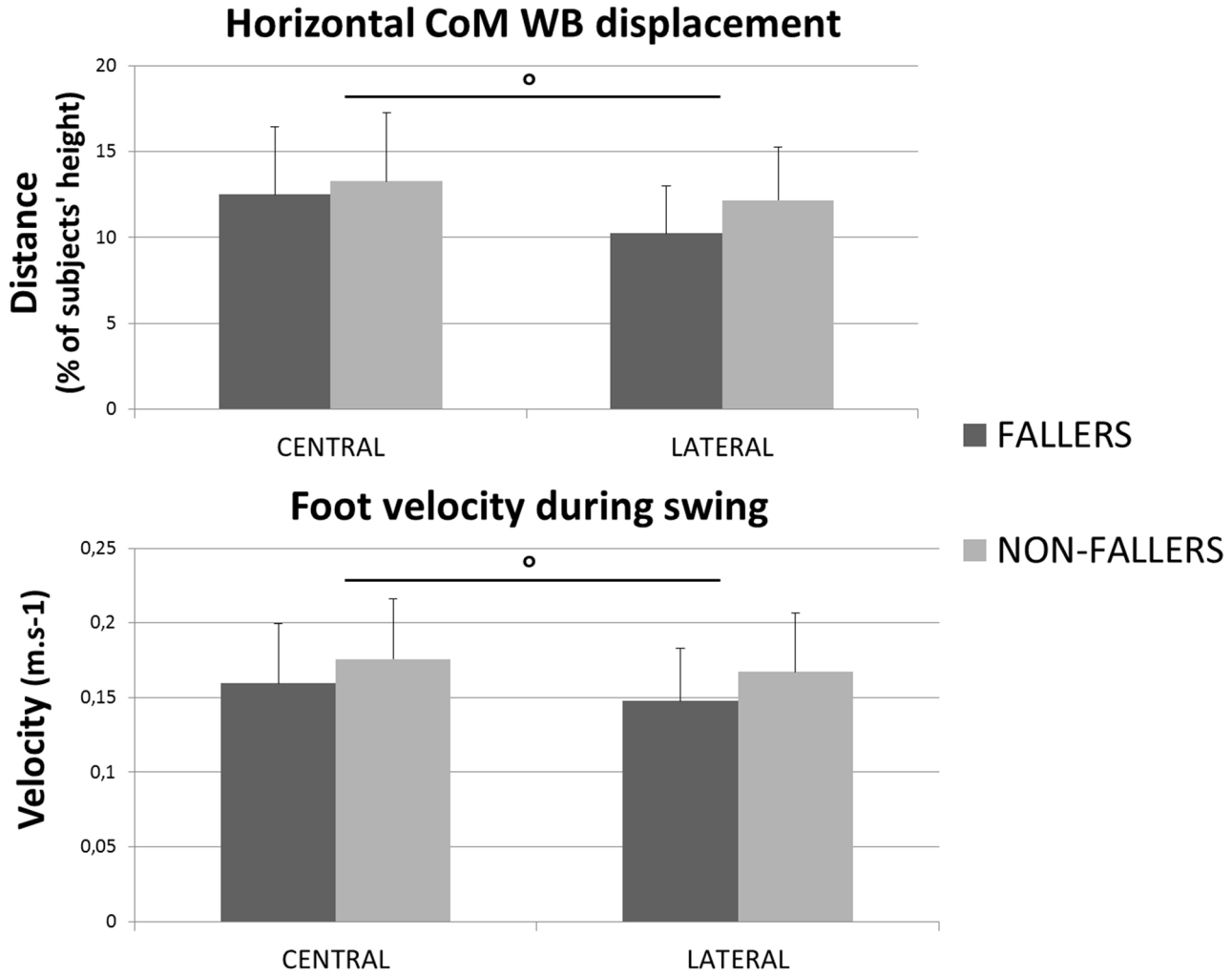

FIGURE 5 | Mean values (with standard deviations) measured of the CoM_{WB} displacement (top) and the velocity of the swing foot (bottom) for both groups and targets. °Indicates a significant effect of the main factor "Target".

with a history of fall and with a high risk of fall, respectively. It could be explained by the fact that Sparto et al. (2014) used purely lateral targets and reported an "error" when a loading subphase was observed, which is a very strict criterion (the presence of a loading subphase being more a sub-optimal response than an error). In St George et al. (2007) study subjects were under dual-task most of the time, which could have complicated the target identification for F. To sum-up, we found that elderly F are slower but able to execute the same step as NF during the CSRT and that the presence of an APA error is apparently not a reason to explain why they need more time to step during this test.

Regarding the step phases independently we found similar RT phase duration for F and NF. The mean value obtained for the RT is close to previous measurements in elderly (Luchies et al., 2002), but differs from the longer durations measured by Patla et al. (1993) (∼400 ms vs. 280 ms in our study) and St George et al. (2007) in their condition without secondary task (∼350 ms). In Patla et al. (1993), targets also involved posterior steps. As the CoP has to move first forward in posterior steps, subjects may have taken more time to ensure the identification of the direction of the target before starting APA. In St George et al. (2007) study, this difference could be explained by the determination of the beginning of APA: they took the first activation of gastrocnemius that, as soleus, are ankle plantar flexors who are firstly turned off during the forward step initiation (Crenna and Frigo, 1991). Moreover, our results indicate that the F and the NF have similar SP durations and swing foot velocity (see **Figures 4**, **5**).

So, an important result of this study is that the total duration of the step is elongated in elderly F compared to NF because their APA phase is elongated. This result is similar to what Patla et al. (1993) found for elderly compared to young adults, and the timing difference between F and NF related here is similar to St George et al.'s (2007) measurements in their condition without secondary task. It confirms the hypothesis that the

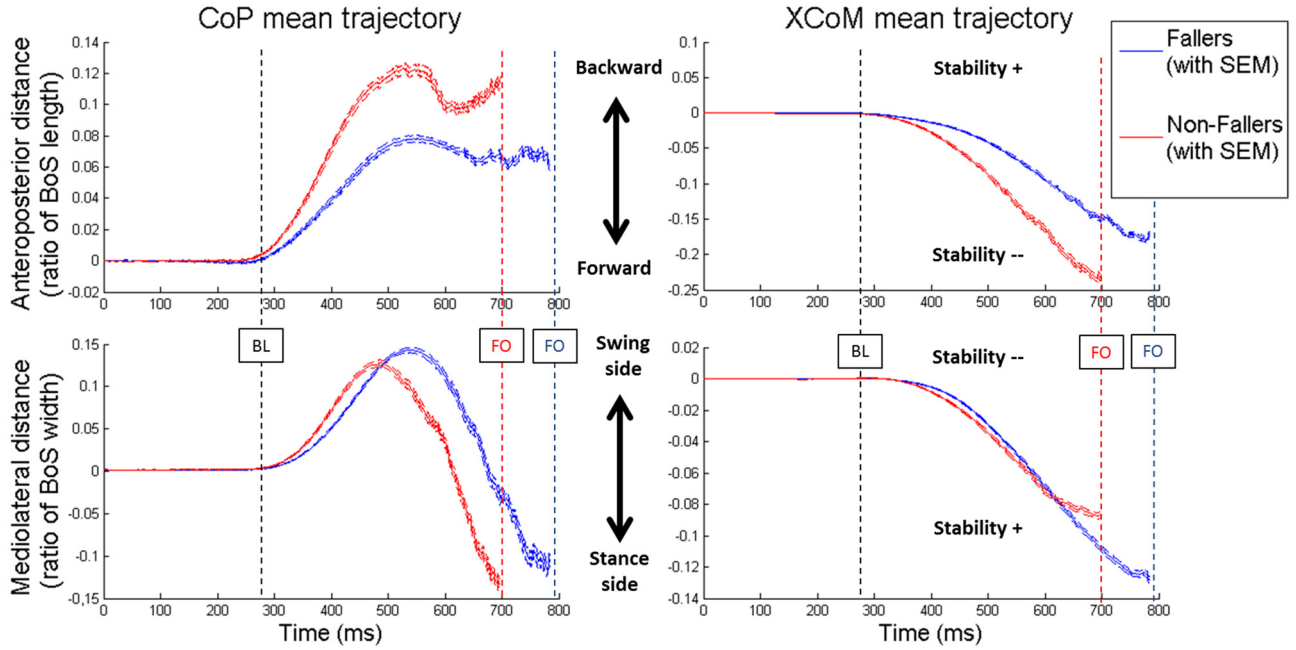

FIGURE 6 | Mean values of the CoP (on the left) and XCoM (on the right) trajectories from T0 to FO in Lateral targets. For both groups the two components of the movement are presented: anteroposterior (on top) and mediolateral (on the bottom). Blue lines are the results for Fallers (F) and red lines for Non-fallers (NF). The lines represent the mean value and the standard error to the mean (SEM). For clarity, the BL is the mean of the two groups. Note that for the anteroposterior displacement of the XCoM (top right) the less negative the XCoM indicates a better stability while for the mediolateral displacement of the XCoM (bottom right) the less negative XCoM indicate a worst the stability. For this representation, the base of support (BoS) width has been calculated between the positions of the two 5th metatarsal head markers, along the mediolateral axis.

difference between F and NF is made during the mechanisms preceding the step execution. Our result is reinforced by the fact that APA of elderly F last longer than those of NF, independently of the direction of the target (see **Figure 4**). Indeed, even for the Lateral targets, a situation that needs *a priori* reduced APA because of the advantages of the gravity effects on the frontal plane during the SP (Patla et al., 1993; Lepers and Brenière, 1995; Lyon and Day, 1997; Sparto et al., 2014), this difference is highly significant ($p < 0.001$). So, as Patla et al. (1993) observed for elderly in lateral steps, elderly F may chose not to take advantage of the gravity as much as elderly NF do during the execution of APA for lateral steps.

Two Different Balance Strategies, Depending on the Axis

Looking at the biomechanical mechanisms occurring during the APA, we showed that elderly F tend to keep their XCoM closer to the stance foot at FO than NF (see **Figure 6**). This situation allows them to increase their conditions for dynamic stability at this particular instant, i.e., when the BoS is reduced to only one foot (although this result was not significant in the ML direction for the Central targets). Moreover, as the body behaves almost as a passive mechanism during the SP (Lyon and Day, 1997) and as the swing characteristics observed here (foot location at FL and SP duration) are unchanged between F and NF, differences in dynamic stability at FL could be expected from the differences in XCoM locations at FO. In particular, the XCoM is further from the stance foot at FO for NF (see **Figure 6**). It likely induces a larger ML displacement of the XCoM during the SP and could result in a smaller dynamic stability at FL for NF compared to F, similar to what was observed at FO. This should nevertheless be confirmed by proper estimations of the XCoM and of the BoS at FL. Interestingly, the increased conditions for stability were obtained

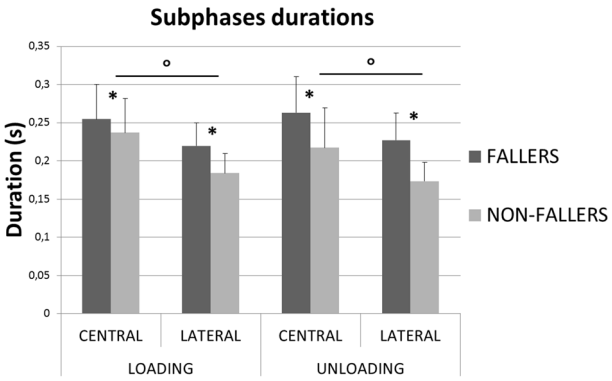

FIGURE 7 | Mean durations (with standard deviations) measured for the two subphases of APA for both groups and targets. *Indicates a significant effect of the main factor "Group". °Indicates a significant effect of the main factor "Target".

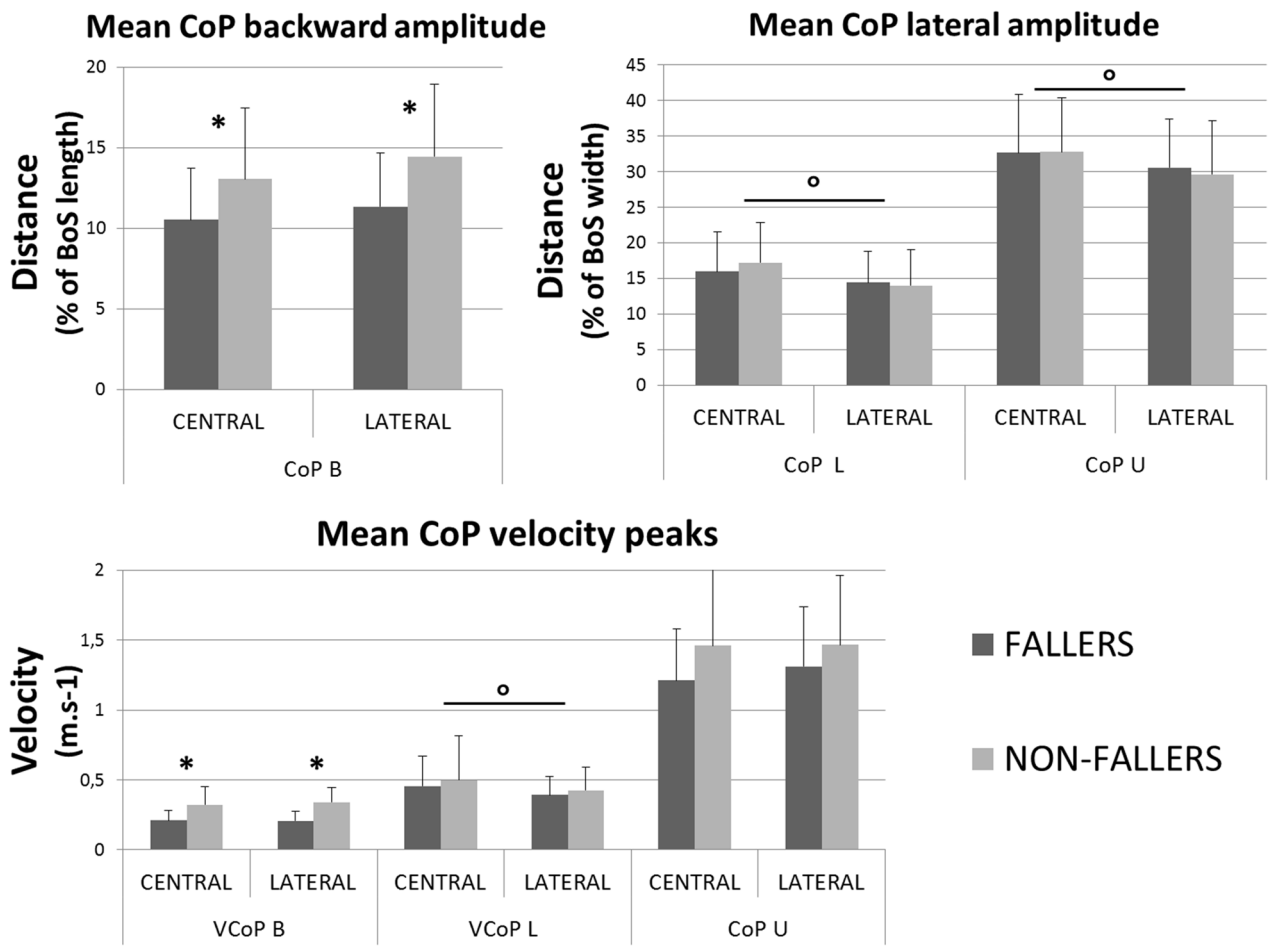

FIGURE 8 | Mean characteristics (with standard deviations) of CoP movement measured for both groups and targets during APA. Backward (top left) and mediolateral (top right) maximal amplitudes are presented with velocity peaks (bottom). *Indicates a significant effect of the main factor "Group". °Indicates a significant effect of the main factor "Target". Note that here the BoS width refers to the initial BoS width, which is calculated between the positions of the two 5th metatarsal head markers, along the mediolateral axis.

through two different strategies observed in the ML and AP directions.

In the ML direction, we did not find any statistical difference in the CoP trajectory between F and NF, both in amplitude and velocity variables (CoP_L, CoP_U, $VCoP_L$ and $VCoP_U$, respectively, see **Figures 6**, **8**). Longer durations of both loading and unloading subphases (see **Figure 7**) implied however that the CoP stayed lateral to the CoM_{WB} on the swing foot side for a longer time in F than in NF. Consequently, the torque that propels the CoM_{WB} toward the stance leg is more efficient in F and so the XCoM is more shifted toward the stance foot (see **Figure 6**). Thus, the ML instability at FO is reduced: MoS_{ML} is less negative (although it was only significant for Lateral targets, see **Figure 9**). This elongated duration implies a poorer performance in the CSRT task (Patla et al., 1993; Lord and Fitzpatrick, 2001). Interestingly, a similar result in terms of stability could be obtained without lengthening the APA phase duration. It would consist in increasing the CoP peak velocity or excursion, i.e., in performing more efficient APA than NF. Why F do not to use this later strategy remains an open question. Two hypotheses could be proposed: (1) a physical limitation, in particular in the hip abductors/adductors that are primarily responsible for the CoP ML displacement (Winter, 1995); and (2) the FoF that would prevent the subjects to unbalance themselves more quickly. This study does not bring firm arguments for or against one of these hypotheses. By elongating their APA without modifying the amplitude, F subjects may have tried to minimize the muscular effort (Zettel et al., 2002). Indeed, a larger CoP displacement in the mediolateral direction (excursion and peak velocity) will require a high level of muscular strength at the hip abductors/adductors. It has been reported that elderly and particularly F have both weaker hip adductor/abductors capacity (Johnson et al., 2004; Inacio et al., 2014; Morcelli et al., 2016) and a reduced lateral stability (Rogers et al., 2001; Johnson-Hilliard et al., 2008). Elderly F also have a

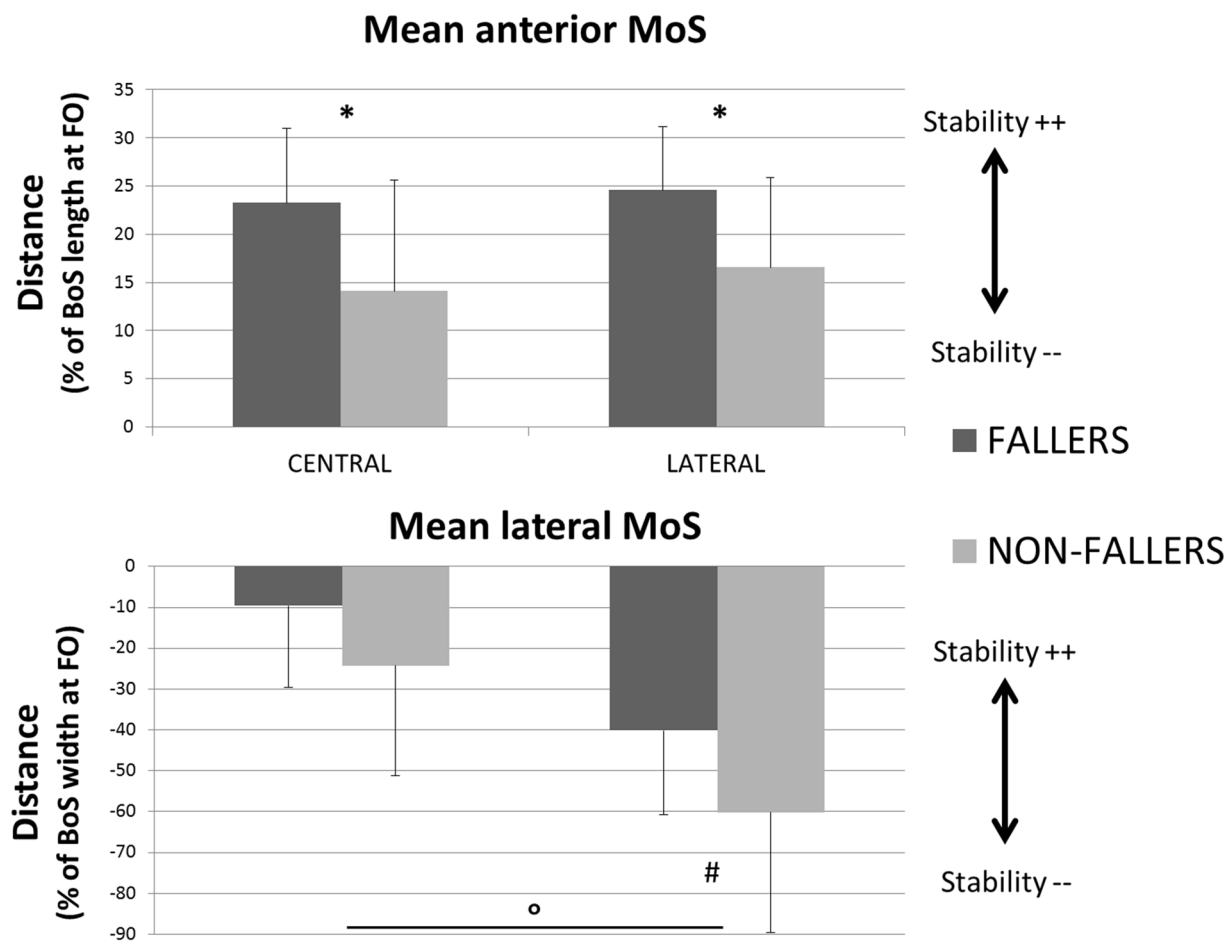

FIGURE 9 | Mean values (with standard deviations) of the MoS measured at FO for both the two groups and targets. Anteroposterior component is presented on the top and mediolateral component on the bottom. Indicators of the quality of stability are provided for each of them (Stability ++ = a higher stability, Stability −− = a smaller stability). *Indicates a significant effect of the main factor "Group". °Indicates a significant effect of the main factor "Target". #Indicates a significant difference between F and NF measured with the *post hoc* test. Note that here the BoS width is the width of the stance foot, the current BoS at FO.

higher FoF (Maki et al., 1991; Vellas et al., 1997; Lajoie and Gallagher, 2004). A high FoF affects the development of APA (Adkin et al., 2000; Yiou et al., 2011), and so F subjects may have tried to reduce the risk to fall on a particular side. Finally, it could be a combination of these two hypotheses. Nevertheless, it is remarkable that in the present study F performed at least as well as NF in terms of CoP excursion and peak velocity in the ML direction. As such, a lengthened APA phase measured during a CSRT test appears to be an earlier indicator of the risk of fall for community-dwelling elderly subjects than the capacity to move the CoP during the APA.

The situation is different in the AP direction: elderly F limited the CoP backward excursion (CoP_B) and peak velocity ($VCoP_B$) compared to NF (see **Figure 8**). According to Brenière and collaborators model (Brenière et al., 1987; Lepers and Brenière, 1995), it means that during APA the F reduced the distance between the CoP and the CoM_{WB} in the AP direction. Consecutively, F did not create a forward propulsive torque as efficient as NF. This mechanism led to a smaller displacement of the XCoM in the forward direction and to an increased stability at FO. This is typically what we observed for F compared to NF (see **Figures 6**, **9**). We could interpret these results in two different ways: (1) F cannot move their CoP further or faster backward, due to physical limitations or a higher FoF, and the APA last as long as the XCoM is forward enough to step; and (2) F chose to decrease the CoP excursion in order to enhance the stability at FO. In this case the decrease is even more pronounced that APA duration is increased, probably due to limitations in the ML direction (see paragraph above). Nonetheless, our results on elderly F show that they were as able as NF in: (1) moving their CoP in the ML direction inside the BoS; and (2) moving their foot during the SP (a part of the movement that also engages muscular capacity). Again, this study does not bring enough firm arguments pro or against any of these interpretations. According to our results

the second interpretation seems however to correspond the best.

Different APA strategies in ML and AP directions are used by F compared to NF. Both resulted in an increase of the dynamic stability at FO. It seems that the increase in APA duration is primarily due to limitations of the ML direction. A lengthened APA phase measured during a CSRT appears to be an earlier indicator of the risk of fall than the capacity to move the CoP, in community-dwelling elderly subjects.

Two Strategies that Aim to Increase Stability Instead of Rapidity in Elderly F

As discussed previously, elderly F displays a higher stability at FO. One of the counterpart is that they take less advantage of the disequilibrium torque given by gravity to propel the body in the direction of the targets, at the beginning of the SP (Lepers and Brenière, 1995; Lyon and Day, 1997). Another negative consequence is that it necessitates longer APA duration that decreases performances at the CSRT (Lord and Fitzpatrick, 2001).

To interpret those results, we can see the CSRT as a test involving two "tasks" for the CNS: stepping on the target as fast as possible (rapidity) and maintaining balance (stability). The results we observed in this study resemble to a "safer" strategy—as previously suggested by Patla et al. (1993), Brauer et al. (2002) and Luchies et al. (2002)—where the elderly F seem to enhance stability to the detriment of rapidity. In a different context, Brauer et al. (2002) showed that elderly having balance troubles prioritize stability instead of a dual task, probably because they involve maximal attentional resources in the accomplishment of the primary "task" (i.e., maintain balance). Similarly to what they suggested, a hypothesis would be that elderly F may see stability as the "primary task" during the CSRT and choose to prioritize it. We suggest that F make a choice because they "go against" the instructions of the test which were clearly to give priority to the rapidity.

This choice could also be qualified as a "conservative" strategy (Nakano et al., 2016), because elderly F seems to use unnecessary large conditions of stability at FO—as elderly do regarding to young adults in lateral steps (Patla et al., 1993). This inability of F to limit, in reasonable proportions, their stability at FO could even be seen as a limited capacity to adapt their motor command to the external context. Elderly F may perform this "conservative" strategy during the CSRT because the initiation of a voluntary step can always be delayed. In a more demanding context, such as a protective step (Rogers et al., 1996; Maki and McIlroy, 1997), this strategy would probably induce balance issues and a higher risk of fall. During protective steps the APA are usually shortened in time and reduced in amplitude in the ML direction to adapt to the perturbation (McIlroy and Maki, 1999) and the lateral balance has been shown to be the most determinant capacity for F to prevent from falling (Rogers et al., 2001; Johnson-Hilliard et al., 2008). The results pointing out that elderly F prioritize a more stable strategy than NF at FO could be interpreted as a poorer control of balance and an increased risk of fall. It has recently been suggested that an increased MoS is an indicator of a decreased control of lateral balance and a higher risk of fall during gait (Vistamehr et al., 2016).

Why would elderly F prioritize a more stable strategy than NF at FO? As the postural control is complex and involve multiple capacities and processes (Horak, 2006), there is never only one reason. If elderly F are effectively choosing a more stable balance strategy, it is probably because of the use of different processes and the integration of their own capacities, which are different from one subject to another. Reasons could be found in numerous capacities and processes, as the literature has already shown in the past (sensorial, cognitive, muscular, psychological). It appears important to us to point out that all subjects of our group of elderly F have one characteristic in common: they fell in the past year. This has probably significantly increased their FoF (Maki et al., 1991; Lajoie and Gallagher, 2004). Then, as the FoF reduces attentional resources available (Gage et al., 2003) and movement reinvestment (Huffman et al., 2009), an interaction between FoF and cognitive processes that acts in APA elaboration may have influenced their choice. A higher FoF is probably the most important reason why we observed this balance strategy in elderly F.

Limitations

This study presents several limitations. The location of our "Lateral" targets may not have been enough lateral (see **Figure 1**). The main limitation for balance in elderly F seems to come from the ML control of the CoP and our results are the most significant for these targets. More pronounced effects may be obtained using, for instance, 45° targets rather than 30°.

Another limitation comes from the fact that there is no simple RT test in that study, such as in Luchies et al. (2002). Such data could have helped to determine if sensory processing was reduced in our group of F and/or if they needed more time than NF to program the correct APA during a CSRT.

We did not study our population under a secondary task during this test, making impossible to know if our F subjects suffered from reduced attentional or inhibition capacities. As the balance strategy observed may come from a choice of a more "safer" or stable strategy, it could have been interesting to see if FoF has an interaction with the decisional process. We cannot currently conclude on those processes, which need to be further investigated.

CONCLUSION AND PERSPECTIVES

The results presented here confirmed our hypothesis. Elderly F have an elongated performance in the CSRT due to longer APA phase. By lengthening the APA duration in the ML direction without increasing the CoP displacement performance (excursion and peak velocity), F increase the MoS at FO.

This strategy can be qualified as a "safer" strategy—as suggested previously by Patla et al. (1993), Brauer et al. (2002) and Luchies et al. (2002)—used to the detriment of the CSRT

performance. This strategy probably comes from a choice due to a higher FoF, which changes the way posture and balance are controlled (Maki et al., 1991; Adkin et al., 2000; Brauer et al., 2002; Huffman et al., 2009; Yiou et al., 2011) and/or an attempt to minimize the muscular effort (Zettel et al., 2002). In a more demanding environment, this incapacity to adjust the stability to the task would probably induce balance issues and a higher risk of fall. Programs for the risk of fall prevention in community-dwelling elderly adults should focus on helping elderly F to get confidence back in their capacity to manage balance in different situations and, by so, improve balance performances.

In perspective of this study, we will look more specifically at the trials with APA errors. It would be indicative to know how elderly F correct these errors. Such information would particularly inform about their inhibition capacity, as Sparto et al. (2014) showed. Further improvements of this test are also to consider, like for example use of 45° targets during a CSRT.

AUTHOR CONTRIBUTIONS

RT contributed with project creation, data collection, data analysis and drafted the manuscript. TR contributed with project creation and data analysis. PC contributed in data analysis. MB contributed with project creation and recruitment of the subjects. LC contributed with project creation, data collection and data analysis. All authors discussed the results and participated in the revision of the manuscript.

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frontiers in Human Neuroscience

ORIGINAL RESEARCH
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Anodal Transcranial Direct Current Stimulation Does Not Facilitate Dynamic Balance Task Learning in Healthy Old Adults

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Older adults frequently experience a decrease in balance control that leads to increased numbers of falls, injuries and hospitalization. Therefore, evaluating older adults' ability to maintain balance and examining new approaches to counteract age-related decline in balance control is of great importance for fall prevention and healthy aging. Non-invasive brain stimulation techniques such as transcranial direct current stimulation (tDCS) have been shown to beneficially influence motor behavior and motor learning. In the present study, we investigated the influence of tDCS applied over the leg area of the primary motor cortex (M1) on balance task learning of healthy elderly in a dynamic balance task (DBT). In total, 30 older adults were enrolled in a cross-sectional, randomized design including two consecutive DBT training sessions. Only during the first DBT session, either 20 min of anodal tDCS (a-tDCS) or sham tDCS (s-tDCS) were applied and learning improvement was compared between the two groups. Our data showed that both groups successfully learned to perform the DBT on both training sessions. Interestingly, between-group analyses revealed no difference between the a-tDCS and the s-tDCS group regarding their level of task learning. These results indicate that the concurrent application of tDCS over M1 leg area did not elicit DBT learning enhancement in our study cohort. However, a regression analysis revealed that DBT performance can be predicted by the kinematic profile of the movement, a finding that may provide new insights for individualized approaches of treating balance and gait disorders.

Keywords: dynamic balance task, balance learning, healthy aging, non-invasive brain stimulation, kinematics, transcranial direct current stimulation

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Abbreviations: a-tDCS, anodal transcranial direct current stimulation; DBT, dynamic balance task; M1, primary motor cortex; s-tDCS, sham transcranial direct current stimulation; tDCS, transcranial direct current stimulation; TD, Training Day; TiB, Time in Balance; ZC, number of zero crossings.

INTRODUCTION

Due to the demographic change, the older population is constantly increasing. Therefore, understanding the mechanisms of aging processes and examining strategies to decelerate age-related decline is of great importance. One significant problem of the aging process is impaired motor ability (Smith et al., 1999; Krampe, 2002) which is the result of a complex interaction of peripheral and central processes involving losses in muscle strength/power (Frontera et al., 1991; McNeil et al., 2007) and alterations in the central nervous system (CNS; Burke and Barnes, 2006). Age-related decline in muscle strength most severely affects the dorsiflexor and extensor muscles of the lower extremities (Frontera et al., 1991; McNeil et al., 2007), which is why older adults often show increased postural sway (Baloh et al., 1994; Liaw et al., 2009). On the other hand, older adults, compared with younger adults, show a reduced amount of structural and functional brain plasticity (Burke and Barnes, 2006) and also learning-dependent plasticity decreases with age (Sawaki et al., 2003). All these factors contribute to an age-related decrease of postural stability, which is an important risk factor for falls (Granacher et al., 2008; Panel on Prevention of Falls in Older Persons, American Geriatrics Society and British Geriatrics Society, 2011). According to the Clinical Practice Guidelines for Prevention of Falls in Older Persons from 2011, exercise in the form of strength, balance, gait, and coordination training was shown to be effective in reducing falls in older adults (Panel on Prevention of Falls in Older Persons, American Geriatrics Society and British Geriatrics Society, 2011). Besides reducing the number of falls (Gardner et al., 2000), balance training also had a positive effect on gait and reduced the fear of falling (Wolf et al., 1996; Liu-Ambrose et al., 2004) and therefore is considered an effective intervention for treating age-related mobility losses. One study revealed that balance training is also capable of inducing neuroplastic changes in elderly but also in patients suffering from Parkinson's disease (Sehm et al., 2014). Interestingly, these neuroplastic changes were correlated with the learning performance (Sehm et al., 2014) and therefore seem to be an important prerequisite for balance learning. Techniques of non-invasive brain stimulation have also been shown to induce neuroplastic changes and thereby also successfully facilitate task performance (Nitsche and Paulus, 2000; Madhavan and Shah, 2012). Transcranial direct current stimulation (tDCS) can facilitate motor performance by up-regulating neural activity in the underlying brain tissue (Nitsche and Paulus, 2000). Following on training studies attempting to enhance postural stability, recent studies have successfully targeted the leg area of the primary motor cortex (M1) by means of anodal tDCS (a-tDCS) to improve static balance (Dutta et al., 2014) and locomotion (Kaski et al., 2012) in young adults. A study in hemiplegic stroke patients showed that single-session tDCS can improve patients' balance ability and increases the isometric strength of the affected lower extremity (Sohn et al., 2013). Therefore, combining the assessment of older adults balance ability with concurrent use of lower limb tDCS seems reasonable to evaluate the effect of brain stimulation on balance learning. In our previous study, the effect of tDCS on balance learning ability was investigated in healthy young subjects using a dynamic balance task (DBT; Kaminski et al., 2016). Our results showed that tDCS over M1 leg area is capable of enhancing balance performance in the DBT as participants showed higher task performance and lower error rates during and after tDCS compared to a control group. To follow up on these findings, in the present study we wanted to examine the feasibility of using the DBT as a balance learning task in elderly participants. Our main objective was to evaluate the effect of a-tDCS on DBT learning in older adults. Additionally, we analyzed the kinematic profile of DBT learning performance in our aged cohort as kinematic variables have been shown to be sensitive markers of postural stability (Yu et al., 2008; Bisson et al., 2014). In specific, we aimed to identify whether kinematic variables velocity, acceleration, jerk and postural sway frequency can predict balance performance in healthy elderly. In our previous study, we found that kinematic variables can well predict DBT performance in younger adults (Kaminski et al., 2013). Additionally, our results showed that performance improvements were mediated by tDCS-induced changes in movement velocity. According to this previous study, we hypothesized that (A) a-tDCS over M1 leg area during DBT learning facilitates learning performance compared with a group receiving s-tDCS in an older age cohort. Additionally, we expected that (B) the kinematic profile assessed during DBT learning predicts the DBT performance level of elderly with a special impact of velocity on performance improvement.

MATERIALS AND METHODS

Participants

Thirty healthy elderly participants (17 females, mean age = 67.7 ± 6 years) were enrolled in this study. All participants gave written informed consent and the study procedures were approved by the local ethics committee of the University of Leipzig and conducted in accordance with the Declaration of Helsinki and only healthy participants were included. To exclude the presence of any neurological disease and/or contraindications, all participants underwent a detailed neurological examination prior to the testing phase. All participants were free of any medication affecting the CNS and were task naïve. All participants were right-handed as assessed by the Edinburgh Handedness Inventory (mean score 90.03; range 55–100; Oldfield, 1971) and did not show any signs of cognitive impairment, measured by the Mini Mental State Examination (MMSE, mean score: 29.23, range: 27–30; Folstein et al., 1975). Furthermore, we assessed participants standing balance ability before the experimental procedure using the Fullerton Advanced Balance (FAB) Scale (Rose et al., 2006), a multidimensional balance scale specifically designed to evaluate balance ability of functionally independent older adults. We also assessed participants' level of physical activity with the long version of the International Physical Activity Questionnaire (IPAQ; Craig et al., 2003).

Study Design

The study was comprised of two consecutive training sessions that were separated by 24 h. On the first training day (TD1), participants performed 15 trials of DBT training while 20 min of tDCS were applied over the leg motor cortex (M1 leg area). Participants were randomly assigned to either the experimental condition, where they received 20 min of a-tDCS, or the sham-control condition, where s-tDCS was applied. On the second training day (TD2), another 15 trials of DBT training were performed without tDCS. This was done to examine the effects of a-tDCS on consolidation of the newly acquired motor skill and to capture longer lasting a-tDCS effects on a consecutive training session. During each session, the platform position of each subject in each trial was continuously recorded using the Spike2 (Cambridge Electronic Design Ltd., Cambridge, UK) software.

Whole-Body Dynamic Balancing Task (DBT)

The DBT was performed on a stability platform (model 16030, LaFayette Instruments, Lafayette, IN, USA) with a maximal deviation of 26° to each side. A detailed description of the procedure is provided elsewhere (Taubert et al., 2010; Kaminski et al., 2013). In brief, subjects were instructed to stand on the movable platform and to keep it in a horizontal position as long as possible during a trial length of 30 s. On each training day, 15 trials were performed with between-trial rest intervals of 90 s to avoid muscle fatigue. Hence, each training session lasted approximately 29 min, including breaks. To prevent falls, participants were secured with a safety harness during training. The primary performance measure was the total time participants were able to keep the platform in a horizontal position within a range of ±3° to each side, henceforth referred as Time in Balance (TiB). After each trial, participants were provided with their TiB value as verbal feedback but besides that, no strategy on how to best perform the task was provided (discovery learning approach; Wulf et al., 2003; Orrell et al., 2006).

Transcranial Direct Current Stimulation (tDCS)

For tDCS, a weak direct current of 1 mA was delivered for 20 min using a battery driven stimulator (neuroConn GmbH, Ilmenau, Germany). On TD1, either a-tDCS or s-tDCS was applied to the bilateral M1 leg area during the first 10 trials of DBT performance. While the anode (5 cm × 5 cm) was placed over the M1 leg area target region, the cathode (reference electrode) was placed over the right frontal orbit (10 cm × 5 cm). The anatomical landmark for M1 leg area was chosen according to the 10–20 system and the anode was placed 1 cm behind the vertex on the mid-sagittal line (Madhavan and Stinear, 2010; Laczó et al., 2014). TDCS was applied using a highly conductive electrode paste (Ten20 CONDUCTIVE Neurodiagnostic Electrode Paste, Weaver and Company) and flexible elastic straps were used to fixate the electrodes on the head. Current was ramped up for 30 s in the beginning of tDCS eliciting a transient tingling sensation on the scalp that faded over seconds (Nitsche et al., 2003; Gandiga et al., 2006) and also ramped down for 30 s. During s-tDCS, the current was increased, maintained and decreased for 30 s each. Before and after tDCS, participants rated their level of attention (1 = not attentive, 10 = very attentive), fatigue (1 = very tired, 10 = not tired at all) and discomfort (1 = no discomfort, 10 = strong discomfort) on a visual analog scale (VAS).

Data Analysis

For detailed data analysis, we recorded the platform position of each subject in each trial. This was done by transforming voltage to an amplifier that translated the signal into a Spike waveform at 5000 Hz. Before parameters were calculated, data was preprocessed using custom-built scripts in MATLAB version 8.2 (see also Kaminski et al., 2016). Data preprocessing included low-pass-filtering at 5 Hz using a 2nd order low-pass Butterworth filter to remove hardware derived artifacts and data resampling to 500 Hz. TiB was then calculated by calculating the total time per trial, subjects spent within a range of ±3° to each side. Additionally, we aimed to decode the kinematic profile of DBT performance using additional variables. Therefore, we calculated the first, second and third derivatives of position representing velocity, acceleration, jerk/smoothness. In addition, the number of zero crossings (ZC) was calculated as the total number of times that signal passed from one side of the horizontal position (0°) to the other. Statistical analyses were performed using IBM SPSS version 22.

Demographics

An independent-samples *t*-test was performed on each demographic variable (age, MMSE-score, total score of physical activity in IPAQ, total score in FAB-scale) to exclude that potential group differences in demographic variables might have influenced task performance. Repeated-measures analysis of variance (RM-ANOVA) with factor GROUP (a-tDCS, s-tDCS) and TIME (pre-post training) were used to assess changes in VAS scores.

Performance Measure Time in Balance (TiB)

Performance data was tested for normality using the Shapiro-Wilk test. As the test showed that the data was not normally distributed, non-parametric tests were used to examine learning improvement.

Training day 1

The Mann-Whitney U Test (MWU) was performed to assess baseline (trial 1) differences between groups. Overall learning was evaluated by performing a Friedman Test on factor TRIAL. First training session improvements were divided in online (trial 1–10) and offline (trial 11–15) learning improvements to disentangle acute tDCS effects and immediate tDCS after effects. Absolute improvement was calculated by subtracting last trial performance from first trial performance (online: t10–t1, offline: t15–t11) and compared between groups using the MWU. Additionally, percentage performance improvement was calculated by subtracting participants first trial performance

(t1) from performance of training trial 15 and normalizing the difference to t1 performance and multiplying the term by 100 to create percentage values (online: (t10−t1)/t1*100, offline: (t15−t11)/t11*100). Percentage improvements were compared between groups using the MWU.

Consolidation and training day 2

To investigate skill consolidation from TD1 to TD2, the retention score, calculated as the difference between t15 TD1 performance and t1 TD2 performance, was compared between the two groups using MWU. Overall learning was evaluated by performing a Friedman Test on factor TRIAL. Absolute and percentage performance improvement on TD2 was calculated analogous to TD1 and compared between groups using the MWU.

Predicting DBT Performance by Kinematic Variables

Multiple regression

A partial correlation was performed between each kinematic variable and performance variable TiB. Subsequently, all variables having significant relations with TiB were entered in a regression model. The regression analysis was performed to decode the contribution of specific kinematic variables on overall DBT performance and thereby unravel the predictive power of the kinematic profile for balance performance measures. All variables were log-transformed before entering them into the model, thereby we created residuals with a normal distribution. In the regression model, TiB was defined as the dependent variable and the kinematic variables velocity, acceleration, ZC and trial were predefined as predictor variables. All main variables were entered at the same time and a full-model fit was examined.

tDCS effects on kinematic variables

To evaluate the effect of tDCS on our kinematic data, we calculated the absolute and percentage change of each variable analogous to our absolute and percentage improvement calculation (absolute: t15–t1, percentage: (t15–t1)/t1*100) and compared these values between groups using MWU.

For all analyses, a p-value of < 0.05 was considered to be significant.

RESULTS

Demographics

There were no significant between-group differences in age (independent-samples t-test, $t_{(28)} = -0.82$, $p = 0.42$), MMSE-score (independent-samples t-test, $t_{(28)} = 0.63$, $p = 0.53$), total amount of physical activity (independent-samples t-test, $t_{(28)} = 0.85$, $p = 0.4$) or balance ability on the FAB-scale (independent-samples t-test, $t_{(28)} = 0.13$, $p = 0.9$); see also **Table 1** for mean values of all variables). All participants tolerated the stimulation well. None of the participants reported any side effects from tDCS stimulation but most experienced the tingling sensation on the skin during the ramp-up phase of tDCS. Groups did not differ in their level of attention (RM-ANOVA Time × Group interaction, TD1: $F_{(1,28)} = 2.87$, $p = 0.1$, TD2: $F_{(1,28)} = 1.26$, $p = 0.27$), fatigue (RM-ANOVA Time × Group interaction, TD1: $F_{(1,28)} = 0.19$, $p = 0.67$ TD2: $F_{(1,28)} = 0.05$, $p = 0.98$) or discomfort (RM-ANOVA Time × Group interaction, TD1: $F_{(1,28)} = 0$, $p = 1$, TD2: $F_{(1,28)} = 0.2$, $p = 0.89$) before and after each of the DBT training days (see also **Table 2** for mean values).

TABLE 1 | Group demographics.

Group	Age (years)	MMSE	IPAQ	FAB
a-tDCS, $n = 15$	66.8 ± 5.63	29.33 ± 0.72	6855.6 ± 5682	36.67 ± 2.72
s-tDCS, $n = 15$	68.6 ± 6.00	29.13 ± 0.99	5383.8 ± 3590	36.53 ± 3.02

MMSE: Mini Mental State Examination, total score range of 1–30; cut-off score for exclusion: ≤26. IPAQ: International Physical Activity Questionnaire, total score of physical activity in metabolic equivalent of task minutes per week (MET-minutes), cut-off for high level of physical activity per week: ≥3000. FAB: Fullerton Advanced Balance Scale, total score range of 1–40, cut-off score for higher risk of falls: ≤25. All values are depicted as mean ± standard deviation of the mean.

Performance Measure Time in Balance (TiB)

Training Day 1 (TD1)

There was no baseline difference in TiB between the two groups (MWU: $U = 101.5$, $p = 0.65$), indicating that all participants started at the same performance level. Both groups significantly improved their DBT performance over time (Friedman: $\chi^2_{(14)} = 51.81$, $p < 0.001$, **Figure 1A**). TiB under a-tDCS increased from 2.87 ± 1.09 s at baseline to 3.9 ± 1.74 s, while TiB under s-tDCS increased from 3.13 ± 1.22 s to 5.22 ± 2.77 s. We did not find significant differences between groups regarding their absolute performance improvement neither during tDCS stimulation (online effect, MWU: $U = 106$, $p = 0.78$) nor immediately after tDCS stimulation (offline effect, MWU: $U = 85$, $p = 0.25$). We also did not find significant group differences regarding percentage improvement gain neither during tDCS (MWU: $U = 105$, $p = 0.76$) nor after tDCS (MWU: $U = 103$, $p = 0.69$; see also **Figure 1B**).

TABLE 2 | Visual analog scale (VAS).

	TD1		TD2	
	Before	After	Before	After
a-tDCS				
Attention	9.47 ± 0.74	9.60 ± 0.74	9.27 ± 1.16	9.40 ± 1.18
Fatigue	9.40 ± 1.12	9.47 ± 0.92	9.60 ± 0.74	9.67 ± 0.72
Discomfort	1.20 ± 0.56	1.20 ± 0.56	1.13 ± 0.35	1.20 ± 0.50
s-tDCS				
Attention	9.53 ± 0.74	9.33 ± 1.18	9.47 ± 0.92	9.40 ± 1.12
Fatigue	9.27 ± 1.03	9.28 ± 0.98	9.27 ± 1.44	9.33 ± 1.40
Discomfort	1.13 ± 0.52	1.20 ± 0.53	1.27 ± 1.04	1.21 ± 0.99

Attention, fatigue and discomfort were assessed on a VAS before and after the dynamic balance task (DBT) was performed on TD1 and TD2. Attention scale, ranging from 1 (no attention) to 10 (highest attention level). Fatigue scale, from 1 (high fatigue level) to 10 (no fatigue). Discomfort scale, ranging from 1 (no discomfort) to 10 (highest level of discomfort). All values are expressed as mean ± standard deviation. Please note that there were no changes in attention, fatigue or discomfort within groups (Before vs. After) or between groups (a-tDCS, s-tDCS) on TD1 or TD2.

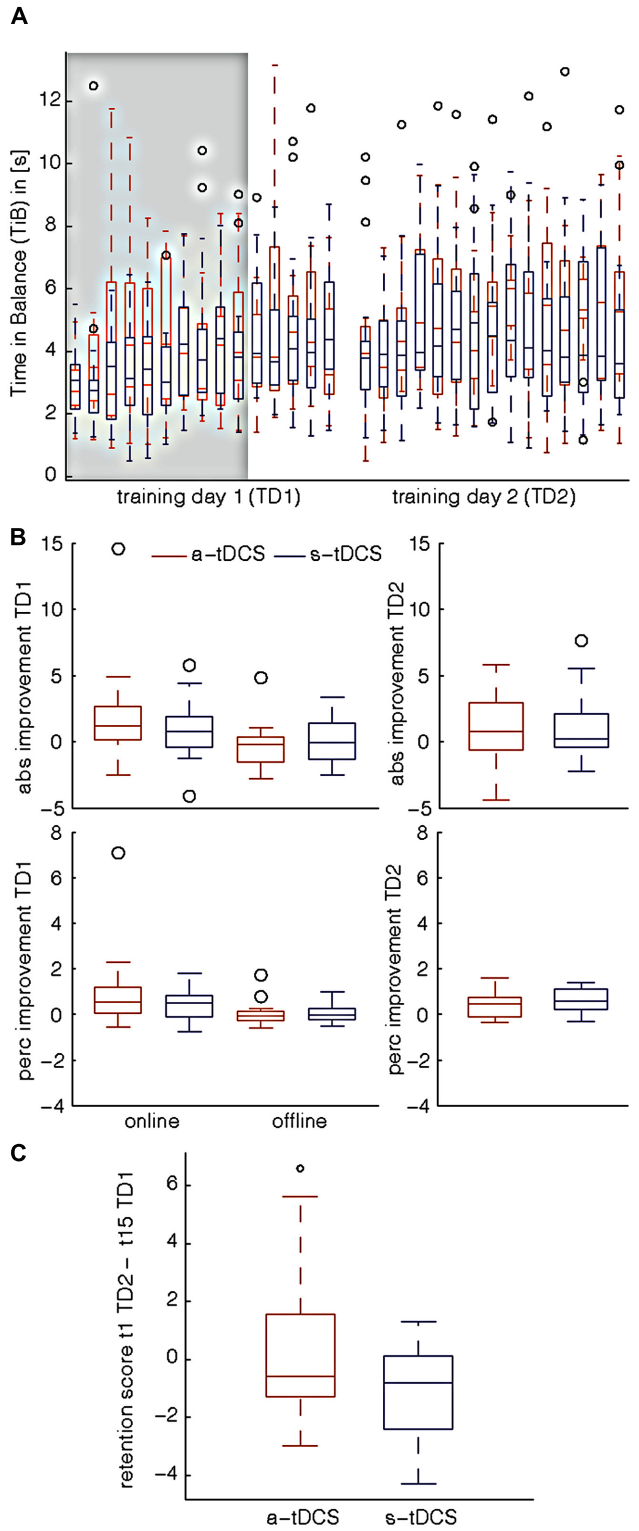


FIGURE 1 | Dynamic balance task (DBT) performance. Results are shown for Training Day 1 (TD1) and Training Day 2 (TD2), which were separated by 24 h. a-tDCS: anodal tDCS, s-tDCS: sham tDCS, abs improvement: absolute improvement, abs improvement TD1: online improvement: trial10–trial1, offline improvement: trial15–trial11, TD2: trial15–trial1, perc improvement: percentage improvement, weighted difference of first and last trial performance multiplied by 100, perc improvement TD1: online improvement: ((t10−t1)/t1*100), offline improvement: ((t15−t11)/t11*100), TD2: ((t15−t1)/t1*100), retention score: difference between trial 15 TD1 and trial 1 TD2 performance (t15TD1–t1TD2). **(A)** Behavioral results for Time in Balance (TiB) performance on both training sessions. There was no baseline difference in TiB between the two groups (trial1, TD1) which indicates that all participants started at the same performance level. Both study groups significantly improved their level of performance over time on TD1 as well as on TD2. Gray shaded box indicates the time of a-tDCS/ s-tDCS stimulation. **(B)** Absolute/Percentage Improvement for TD1. No significant differences between a-tDCS and s-tDCS group were observed when comparing their absolute or percentage improvement gain. On TD1, neither online (t1–10) nor offline effects (t11–15) of tDCS showed a significant group difference. Therefore, one can conclude that the concurrent application of tDCS over M1 leg area did not elicit DBT performance enhancement in our study cohort **(C)** Retention score. There was no significant difference regarding the retention scores of the two groups, which indicates that tDCS did not affect skill retention from TD1 to TD2.

Consolidation and Training Day 2 (TD2)

When comparing the retention scores of the two groups, we found no significant difference (MWU: $U = 76$, $p = 0.13$), which indicates that a-tDCS did not affect skill retention from TD1 to TD2 (**Figure 1C**). Similar to TD1, DBT-learning in both groups improved over time (Friedman: $\chi^2_{(14)} = 34.68$, $p = 0.002$, **Figure 1A**). However, no significant difference regarding the absolute (MWU: $U = 110$, $p = 0.94$) or the percentage improvement gain (MWU: $U = 109$, $p = 0.9$) of the two groups was detected (**Figure 1B**). TiB increased from 4.24 ± 2.87 s to 5.33 ± 2.82 s under a-tDCS, while performance under s-tDCS increased from 3.5 ± 1.03 s to 5.05 ± 3.35 s.

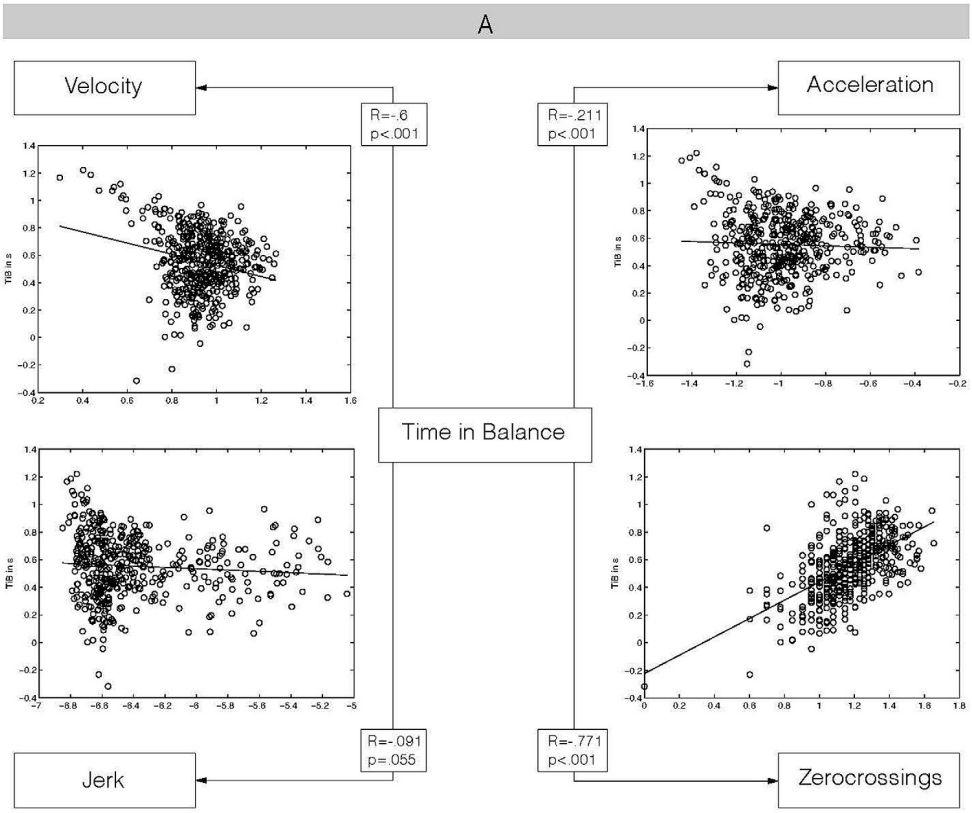
Relationship between Kinematics and Performance

Multiple Regression

Figure 2A depicts the significant partial correlations between our dependent variable TiB and the kinematic variables velocity, acceleration and the number of ZC. As there was no significant correlation between TiB and jerk (see **Figure 2A**), we did not include jerk as a factor in the model. All other kinematic variables and variable trial were included as predictors in the model. The regression model revealed that each independent variable was significantly related to the dependent variable TiB (adjusted $R^2 = 0.72$, $F_{(4,443)} = 285.71$, $p < 0.001$). Larger ZC- and larger acceleration values were associated with greater TiB values (positive correlation), while lower velocity values were associated with higher TiB values (negative correlation). Additionally, TiB and trial showed the expected positive association, indicating that TiB increased with ascending trial numbers (see also **Figure 2B** for regression weights).

tDCS Effects on Kinematic Variables

We did not detect any group difference regarding absolute or percentage change from t1 to t15 in our kinematic variables velocity (abs: $U = 93$, $p = 0.42$, perc.: $U = 103$, $p = 0.69$), acceleration (abs: $U = 78$, $p = 0.15$, perc.: $U = 80$, $p = 0.18$) or the number of ZC (abs: $U = 100$, $p = 0.6$, perc.: $U = 105$,



B

Predictor	B	β	t	p
velocity	-1.582	-.918	-15.75	<.001
acceleration	.306	.247	4.02	<.001
ZC	1.08	.891	28.08	<.001
trial	.007	.13	5.09	<.001

FIGURE 2 | Relationship between kinematic variables and balance performance. **(A)** Results of partial correlation analysis, controlling for the other three kinematic variables, respectively. This analysis revealed a specific relationship between time in balance performance and kinematic variables velocity, acceleration and the number of zero crossings (ZC), but not for jerk. Additionally, scatterplots of the relationships between kinematics and performance are added. **(B)** Results from multiple regression analysis, Time in Balance (TiB) as dependent variable, velocity, acceleration, number of ZC and trial as independent predictors. ZC: number of zero crossings, B: unstandardized regression coefficient, β: standardized regression coefficient, t = t test value (t-statistic), p = p-value of t-statistic. Our multiple regression analysis revealed a significant relationship between each of the included variables and our dependent variable TiB. The kinematic variable velocity was negatively correlated with performance, while acceleration and ZC showed a positive relation with TiB. Trial was also positively correlated with TiB.

$p = 0.76$). Interestingly, we found a significant group difference in jerk for absolute ($U = 46$, $p = 0.006$) as well as percentage change ($U = 52$, $p = 0.012$) from t1 to t15, even though the change in jerk was relatively small. While the a-tDCS group showed a small increase in jerk values from t1 to t15 (absolute change: 0.0002 m/s^3, percentage change: 18%), jerk in the s-tDCS group rather decreased from t1 to t15 (absolute change: −0.0035 m/s^3, percentage change: −28%). However, our partial correlation analysis did not reveal a significant association between jerk and TiB; therefore we assume that the group difference in jerk change did not affect our global learning measure TiB.

DISCUSSION

In the present study, our main objective was to examine whether a-tDCS over M1 leg area is capable of enhancing DBT learning in healthy elderly. We expected that, analogous to a younger cohort (Kaminski et al., 2016), targeting the M1 leg area region by means of tDCS would support DBT learning in the elderly and

translate into superior learning performance compared to sham stimulation. However, even though both groups successfully increased their level of DBT performance over time, in the present study we found no difference between the a-tDCS and s-tDCS groups' amount of learning. Thus, our results indicate that the application of tDCS over M1 leg area during DBT performance did not elicit performance enhancement in our aged study cohort. But the results also indicate that older adults are able to perform the DBT (Sehm et al., 2014) and significantly improve their performance even within a single training session. Future studies can use this knowledge to directly compare DBT performance between different age cohorts to further investigate age-related deficits in balance learning ability and identify related neural correlates using combined neurophysiological assessments of brain activation with behavioral outcome measures. Furthermore, our results show that a large amount of variance in DBT learning performance can be predicted by kinematic variables, a result that can particularly be important when diagnosing and treating balance and gait disorders.

No Effects of tDCS on Complex Balance Learning in Elderly

Several studies have shown beneficial effects of tDCS over M1 leg area on postural control and locomotion. While Kaski et al. (2012) showed enhanced motor adaptation aftereffects in healthy young adults after using tDCS over M1 leg area, Sohn et al. (2013) were able to demonstrate that tDCS enhanced the overall stability index of hemiplegic stroke patients after only a single session (Sohn et al., 2013). In a previous study, we found that tDCS over M1 leg area does elicit performance improvements in DBT learning in a younger study cohort (Kaminski et al., 2016). However, using the same parameters of tDCS stimulation in our older study sample, we did not see behavioral improvements in DBT learning, a finding that might indicate age-related differences in the capacity for tDCS-induced behavioral changes. One potential explanation for this discrepancy is that the brain regions that are involved in initial DBT learning differ between younger and older adults. In a recent study, it was demonstrated that a single DBT training session results in cortical thickening of M1 leg area in healthy young adults (Taubert et al., 2016). This finding suggests a specific involvement of the leg area sub-region of M1 during initial DBT learning in a younger cohort. However, nothing is known so far about brain activation changes after a single DBT session in older adults. It might be that brain regions other than M1 leg area are more important during initial DBT learning in older age. Another issue that needs to be considered is the timing of the stimulation. It is known that neurophysiological effects of tDCS differ between older and younger adults with older adults showing delayed plasticity of M1 (Fujiyama et al., 2014). Therefore, future studies should consider applying tDCS in older adults before a motor task is performed. What is also known is that older adults exhibit more elaborate brain activation than younger controls when performing a motor task, potentially to compensate for an age-related decline of neuronal efficacy (Heuninckx et al., 2008). Therefore, one could argue that stimulating a single brain region by means of tDCS may not have been sufficient to activate the whole large-scale network responsible for successful performance of this complex task in older adults. This would also be in line with previous studies demonstrating that older individuals show different responses to non-invasive brain stimulation protocols as compared with younger adults (Müller-Dahlhaus et al., 2008; Ridding and Ziemann, 2010). It is also known, that the effects of tDCS on motor outcomes are highly variable (Horvath et al., 2016) and tDCS effects also vary across sessions and individuals (Chew et al., 2015). Additionally, large differences in brain structure as well as in brain function exist in older adults (Stewart et al., 2014), which may also affect task performance and responsiveness to tDCS protocols. Therefore, it may be that the inter-individual variability in older adults is greater than that of younger adults, and may impair our ability to detect differences between groups.

Taken together, we are not able to determine which factor or combination of factors, if any, may have contributed to a facilitatory effect of tDCS on DBT performance in older adults. As argued above, the outcome of tDCS is affected by multiple factors involving task characteristics and individual determinants (Ridding and Ziemann, 2010) and little is known about neuronal correlates of DBT performance in older adults. Therefore, more research is needed to draw a comprehensive picture on dynamic balance ability in the elderly and how non-invasive brain stimulation techniques may interact with such complex coordinative behavior.

Relationship between Kinematic Variables and Balance Control

Previous studies suggest an association between changes in postural control and changes in parameters of movement kinematics. Our regression results are in line with previous findings, showing that the kinematic parameters velocity (Jeka et al., 2004), acceleration (Jeka et al., 2004; Yu et al., 2008) and information on postural sway (Manor et al., 2010) provide important information for maintaining postural control. While velocity showed a strong negative relationship with performance, acceleration and performance were weakly positively correlated. Both velocity and acceleration seem to be sensitive markers of postural stability (Yu et al., 2008), however, we also found that the number of ZC, reflecting postural sway speed, were strongly positively correlated with performance. It has already been shown that greater velocity is associated with higher center of pressure deviation and, thereby, lower postural control (Paillard, 2012). Postural sway velocity, especially in the medial–lateral direction, has high predictive value for individual fall risk (Bigelow and Berme, 2011). As slowing down walking speed can also be an effective strategy to reduce the risk of falls (Roos and Dingwell, 2013), our finding that lower velocity values are associated with higher DBT performance is in good agreement with the literature. Given that DBT learning is associated with higher-frequency movement adjustments, the positive relationship between the postural sway speed and performance is an indicator of greater movement automaticity

(Wulf and Lewthwaite, 2009) and therefore also a marker for learning. Taken together, our data suggest that DBT learning performance can be predicted by the kinematic profile of the movement. This result could be of functional relevance for diagnostics of balance related disorders or individualizing gait retraining or fall prevention treatments.

In a second analysis, we aimed to evaluate the effect of tDCS on our kinematic data. Interestingly, we found a significant effect of tDCS on absolute and percentage change in jerk on training day 1, suggesting that a-tDCS resulted in a small increase of jerk values, while during s-tDCS, jerk was decreased. Higher jerk values reflect "jerkier" movements with more deviation in motion, while lower jerk values represent movements with higher smoothness. However, as we found no correlation between jerk and TiB, we assumed that the effect on jerk did not affect our global learning parameter TiB. While some studies suggested that a decrease in jerk is associated with better performance (e.g., James, 2014), another study rather stated a positive relation of higher jerk values and performance increase (Slaboda, unpublished data). As there are not many studies investigating jerk effects during highly complex, multi-joint movements, the effects of different jerk patterns remain ambiguous and have to be further explored.

Balance and Aging

Older adults show reduced postural stability as declines in muscular strength most severely affect the lower extremities (Frontera et al., 1991; McNeil et al., 2007). However, postural instability also represents an insufficiency of attentional resources since maintaining posture requires the integration of many different modalities of information including vision, proprioception and vestibular feedback (Granacher et al., 2008). In daily life, posture is held during changing environmental conditions, thus making it necessary for the balance system to interact with an external dynamical system (Chagdes et al., 2013). It has been shown that interventions that focus on improving balance in the elderly are most effective when they incorporate more complex exercises (Halvarsson et al., 2015) and also involve cognitive components. The DBT provides a nice setting to evaluate balance ability in older adults as it forces the user to dynamically adjust posture to continuous changes in the environment, thus demanding high attentional resources as well as flexible adaptations. The unstable platform of the balance board nicely mimics continuous changes in the environment and thereby creates an ideal setting for evaluating and training complex postural behavior (Chagdes et al., 2013). Our results show that older adults are able to improve their balance ability during a single session of DBT training and maintain this motor skill at least until a second day of training. Therefore, using the DBT in a longer-term setting may support and improve classical fall prevention trainings and provide an interesting setup for training on instable platforms. However, even though we observed significant learning improvements, DBT learning curves of both groups were characterized by irregular increases and decreases of performance. The underlying mechanism remains unclear, however, one potential explanation might be the difficulty of the motor task. Since we wanted to maintain conditions from our younger study sample (Kaminski et al., 2016), older adults were tested with a TiB range of only 3° while in our previous study, 5° of TiB range were tested (Sehm et al., 2014), thus making it easier for older adults to meet the criterion for successful performance. Therefore, the task may have been more difficult and irregularities in performance may represent difficulties in maintaining better performance over the time course of the training session. On the other hand, decreases in TiB performance may be the result of muscle or cognitive fatigue since the DBT is both physically and attentionally demanding. This, however, seems rather unlikely, since changes in levels of attention but also both muscle and cognitive fatigue were assessed using a VAS and no significant changes were detected.

Study Limitations

In the present study, we used behavioral measurements to assess motor learning in an aging population. However, since no neuroimaging measurements were included, it was not possible to investigate whether specific brain structures or specific brain states may have predicted DBT performance. Additionally, we cannot relate the variance in response to tDCS to a specific brain network. To get a better understanding of the neuronal correlates of DBT learning in older adults and potential tDCS effects on neuronal networks, further studies that combine neurophysiological assessments of brain activation with behavioral outcome measures are needed. Furthermore, our aged study cohort was selected according to relatively strict inclusion criteria and can therefore be considered healthy and active. In the long term, one goal would be to incorporate tDCS-usage as an add-on interventional strategy to treat balance and gait disorders; therefore older adults facing an increased risk of falls should be in the center of interest. Even though we did not detect any tDCS-induced effect on DBT performance in healthy older adults, it is possible that tDCS affects dynamic balance in patients. Additionally, we did not investigate the role of multiple tDCS-sessions on balance performance and did not test for any long-term effects. It is worth considering that multiple tDCS application sessions may have induced stronger behavioral effects that could be more persistent, as suggested by previous studies (Reis et al., 2009; Dell'Osso et al., 2011; Galletly et al., 2012). However, this study was the first step in understanding the role of single-session tDCS during the initial learning phase of a dynamic balancing task in older adults. While we provide initial evidence that tDCS over M1 leg area does not facilitate initial DBT learning in healthy older adults, future studies should be conducted investigating different time scales of DBT learning including also patient populations to draw a comprehensive picture of the effects of tDCS on dynamic balance performance.

CONCLUSION

Combining measures of balance evaluation with methods of non-invasive brain stimulation in older adults is important to advance the knowledge on how to enhance treatment success in terms of fall prevention and gait training. Our results

indicate that even though older adults are able to learn a dynamic balancing task over the time course of a single training session, concurrent application of tDCS over M1 leg area did not elicit DBT performance enhancement in our study cohort. More knowledge on neuronal processing of DBT learning in older adults, the influence of tDCS parameters, and the effect of inter-individual differences is required in order to draw a comprehensive picture of whether tDCS can help to enhance older adults dynamic balance learning. However, we also found that balance performance can be predicted by the kinematic movement profile, a result that could be of functional relevance to individualize gait retraining or fall prevention treatments for patients suffering from balance impairments.

AUTHOR CONTRIBUTIONS

EK: study design, study planning, execution, analysis, manuscript writing. MH: study execution, ideas for analysis, suggestions for manuscript writing. VR: study execution, suggestions for manuscript writing. CJS: data analysis, help with figure creation, suggestions for manuscript writing. CG: data analysis. BS: data analysis, suggestions for manuscript writing. AV: suggestions for manuscript writing, study design, interpretation of results. PR: corresponding author, study idea, hypotheses, study design, data analysis, manuscript writing.

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Electromyographic Pattern during Gait Initiation Differentiates Yoga Practitioners among Physically Active Older Subjects

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During gait initiation, postural adjustments are needed to deal with balance and movement. With aging, gait initiation changes and reflects functional degradation of frailty individuals. However, physical activities have demonstrated beneficial effects of daily motor tasks. The aim of our study was to compare center of pressure (COP) displacement and ankle muscle co-activation during gait initiation in two physically active groups: a group of walkers (n = 12; mean age ± SD 72.6 ± 3.2 years) and a yoga group (n = 11; 71.5 ± 3.8 years). COP trajectory and electromyography of leg muscles were recorded simultaneously during five successive trials of gait initiation. Our main finding was that yoga practitioners had slower COP displacements ($p < 0.01$) and lower leg muscles % of coactivation ($p < 0.01$) in comparison with walkers. These parameters which characterized gait initiation control were correlated ($r = 0.76$; $p < 0.01$). Our results emphasize that lengthy ankle muscle co-activation and COP path in gait initiation differentiate yoga practitioners among physically active subjects.

Keywords: anticipatory postural adjustments, gait, aged, yoga, electromyography

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INTRODUCTION

In older adults, physiological changes and physical inactivity are associated with a decrease in personal independence in general and in walking ability in particular. Indeed, older subjects with impaired gait are scared of falls and thus limit their physical activity and activities of daily living (Alexander, 1994; Maki and McIlroy, 1996). For example, individuals adopt a more conservative, basic gait pattern (Menz et al., 2003). Because of socio-economics impact of falling, several studies were lead to determine predictive factors of falling in older population. Gait initiation parameters (as described below) may be sensitive indicators of balance dysfunction and the risk of falls in older adults (Chang and Krebs, 1999). Indeed, gait initiation is a transient phase during which postural control and balance maintenance systems are highly active. Specifically, gait initiation consists in creating forward momentum from a quiet stance. Muscle activity creates internal forces that dissociate the center of pressure (COP) from the center of gravity (COG), in order to produce the initiation step (Mann et al., 1979; Brunt et al., 1991). While momentum creation disturbs balance, anticipatory postural adjustments (APA) are needed to deal with balance and allow efficient step initiation.

Several studies have evidenced the degradation of gait initiation with age. The older people show a decrease in the peak moment arm between the body's COG and the COP (Brunt et al., 1991; Polcyn et al., 1998; Chang and Krebs, 1999). The decrease in this forward momentum is associated with lower COG velocity and lower first step amplitude (Patchay et al., 1997, 2002; Halliday et al., 1998). It has been suggested that this change in kinetic gait initiation parameters occurs because older subjects do not tolerate a deviation of the body as a whole (COG) from the ground reaction forces (COP). In order to initiate gait and compensate for impairments in the moment arm, older subjects have to perform additional trunk movements (Martin et al., 2002).

The observed changes in kinetic parameters have also been explained in terms of impaired muscle activation patterns. The role of muscle activity is to create internal forces in order to dissociate the COP from the COG (Mann et al., 1979; Brunt et al., 1991). For that reason, the electromyographic (EMG) sequence recorded during gait initiation can be considered as "a motor program that adjusts the configuration of external forces, which acts directly on the position of the COP and joint position" (Crenna and Frigo, 1991). Several studies described a stereotypical pattern of muscle activation in healthy, younger adults: (i) starting from a postural quiet stance, postural muscles are activated in order to maintain postural alignment; and (ii) in order to initiate gait *per se*, postural muscle activity is inhibited and motor muscles are then activated (Mann et al., 1979; Brunt et al., 1991, 1999). Difficulties in inhibiting antigravity muscles prior to movement are correlated with the age-related loss of Betz cells in the motor cortex (Scheibel et al., 1977; Scheibel, 1985). Higher levels of muscle coactivation have been reported in older subjects during activities of daily living–such as bipedal stance (Laughton et al., 2003; Nagai et al., 2011) and dynamic balance (Hortobágyi and DeVita, 2000; Larsen et al., 2008; Schmitz et al., 2009; Pereira and Goncalves, 2011). During gait initiation, the duration of postural and motor muscle coactivation increases with age. Indeed, it appears that the degradation of central mechanisms in gait initiation translates into a decrease in the ankle muscle antagonist coordination pattern (Polcyn et al., 1998; Henriksson and Hirschfeld, 2005), i.e., coactivation of the tibialis anterior (TA) and triceps surae muscles. The difference between young adults and older adults is more obvious for the swing limb (SWL), which shows greater degradation than the stance limb (STL) does (Polcyn et al., 1998).

It has often been suggested that physical activity improves functional ability in older people (Lord and Castell, 1994; Maki and McIlroy, 1996; Lelard and Ahmaidi, 2015). As an indicator of functional status, physically active olders show higher walking velocity compared to aged-matched sedentary adults. However, it seems that the characteristics of the physical activity, duration and frequency of training sessions induce differentiated effects on motor ability. Tai Chi training also showed an enhancement of gait initiation control (Hass et al., 2004; Vallabhajosula et al., 2014). These studies focused on CoP-CoG displacements during APA. These findings demonstrated that proprioceptive physical activity could help to improve gait initiation control via better COP displacement. Gait initiation is a pre-programmed task (Fiolkowski et al., 2002) which need APA controlled by an open-loop mechanism (Massion, 1992). As neuromuscular activity reflects motor program, previous results may explain this improvement by enhanced neuromuscular coordination after proprioceptive training (Chen et al., 2012a,b). Indeed, Nagai et al. (2012) have demonstrated significant changes in muscle coactivation after balance training (relative to an untrained group). Most of these studies reported beneficial effects of proprioceptive practice on postural control, however, differential effects depending on the type of practice were described on postural control (Gauchard et al., 2003). As described by these authors, proprioceptive activities such as yoga consist to produce a sequence of postures that need to deal with balance and movements improving body schema knowledge. To our knowledge, no study was performed to compare the effects of different types of physical activity on gait initiation.

Since differentiated effects on postural control were previously reported according the type of training program, we hypothesize that practicing different type of physical activity would show differences in APA during gait initiation. To initiate the first step, the central nervous system has to deal with the antigravity function of the posture and production of movements. Motor program has to switch from postural activity (Triceps Surae) to focal movements (TA). A time course analysis of co-activation and COP displacement might then be an effective indicator of efficiency of gait initiation. The aim of the present study was thus to investigate potentially differentiating patterns of leg muscle co-activation and COP displacements during gait initiation in yoga practitioners and physically active group (regular walkers).

MATERIALS AND METHODS

Subjects

Twenty-three volunteers healthy subjects aged from 68 years to 78 years took part in the study. Regular yoga practitioners (n = 11; 71.5 ± 3.8 years old; 1.59 ± 0.08 m height; 66.8 ± 9.3 kg weight) and walkers subjects (n = 12; 72.6 ± 3.2 years old; 1.61 ± 0.03 m height; 64.3 ± 8.6 kg weight) were recruited from community dwelling. The group of yoga practitioners was standardized in terms of time (more than 1 year) weekly sessions (1) and sessions duration (1 h) of practice. The physically active group was selected on the basis of a questionnaire. Their physical activity level was equal or higher than 1 h of walking per week. All subjects signed prior the study an informed consent which was accepted by the local ethical committee (Comité de protection des Personnes Nord Ouest 2, Amiens, France) in accordance with Helsinki Declaration of 1975. Prior to taking part in the study, all participants reported their medical history. Clinical examination and questioning was conducted in order to exclude subjects showing any possible causes of balance alteration (medication or disease). Subjects were free from any disease which could influence postural maintaining and were able to walk without external help. Subjects did not show cognitive impairments with

a score superior to 24 points in Mini-Mental State Evaluation (Folstein et al., 1975). The participants were independent as revealed by a maximal score in the Activities of Daily Living (Katz et al., 1963).

Experimental Devices

A Piezoelectic force plate (Kistler type 9281 B11, Kistler AG, Winterthur, Switzerland) associated with a calculator was used to assess the temporal time-course of the COP displacements in antero-posterior (AP) and medio-lateral (ML) from the ground reaction forces and their moments in the three planes. The analogic signal was digitized at a sampling frequency of 1000 Hz.

Electromyograms (EMG) of leg muscles were collected using bipolar Ag/AgCl surface electrodes (Beckmann, 8-mm diameter) on the first leg that leaves the floor (initial SW limb). Before the electrode positioning, the skin was slightly abraded and cleaned with an alcohol solution in order to reduce the interelectrode resistance to below 5 kΩ. An electrolytic gel was placed between the skin and the electrodes to insure electrical contact. The electrodes were fixed (2 cm apart center to center) over the muscle bellies for TA and lateral gastrocnemius (LG) muscles. The EMG signals were amplified and filtered using a bandwidth of 10–1000 Hz (Gould 6600), and then addressed to an analog-digital converter piloted by the Turbolab software (SM2I, France) for their digitization at a sampling rate of 1000 Hz.

Procedure

After two learning trials, the subjects performed five gait initiation trials. In order to standardize the starting conditions, the subjects placed their bare feet on foot marks drawn on the platform. They had to keep their arms by their sides, relax their jaw and fix a spot on a wall 10 m in front. The experiments took place in a quiet room with no visual perturbations.

In each test, the experimenter triggered the acquisition of the COP displacement and EMG signals. The order to initiate gait was given by the experimenter after at least 2 s of steady-state postural recording (judged by visual inspection of the EMG signal).

Data Analysis

Usually, based on COP displacement, three gait initiation phases were described (Halliday et al., 1998; Martin et al., 2002; Hass et al., 2004), the first phase represents the backward COP displacements that create the forward momentum thanks to COP-COG dissociation, the second the weight bearing transfer from SWL to STL, and the third the forward COP displacement.

These phases were identified in our study thanks to the gait initiation events using landmarks on the COP trajectory (**Figure 1**). Landmark 1 (L1) represents the mean position of COP during quiet stance. Landmark 2 (L2) represents the most posterior and lateral position toward the SWL of COP location. Landmark 3 (L3) represents the most posterior and lateral position toward the STL of COP location. The end of the recording of COP displacement represents the outgoing of

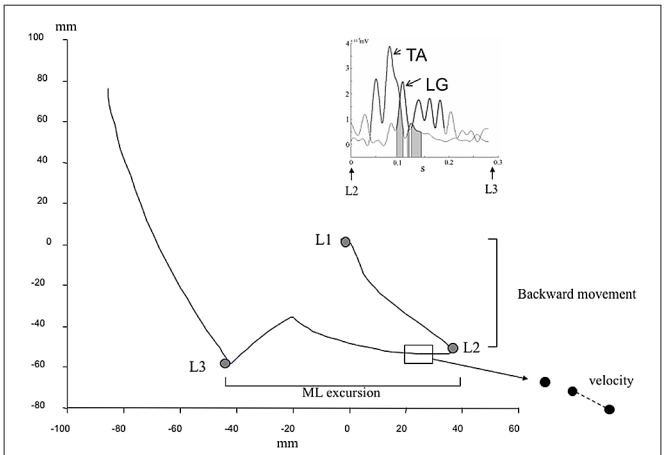

FIGURE 1 | Kinetic and electromyographic (EMG) data used to describe gait initiation. Center of pressure (COP) displacement during gait initiation. L1 represents the position of the COP in normal quiet standing. L2 represents the backward of COP. L3 represents the COP displacement toward the stance limb (STL). Parameters used were the backward COP position during the phase 1 (L1–L2), the medio-lateral (ML) excursion, the velocity (path reported to phase duration). Insert represents tibialis anterior (TA) and lateral gastrocnemius (LG) vs. time during the weight bearing transfer from swing limb (SWL) to STL (From L2 to L3). The bold lines represent when muscle are activated (>25 ms consecutive above the threshold corresponding to the mean ± 3 standard deviation). Gray area represents the phase of coactivation of LG and TA muscles.

COP from the force plate. The identification of these landmarks was conducted with an application of Matlab Program (The Mathworks, Inc., Natick, MA, USA), under visual control. In order to characterize the COP displacement, we calculated the excursion separating two landmarks, the average velocity (sum of distance separating two points of acquisition related to time elapsed in the phase (**Figure 1**).

For EMG data, we have analyzed the period corresponding to weight bearing transfer from STL to SWL during which an inhibition of postural muscle and activation of motor muscles were reported. From an algorithm developed with Matlab program, we determined phasic activation of LG and TA of the SWL under visual control. The Matlab application was developed using previous methodological studies (Mickelborough et al., 2004). EMG data were smoothed with low-pass filter cut off frequency of 20 Hz. The threshold for EMG activation detection was defined as mean added with 3 standard deviations of reference phase. The muscle was considered as active after 25 ms of consecutive above the threshold. Then, we calculated relative time of coactivation of LG and TA muscles during weight bearing transfer from SWL to STL (ratio of time of coactivation with time elapse in the phase).

Statistics

Statistical analysis was carried out with Statview software (SAS Institute, Cary, NC, USA). Given that the data were normally distributed (according to a Kolmogorov-Smirnov test) and the equality of variance Levene median test) was confirmed, an unpaired *t*-test was used to compare the physically active group and yoga group in terms of kinetic

and EMG values. The threshold for statistical significance was set to $p < 0.05$.

We also assessed the relationship between kinetic COP displacement parameters and muscle coactivation by applying Pearson's correlation test.

RESULTS

COP Movements

The yoga and physically active groups do not differ significantly in terms of displacements during the first phase of gait initiation (**Figure 2A**). The mean ± SD backward movement of COP position shows non-significant lower values in the yoga group than in the group of walkers (−27.8 ± 5.3 vs. −31.1 ± 13.6 mm respectively).

For the second phase of gait initiation, we characterized the excursion and velocity of COP displacement from the SWL to the STL. We did not find significant differences in COP excursion during this phase (110.8 ± 12.1 vs. 102.5 ± 19.7 mm for the yoga and physically active groups, respectively; **Figure 2B**). The COP velocity was significantly lower in yoga practitioners than in the walkers (555.2 ± 32.5 vs. 624.0 ± 50.3 mm.s^{-1}, respectively; $p < 0.01$; **Figure 2C**).

Leg Muscle Co-Activation

During gait initiation, we found significant differences in leg muscle co-activation between the two physically active groups (**Figure 2D**). In fact, leg muscle co-activation is lower in yoga practitioners than in the walkers (3.9 ± 6.0% vs. 10.5 ± 5.1%, respectively; $p < 0.01$).

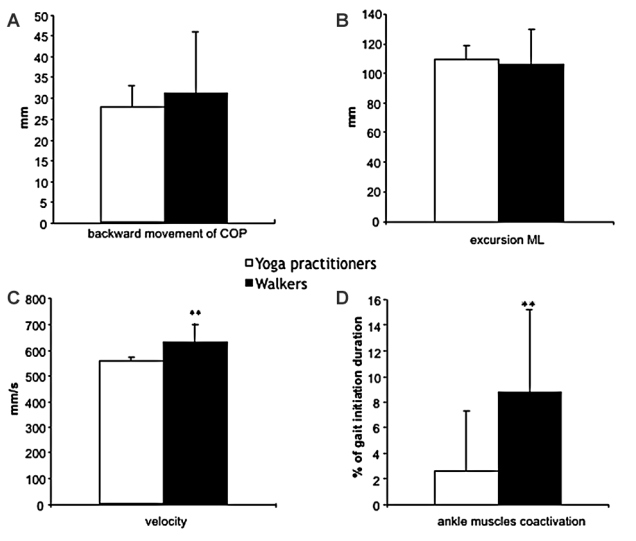

FIGURE 2 | Kinetic and EMG data recorded in yoga (□) and in walkers (■) subjects (mean and standard deviation). **(A)** The backward movement of COP during the phase 1 of gait initiation. **(B)** The excursion of COP displacement (in mm) during phase 2 of gait initiation. **(C)** Velocity of COP displacement (in mm) during phase 2 of gait initiation. **(D)** Percent of time during which LG and TA are coactivated during phase 2 of gait initiation. Significant differences were expressed as $^{**}p < 0.01$.

The relationships between kinetic variables and leg muscle co-activation reveal that muscle co-activation is correlated with the velocity measured during the SWL-to-STL phase ($r = 0.76$; $p < 0.01$).

DISCUSSION

The objective of the present study was to assess the effect of regular yoga practice in gait initiation control in the elderly. This was characterized in terms of COP excursion, COP velocity and muscle co-activation. We hypothesized that Yoga practitioners present differences in APA during gait initiation compared to physically active older adults. Indeed, Gauchard et al. (2003) demonstrated that proprioceptive activities enhance sensory inputs and improve the subject's knowledge of the body scheme and gravity effects. Significant results were reported during the SWL to STL transfer for the COP velocity and % of leg muscle coactivation between the two groups. Lastly, the observed link between COP path and muscle co-activation duration confirmed the interaction between muscle co-activation and the COP trajectory during gait initiation.

During gait initiation, the central postural control system has two main functions: (i) maintenance of balance; and (ii) creation of the anteroposterior moment needed to produce the first step (via a stereotyped pattern of leg muscle activation). In the present study, we did not observe any significant intergroup differences in the rearward COP excursion during the first phase of gait initiation. Previous studies have found that older and disabled subjects exhibit a lower arm peak moment (i.e., a smaller COP-COG distance; Polcyn et al., 1998; Chang and Krebs, 1999; Martin et al., 2002). Based on COP displacements, the present study does not allow to demonstrate differentiated effect between type of physical activity practiced on COP rearward during the first phase of APA.

The second phase of gait initiation consisted in transferring body weight from the initial SWL to initial STL. In the present study, we reported higher average velocity of the COP in the physically active group as compared to the yoga group for a similar ML excursion. In previous studies, smoother COP displacement during gait initiation was seen after 48 weeks of tai chi practice (Hass et al., 2004) and was also described in healthy older subjects (relative to disabled subjects; Martin et al., 2002). The reason for this significant difference remains unclear: the lower COP velocity in the yoga group might be related to the specific, slow movements performed during this activity. Then, it might be the consequence of a behavioral change in yoga practitioners.

However, our results might also be related to adaptations of the central nervous system in the yoga group (relative to the physically active group). To our knowledge, the present study is the first investigation conducted to explore differentiated coactivation of the leg muscles during gait initiation in two types of physical activity practitioners. The time course analysis of EMG data assessed the time during

which muscles were involved in postural maintaining (LG) and movement (TA) (Polcyn et al., 1998; Henriksson and Hirschfeld, 2005). The duration of coactivation (expressed as a % of APA duration) might be an indicator of CNS adaptation to deal with postural constraints induced by gravity and movement production during the preparation phase of gait. This muscle pattern (inhibition of postural muscle) was described in healthy young adults (Mann et al., 1979; Brunt et al., 1991, 1999) and seem to be altered with aging and/or disability (Scheibel et al., 1977; Scheibel, 1985; Polcyn et al., 1998; Henriksson and Hirschfeld, 2005). In the present study, Yoga practitioners present lower TA/LG muscles coactivation than the physically active group. The result should be related to a previous study that demonstrated that muscle activation during gait initiation can reflect different behavior in counteracting and using gravity (Honeine et al., 2014).

One specific feature of the present study was the observed association between COP displacement and the EMG motor program. As previously described, the EMG sequence recorded during gait initiation can be considered as a motor program that acts on the COP's position (Crenna and Frigo, 1991). APA are pre-programmed by an open-loop mechanism, then their improvements need better body scheme knowledge. In our study, we reported a significant correlation ($r = 0.76$; $p < 0.01$) between TA/LG coactivation and COP displacement. The relationship obtained between muscle co-activation (time of coactivation/time) and velocity (path/time), demonstrates that the path length is greater when the duration of muscle co-activation is longer. Leg muscle coactivation previously reported in frailty adults might also reflect hesitation or difficulties in initiating gait (i.e., pain, motor impairment, fear of falls, etc.). Several studies have shown that changes in ankle control occur with age and may be associated with an increased risk of falling. A previous study has shown that ankle dorsiflexion was significantly delayed and its amplitude was lower for fallers during gait (Kemoun et al., 2002). Simoneau et al. (2007) explained the decrease in dorsiflexion maximal voluntary contraction torque with aging by neural factor (Simoneau et al., 2007). The question of the benefit of reducing muscle co-activation in frailty adults should then be explored.

Our results suggest that the neuro-adaptation related to yoga performance can modify leg muscle pattern during gait initiation. This result should also be related to the reduction in muscle coactivation during other dynamic tasks after practice (Chu et al., 2009; Chen et al., 2012a,b; Nagai et al., 2012).

However, the present study may have some limitations inherent to cross-sectional studies. Even if our inclusion criteria allow us to select a healthy elderly population in this cross-sectional study, the two groups might not present similar health conditions. Comparison with other groups should help to understand the effects of physical activity on gait initiation by comparing our results with groups of young adults, sedentary older adults or with other type of physical activity (exercises at a fast pace way requiring balance). We can also note that due to the absence of kinematic data, we could not determine the position of the COG. Therefore, the COP-COG dissociation could not be assessed in the present study.

CONCLUSION

The actual results obtained did not accurately demonstrated that gait initiation is more efficient (in terms of COP-COG dissociation and in term of amplitude of the first step) in yoga practitioners than in regular walkers. However, Yoga practitioners showed slower COP displacement associated with lower leg muscle coactivation. This last point result might be a marker of the use of a different strategy to prepare the first step. Further studies are needed to explore the clinical interests of proprioceptive activities on muscle coactivation during gait initiation and the relationship between gait initiation efficiency (COP-COG, step length) and leg muscle coactivation.

AUTHOR CONTRIBUTIONS

TL, P-LD and SA: project creation. TL: data collection. TL, P-LD and AT: data analysis. TL, P-LD, AT and SA: discussed the results; revised the manuscript. TL and AT: drafted the manuscript.

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frontiers in Human Neuroscience

REVIEW
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The Organization and Control of Intra-Limb Anticipatory Postural Adjustments and Their Role in Movement Performance

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Anticipatory Postural Adjustments (APAs) are commonly described as unconscious muscular activities aimed to counterbalance the perturbation caused by the primary movement, so as to ensure the whole-body balance, as well as contributing to initiate the displacement of the body center of mass when starting gait or whole-body reaching movements. These activities usually create one or more fixation chains which spread over several muscles of different limbs, and may be thus called *inter-limb APAs*. However, it has been reported that APAs also precede voluntary movements involving tiny masses, like a flexion/extension of the wrist or even a brisk flexion of the index-finger. In particular, such movements are preceded by an *intra-limb* APA chain, that involves muscles acting on the proximal joints. Considering the small mass of the moving segments, it is unlikely that the ensuing perturbation could threaten the whole-body balance, so that it is interesting to enquire the physiological role of *intra-limb* APAs and their organization and control compared to *inter-limb* APAs. This review is focused on *intra-limb* APAs and highlights a strict correspondence in their behavior and temporal/spatial organization with respect to *inter-limb* APAs. Hence it is suggested that both are manifestations of the same phenomenon. Particular emphasis is given to *intra-limb* APAs preceding index-finger flexion, because their relatively simple biomechanics and the fact that muscular actions were limited to a single arm allowed peculiar investigations, leading to important conclusions. Indeed, such paradigm provided evidence that by granting a proper fixation of those body segments proximal to the moving one APAs are involved in refining movement precision, and also that APAs and prime mover activation are driven by a shared motor command.

Keywords: intra-limb APAs, precision, motor control, postural control, posturo-focal integration, human

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INTRODUCTION

Anticipatory Postural Adjustments (APAs) are commonly described as unconscious muscular activities aiming to maintain the equilibrium of the whole body during various voluntary motor performances (for a review see Massion, 1992; Bouisset and Do, 2008), but they are also known to contribute to initiate the displacement of the body center of mass when starting gait (Brenière et al., 1987) or whole body reaching movements (Stapley et al., 1998, 1999).

However, the importance of APAs is also apparent when considering motion of one single limb (e.g., Belen'kii et al., 1967 for the upper limb; Alexeief and Naidel, 1972 for the lower limb). In the latter context, the main goal of APAs is to minimize the changes in the body center of mass, in order to keep its projection within the support area, and to counteract the self-initiated postural perturbation. These APAs usually spread over several muscles of different limbs, creating one or more fixation chains. For this reason they may be called *inter-limb APA*.

The role of APAs may look less obvious when considering a movement involving little masses, which are not supposed to threaten the whole body postural stability. In this regard, Aoki (1991) reported a pattern of muscular activity in various arm muscles about 50–60 ms before a rapid wrist movement, and showed that this activity is distributed according to the direction of the movement in space. Moreover, Caronni and Cavallari (2009a) found that during index-finger tapping, in which the moving mass is even smaller, an anticipatory postural chain develops in several upper-limb and trunk muscles. These activities, named *intra-limb APAs* since they are distributed to muscles of the same limb in which the movement occurs, precede the onset of the voluntary movement, are polarized according to the task direction in space and adapt to changes in the postural requirement of the task. In other words, they share the same behavioral properties of *inter-limb APA*, as it will be shown as the *first topic* of the present review.

Nevertheless, it is difficult to envisage a postural role for *intra-limb APAs* in the common sense of its acceptation, i.e., preserving the whole body equilibrium or counteracting a self-initiated perturbation that could threaten the body posture. This *intra-limb* APA pattern seems in fact organized so as to preserve the *local equilibrium* of the limb, which, in a behavioral perspective represents a basic requirement for performing precise movements. The involvement of *intra-limb* APAs in setting movement precision will be treated as the *second topic*.

Moreover, the *finger tap* experimental model allowed us to disclose some key aspects of the central organization of voluntary movement and postural actions, aspects that would hardly be revealed by using the classical *whole body* experimental paradigm. Thus, the *last topic* of this review will be about the organization of voluntary and postural actions, either as two different central commands (a focal and a postural component), as classically proposed (Babinski, 1899; Thomas, 1940; Hess, 1943; Gelfand et al., 1966; Cordo and Nashner, 1982; Brown and Frank, 1987) or as a unique motor command as suggested by more recent evidences (Aruin and Latash, 1995; Caronni and Cavallari, 2009b; Petersen et al., 2009; Leonard et al., 2011).

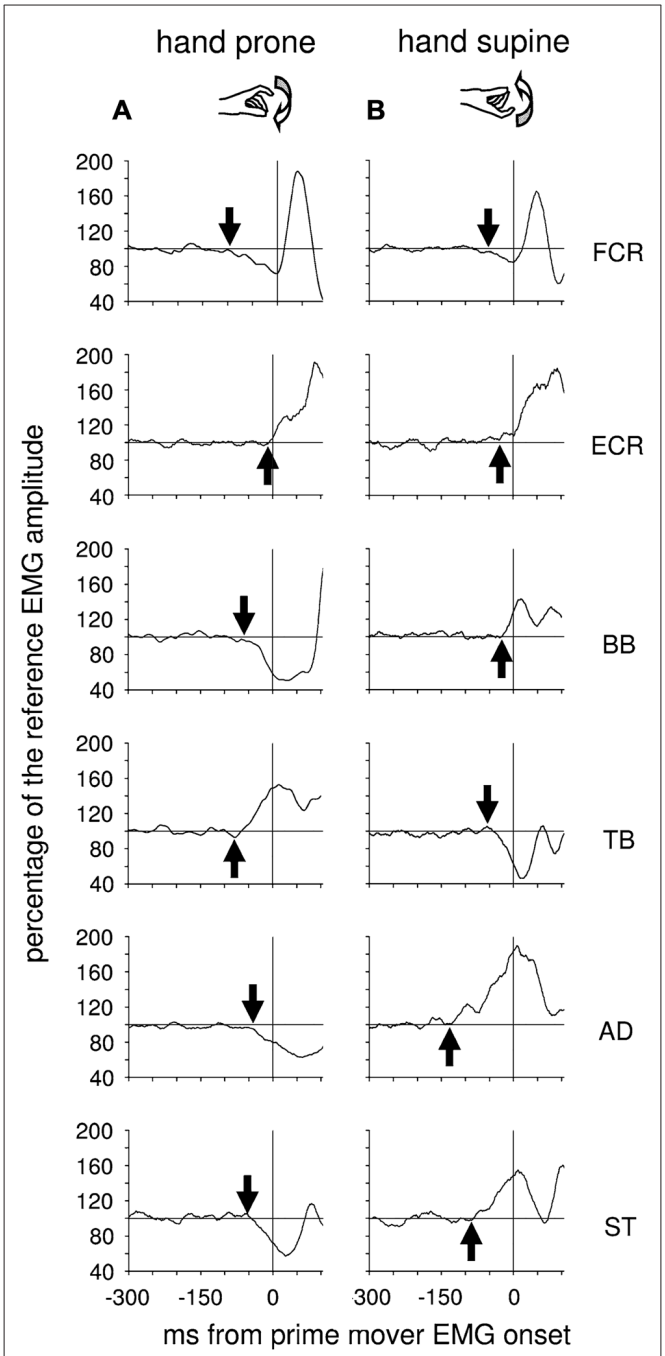

FIGURE 1 | Postural adjustments in upper-limb muscles preceding an index-finger tap with the prone or supine hand. Each graph displays the Anticipatory Postural Adjustments (APA) onset (arrow) and its development on the tonic EMG from different postural muscles of a single representative subject, with the hand resting prone **(A)** or supine **(B)**. Postural muscles: flexor carpi radialis (FCR), extensor carpi radialis (ECR), biceps brachii (BB), triceps brachii (TB), anterior deltoid (AD), superior trapezius (ST). The vertical line at 0 ms marks the onset of the prime mover activity. Note that in the muscles acting at the elbow, the shoulder and the trunk APAs reverts in sign when hand posture changes from prone to supine. EMG is rectified, integrated and averaged (75 trials) and its size expressed in percentage of the mean EMG level recorded 1 s before the go signal. *Reproduced from Caronni and Cavallari (2009a), © Springer-Verlag 2008, with permission of Springer.*

Brief Historical Background on Posture and Voluntary Movement

To the best of our knowledge, the first to describe the rules governing postural and voluntary movement control was Leonardo da Vinci (1452–1519), in his *Libro A, Trattato della Pittura*, which is now conserved within the *Codex Urbinas*

Latinus. Leonardo wrote: "*I say that if a motionless figure is poised on his feet, and his arm is extended in front of the chest, he will throw backward as much natural weight as the natural and accidental weight which he thrusts forward. And I say the same of each part that projects more than usual beyond the whole*". Moreover, Leonardo stated: "*Never will a weight be lifted and carried by a man, without his extending outside himself more than as much weight as that which he wishes to lift, and he thrust it on the side opposite the one where he lifts the weight*". A couple of centuries later, Giovanni Alfonso Borrelli (1608–1679) followed the pathway of Leonardo in his *De Motu Animalium*, where he described some principles that govern the voluntary movement. In particular, Borelli considered the skeleton as multi-linked system of levers, which can maintain the body balance as long as the center of mass falls within the support base.

After the observation of Leonardo da Vinci and Giovanni Borelli, we had to wait until the end of the 19th century to first clinically observe the importance of correct postural tailoring during voluntary movements in order to execute a successful motor act. Joseph Babinski (1857–1932), in his *De l'asynergie cérebelleuse*, first described the lack of harmonious synergies in cerebellar patients; in particular, he observed the forward displacement of the knees and hips to compensate for the backward displacement of the trunk, neck and head when asking a subject to look upward. Babinski also observed that cerebellar patients, who were asked to perform the same *looking upward* task, were unable to coordinate the upper part of their body to their hip and lower limb, so that they usually fell. However, Babinski did not analyze the temporal relationship between the postural adjustments and the voluntary movement, and therefore he lacked to observe that also an anticipatory postural control, adjusted in a feed-forward manner, is needed when performing a voluntary movement.

In the 20th century, studies about the relationship between posture and voluntary movement stood on the shoulders of three giants of movement physiology: Charles Sherrington (1857–1952, Nobel Prize 1932), Walter Hess (1881–1973, Nobel Prize 1949) and Nikolai Bernstein (1896–1966, Stalin Prize for Science 1948). Sherrington sustained the idea of a dual coordinated control system: one for movement and one for posture. This idea was in agreement with the proposals of Hess, who held the view that without anticipation of postural adaptations (a component of his ereismatic-supporting function system), goal-directed movements were doomed to failure. On the other hand, Bernstein was the first to propose a unique motor command for both posture and voluntary movement: "*movements are not chains of details but structures which are differentiated into details; they are structurally whole*" (Bernstein, 1967). However his ideas did not reach western scientists until several years after his death since his articles and books were only recently translated into English.

SHARED BEHAVIORAL PROPERTIES OF INTER AND INTRA-LIMB APAs

This review deals with *intra-limb* APA, since many other reviews (see "Introduction" Section) have been already devoted to all the features characterizing *inter-limb* APAs. However, it is important to briefly recall (see "Inter-Limb APAs" Section) those specific aspects of *inter-limb* APAs which can be directly compared with *intra-limb* APAs. All other features, like the effects of development, aging and fatigue, extensively studied in *inter-* but not in *intra-limb* APAs, have been thus omitted.

With regard to literature selection, this is a narrative more than a systematic meta-analysis review because in the last decade the *intra-limb* APAs has been mainly treated by our research group (for older studies see "Intra-Limb APAs" Section). However, to avoid missing important literature, *Pubmed*® and *Web of Science*® databases were inquired, by searching for *APAs* or *Anticipatory Postural Action(s)* and verifying item by item whether it was dealing with *inter-* and/or *intra-limb* APAs.

Inter-Limb APAs

These are the most frequently studied APAs. For example, when we intend to move a segment of the upper or the lower limb, a chain of muscular actions develops from that moving segment to the nearest fixation point. These actions precede the primary movement (in the range of tenths ms) and in many cases also the prime mover recruitment, the larger advance being observed in the muscles acting near the fixation point.

These *inter-limb* APAs have been documented for various movements such as: shoulder flexion and extension (Belen'kii et al., 1967; Lee, 1980; Clément et al., 1984; Horak et al., 1984; Bouisset and Zattara, 1987; Maki, 1993 in adults; Riach and Hayes, 1990 in children), shoulder lateral abduction (Aruin and Latash, 1995; Vernazza et al., 1996), elbow flexion (Friedli et al., 1984) and similar movements of the lower limb (Rogers and Pai, 1990; Do et al., 1991; Mouchnino et al., 1991; Nouillot et al., 1992). APAs also accompany movement involving the trunk, when bending it (Oddsson and Thorstensson, 1986; Crenna et al., 1987; Pedotti et al., 1989), during whole body reaching (Stapley et al., 1998), rising up on tiptoe (Houtz and Fischer, 1961; Lipshits et al., 1981; Nardone and Schieppati, 1988) and rocking on the heels (Nardone and Schieppati, 1988). In some experimental situations, it was asked to push or pull a handle with the upper limb, both in normal subjects (Cordo and Nashner, 1982; Lee et al., 1987) and in patients with Parkinson disease (Dick et al., 1986). *Inter-limb APAs* are also associated with movements involving a bimanual load-lifting task, when participants hold an object in one hand and the object is voluntarily lifted by the same person (active lifting) or by an experimenter (passive lifting). In the first case, the voluntary activation of the lifting hand is synchronous with an inhibitory APA in the contralateral biceps brachii (BB), thus avoiding an uncontrolled flexion of the elbow (Hugon et al., 1982) and preserving the upper limb posture. On the contrary, when the object is unexpectedly lifted by the experimenter, the BB inhibition starts about 50 ms after the unloading, showing that is it should have a reflex origin (postural reflex). The described experiment, known as "*the barman task*" allowed to make two conclusions: first, even a movement that does not lead to a whole body imbalance is preceded by APAs, aimed at preserving the single segment's

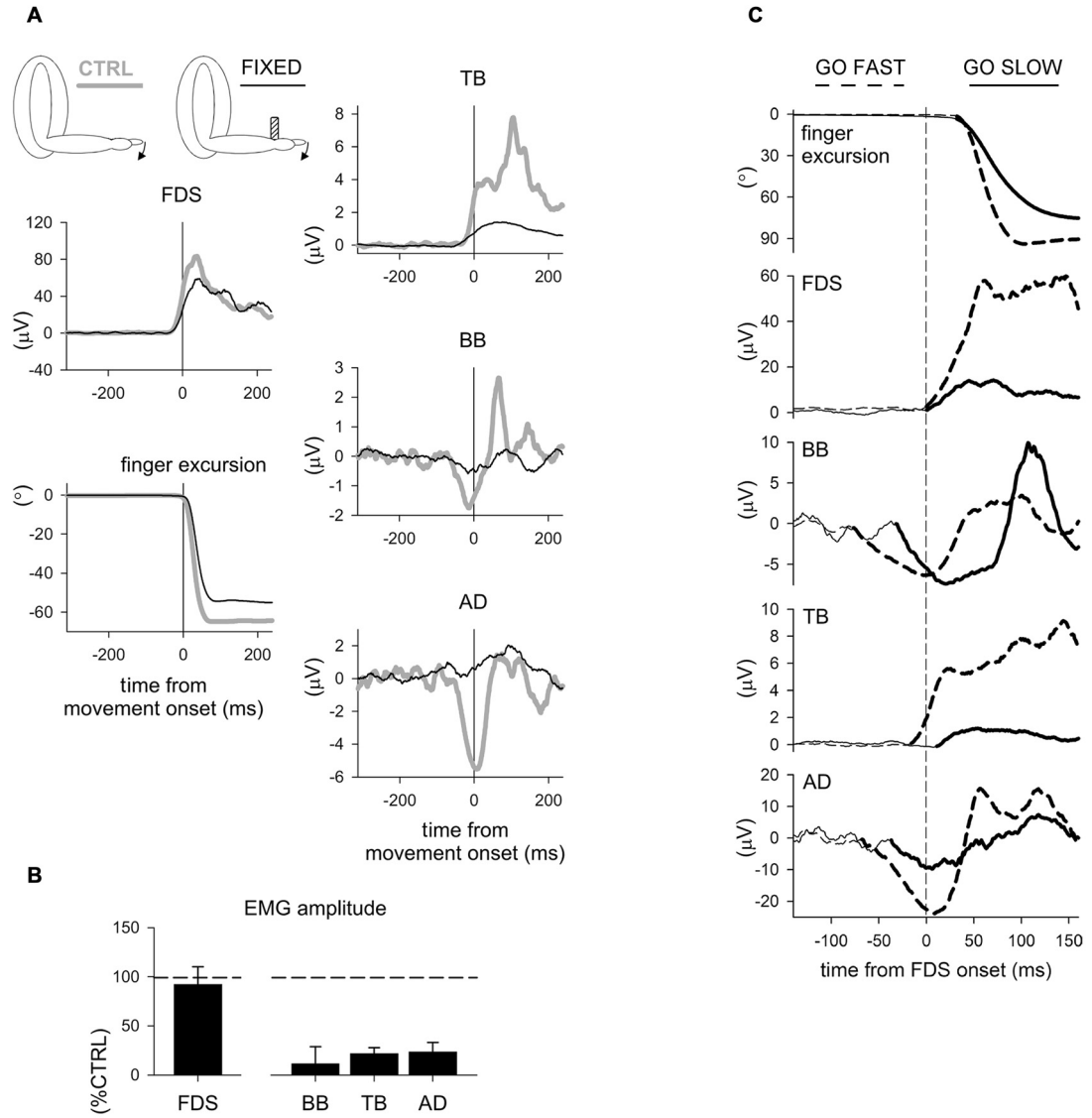

FIGURE 2 | Effects of fixation point and movement velocity on APAs. (A) Recordings of EMG activity in index-finger prime mover and intra-limb APAs in a representative subject, with or without a wrist fixation point. It is evident that both the EMG activity in the prime mover flexor digitorum superficialis (FDS) and the finger movement were comparable both with (FIXED, black) and without (CTRL, gray) the wrist fixation point, while in the FIXED condition APAs were deeply reduced in BB and TB and completely abolished in AD. **(B)** Mean amplitude of pre-movement FDS EMG and of APAs in BB, TB and AD. Values in % of the control sequence (CTRL). A *t*-test showed no CTRL vs. FIXED difference in FDS activation ($t_6 = 0.44$, $p = 0.67$). The average inhibitory effects on BB and AD and excitation in TB revealed a significant reduction in the FIXED condition ($t_6 = 5.01$, $p = 0.002$; $t_6 = 12.41$, $p < 0.0001$; $t_6 = 7.80$, $p = 0.0002$, respectively). *Reproduced from Bruttini et al. (2014), © Springer-Verlag Berlin Heidelberg 2014, with permission of Springer*. **(C)** Go-fast and go-slow movements in a representative subject. Goniometric recording of the index-finger flexion (top panel) and rectified and integrated (25 ms) EMG from the prime mover FDS and from BB, TB and AD. Note that when moving as fast as possible (GO FAST, dashed traces) the prime mover onset was preceded by APAs in BB, TB and AD. APAs (emboldened) were instead clearly delayed when moving at ∼50% of maximal speed (GO SLOW, solid traces). Time 0 (vertical dashed line) refers to prime mover EMG onset. *Reproduced from Esposti et al. (2015), © Springer-Verlag Berlin Heidelberg 2014, with permission of Springer*.

balance. Second, APAs may develop also in muscles that are not usually considered as *postural muscles*, such as muscles in the upper-limb. Moreover, since the degree of elbow rotation was shown to be lower when the subject unloaded the forearm by himself, the APA mechanism showed a greater efficacy in limb stabilization vs. the reflex mechanisms. The involvement of APAs in controlling the segmental stability was also confirmed for movements affecting the whole body balance (Patla et al., 2002).

Classically, APAs are known to be tuned depending on several kinematic aspects of the primary movement; specifically, the amplitude (Aruin and Shiratori, 2004), the speed

(Horak et al., 1984; Shiratori and Aruin, 2007), the movement direction (Aruin and Latash, 1995; Pozzo et al., 2002) and also the mass of the moving segment (Friedli et al., 1984). Moreover, an increase of APAs was shown when the voluntary movement was performed against resistance (Baldissera et al., 2008).

In addition, the CNS is able to adapt *inter-limb APAs* to changes in the postural demand of the motor task (Belen'kii et al., 1967; Cordo and Nashner, 1982; Aruin and Shiratori, 2004; Shiratori and Aruin, 2007). Clear signs of this adaptative process have been observed even after the very first movement trial (Hall et al., 2010), although they usually develop within few movement repetitions.

Another feature of the APAs is that they overtly develop in those muscles which connect the moving segment(s) to the nearest fixation point (Belen'kii et al., 1967; Marsden et al., 1981; Cordo and Nashner, 1982; for a review see Massion, 1992), while they are correctly shaped, but kept subthreshold, in those muscles in which their action is useless (Baldissera et al., 2002). An indirect issue which is strictly correlated to the above observations is that APAs conform to the adequacy of the fixation point, being smaller and smaller or even disappearing when the fixation point does not guarantee the full discharge of the perturbation (Brenière et al., 1987 balance during locomotion; Nouillot et al., 1992 balance during unipedal stance; Dietz and Colombo, 1996 balance in water; Esposti and Baldissera, 2011 balance with two fixation chains).

Intra-Limb APAs

As explained in the introduction, *intra-limb APAs* are those distributed to muscles of the same limb in which the movement occurs. The first evidence of such APAs dates to 1963, when Hopf and Hufschmidt (1963) observed that the anterior deltoid (AD) activity preceded the voluntary recruitment of BB driving elbow flexion. Later on, Aoki (1991) reported that wrist flexions, performed with the hand prone or supine, were accompanied by APAs in muscles acting at the elbow and that these APAs reverted their pattern in relation to the direction of the movement. In this regard, Chabran et al. (2001), observed also that when providing a support to the elbow the level of postural activity in shoulder muscles was deeply depressed, but the *intra-limb* APAs chronology remained unaffected. Examples of intra-limb APAs were also reported for shoulder and elbow movements by Almeida et al. (1995) and by Gribble and Ostry (1999).

More recently, Caronni and Cavallari (2009a,b) also reported that when only the index-finger is flexed, an APA chain develops in several upper-limb muscles to stabilize the *segmental* equilibrium of the arm. Indeed, these authors described that with the hand prone a brisk finger flexion was preceded by an excitatory burst in Extensor Carpi Radialis (ECR), Triceps Brachii (TB) and Superior Trapezius (ST), while Flexor Carpi Radialis (FCR), BB and AD showed a concomitant inhibition of their tonic activity (**Figure 1A**). The ECR-FCR coupled

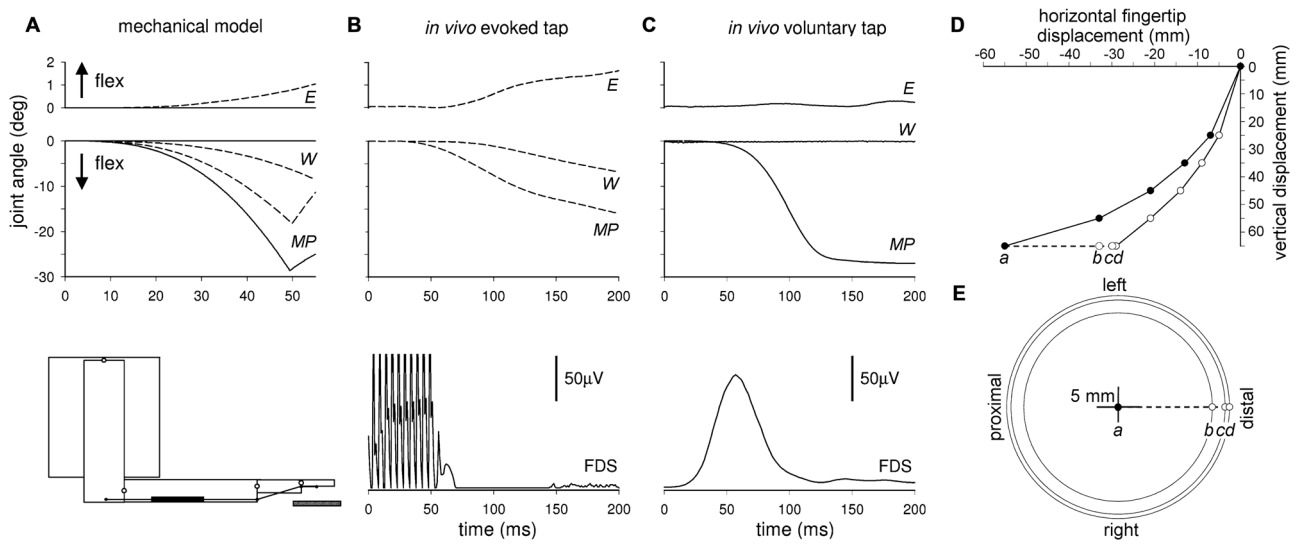

FIGURE 3 | Comparison of arm joint kinematics during a simulated, an *in vivo* evoked and a voluntary finger flexion. Time course of a finger flexion at the metacarpophalangeal (*MP*) joint, and the related changes at wrist (*W*) and elbow (*E*) level, measured in an arm mechanical model (bottom-left inset) when the proximal segments were free to rotate **(A**, dashed lines**)** or when they were immobilized **(A**, solid lines**)**, so as to produce fictive APAs. Angular displacements of the three joints were also recorded when an index-finger tap was passively evoked *in vivo* by electrical stimulation of the median nerve **(B)** and when it was voluntary performed **(C)** Rectified EMG activity of prime mover FDS in the two lower graphs. Note that the mechanical model well predicts the displacements of the proximal joints both during voluntary (solid lines) and evoked (dashed lines) index-finger tap. Panel **(D)** illustrates the simulated fingertip trajectory when the proximal segments were immobilized (filled circles, fictive APAs), and when they were free to rotate (empty circles). Note that for a vertical displacement of 65 mm, the fingertip hits the table surface (dashed line) more proximally with fictive APAs (*a*) then without them (*d*). Dots *c* and *b* mark the hitting position when the fictive APAs were restrained to the sole shoulder or to shoulder plus elbow, respectively. In the planar graph **(E)** the filled circle is the univocal target position theoretically resulting from a fully expressed APA control. Any disturbance of the APA chain would necessarily lead to impact any other point. *Reproduced from Caronni and Cavallari (2009a), © Springer-Verlag 2008, with permission of Springer*.

activities were appropriate for contrasting the by-product wrist flexion torque due to the voluntary contraction of the index-finger flexors. At the same time, the TB-BB and ST-AD actions contrasted the elbow and shoulder flexion torques produced by the upward perturbation that the index-finger flexion discharged on the metacarpophalangeal (MP) joint. Interestingly, when the hand posture was changed from prone to supine (**Figure 1B**), the APA pattern reverted in sign in the elbow and shoulder muscles but not in ECR and FCR. This is consistent with the fact that in this condition the perturbation produced on the MP joint was inverted, i.e., downward, but the by-product of recruiting the index-finger flexors was again a wrist flexion torque. These observations witness that APAs are versatile enough to adapt to the mechanical requirements of the postural context. Another proof that *intra-limb* APAs adapt to changes in the postural context within few trials comes from Bruttini et al. (2014) who illustrated that when tapping with the right index-finger, *intra-limb* APAs were deeply reduced (**Figures 2A,B**) if the right forearm was fixated at the wrist, i.e., closer to the voluntary moving segment. Moreover, Esposti et al. (2015) confirmed that also the *intra-limb* APAs adapt to changes in movement speed (**Figure 2C**).

In conclusion, *intra-limb* and *inter-limb* APAs seem to share similar control mechanisms. Indeed, both of them: (1) are distributed to several muscles creating a postural chain aiming to prevent the effects of the interaction torques generated by the voluntary movement; (2) revert in sign when movement direction is reverted; and (3) adapt to changes of the postural context within few trials of movement repetition. Thus, the central nervous system seems to use the same organization of the motor command for controlling both the segmental and the whole-body posture.

APA AND PRECISION

The idea that the precision of a voluntary movement relies on proper APAs was first proposed in relation to *inter-limb* APAs. When pointing toward targets of different sizes, it has been shown that APAs decreased in size as the accuracy demand increased, i.e., when pointing smaller and smaller targets. This feature has been shown both in the upper-limb

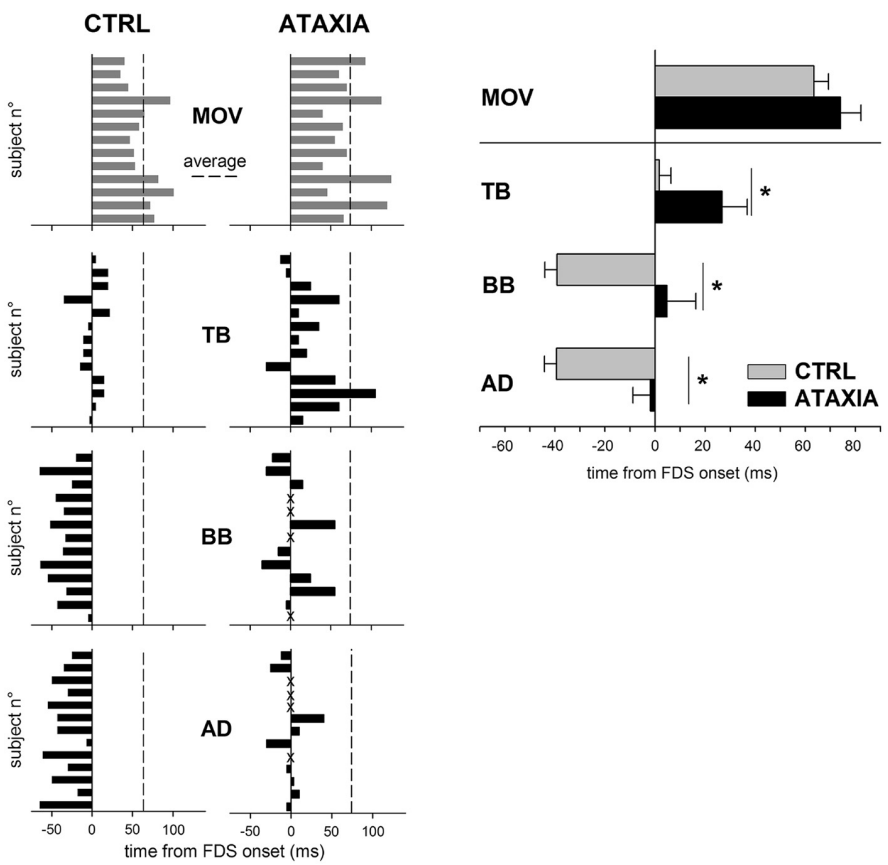

FIGURE 4 | Comparison of the APA chain in healthy (CTRL) and in cerebellar (ATAXIA) subjects. Latencies of finger flexion (MOV) and APA onsets in TB, BB and AD are plotted with respect to the onset of FDS, prime mover. Each single subject is represented. Dashed line marks the average movement latency for either group of subjects. Note that in ATAXIA APAs are delayed or, in some cases absent (marked with X). The right panel shows mean latency (± SE) of the onset of finger flexion and APAs. Asterisks mark significant differences found by the unpaired *t*-test. *Reproduced from Bruttini et al. (2015), © Springer-Verlag Berlin Heidelberg 2014, with permission of Springer*.

(Bonnetblanc et al., 2004; Nana-Ibrahim et al., 2008) and in the lower-limb (Bertucco and Cesari, 2010). Lower limb pointing was also investigated by Duarte and Latash (2007), which have shown that as movement velocity increased, so did APA variability. The relation between movement speed and scattering of the final position around a target was also well described (Schmidt et al., 1979; Fernandez and Bootsma, 2004). All these observations suggest that small and less variable APAs should accompany slow but precise movements. Finally, Berrigan et al. (2006) reported that when pointing is performed towards small targets (i.e., under high accuracy constraints) from an unstable position (i.e., standing vs. sitting), slowing movement speed represents a strategy to reduce the equilibrium disturbance and the associated APAs. However, the above results might simply be an outcome of the relationship between APAs and intended movement speed (Shiratori and Aruin, 2007; Esposti et al., 2015), given the well known inverse relation (Fitts, 1954 law) between target width and movement speed. In order to get rid of such possible bias, Caronni et al. (2013) studied *inter-limb* APAs during an upper limb pointing movement toward a target of fixed dimension, while wearing (or not) prismatic lenses, which shift the binocular eye field and make the subject to miss the target (Redding et al., 2005). Caronni et al. (2013) observed that the focal movement had similar kinematics in the two conditions, but after donning or doffing the lenses appreciable pointing errors occurred. Moreover, when committing such errors, APAs in the lower limb were out of proportion with respect to the recruitment of the upper limb prime mover.

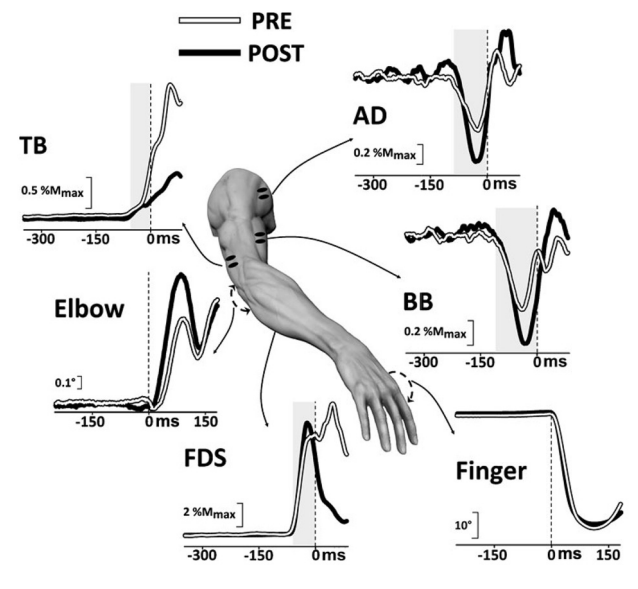

FIGURE 5 | Intra-limb APAs change after short-term immobilization. Average recordings in a representative subject before (PRE, white) and after (POST, black) immobilization. When rapidly flexing the index-finger (prime mover FDS), the arm equilibrium is preserved thanks to APAs (shaded area), which are excitatory in TB and inhibitory in BB and AD. After a 12-h immobilization of the wrist and fingers, FDS activation preceding the movement onset and index-finger movement were unchanged. Instead, inhibitory APAs in BB and AD apparently increased, while excitatory APA in TB was marginally decreased. The changes in the postural chain led to a less effective fixation of the elbow joint, which showed a larger displacement during index-finger acceleration. EMG amplitude was normalized to the maximal motor response (M_{max}) evoked by orthodromic nerve stimulation. *Reproduced from Bolzoni et al. (2012), © Springer-Verlag 2012, with permission of Springer.*

The linkage between APAs and movement precision is also supported by the observation that training induces improvement in the correct tailoring of the APA chain with respect to the prime mover recruitment, both in young adults (Kanekar and Aruin, 2015) and elderly (Kubicki et al., 2012; Aruin et al., 2015). Thus, the increased movement precision observed after training (Hamman et al., 1995; Yang et al., 2013) might be partly due to a more appropriate tuning of the postural adjustments. Other suggestions about the linkage between APAs and precision derive from some motor behaviors in which proper whole-body stabilization is needed to achieve an effective performance. According to shooting coaches and athletes, good postural balance is a vital component of successful shooting. During bipedal standing, top-level rifle shooters stabilized their whole body balance better than naive shooters (Aalto et al., 1990); the capability to reduce the oscillation, especially in the last few seconds before pulling the trigger, expresses better control of posture in athletes and was associated with a better shooting performance (Era et al., 1996; Mononen et al., 2007). More recently, Furuya et al. (2011) demonstrated that professional pianists tended to play using less muscular activity and take greater advantage of shoulder joint rotation during a keystroke than did novice.

In regard to *intra-limb* APAs, Caronni and Cavallari (2009a) suggested that during a brisk index-finger flexion, *intra-limb* APAs not only would guarantee the maintenance of the arm posture, but should also be very important in controlling the trajectory (**Figure 3C**) and thus the final position of the moving segment, i.e., what is clinically indicated as *metria*. Indeed, when simulating an index-finger flexion using a four-joint software mechanical model of the arm (**Figure 3A**), in which only the prime mover was recruited, a clear disturbance of both focal movement and upper-limb posture was observed, with relevant changes at wrist and elbow level. This would affect the final position of the intentional finger movement (**Figures 3D,E**). In the model, the only way to prevent these *collateral effects* was to block all segments but the finger, preventing the proximal joints from rotating (fictive *intra-limb* APAs).

Since this observation was derived from a very simplified system, Caronni and Cavallari (2009a) also looked for a more realistic situation: a finger tap was electrically evoked in a real arm by stimulating the median nerve (**Figure 3B**); such an experiment showed recordings comparable in sign and size to those predicted by the software mechanical model, including the dysmetric motor output. However, both the *software simulation* and the *electrically evoked tap* paradigms did not faithfully represent the *natural dysmetric behavior*, since in the two cases no voluntary command is modeled or generated, respectively. An indirect suggestion of the role of APAs in movement

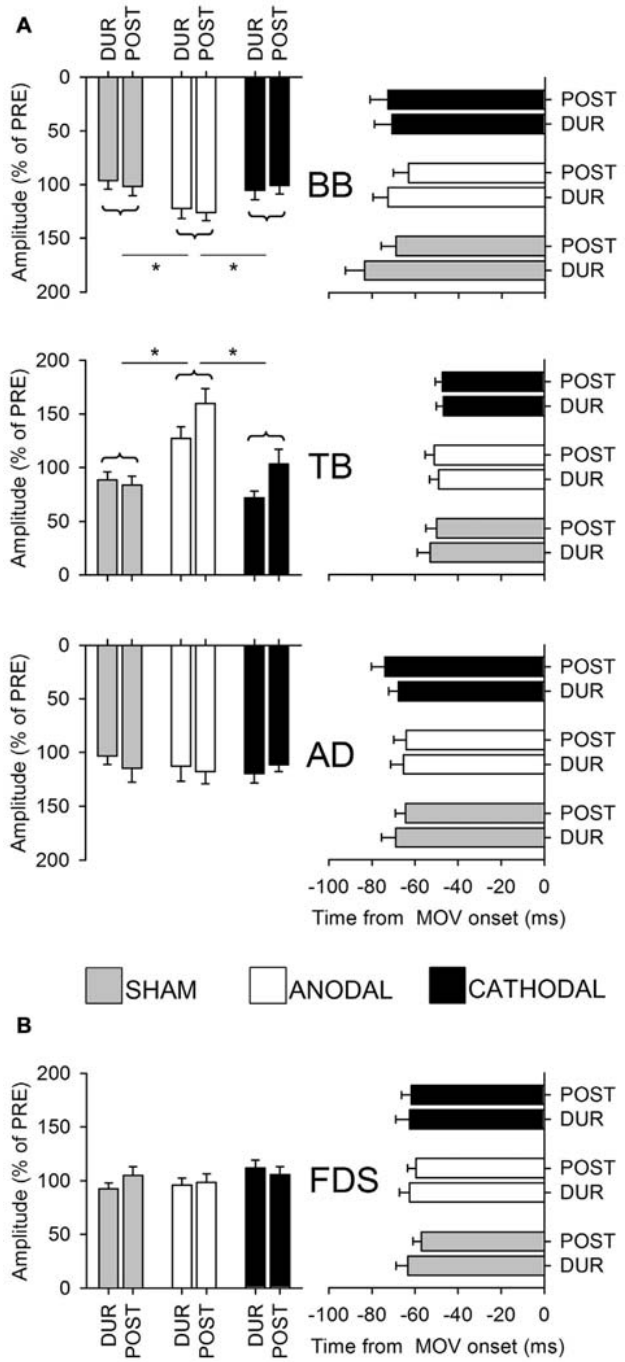

FIGURE 6 | Amplitude and latency of intra-limb APAs (A) and of voluntary recruitment of index-finger prime mover (B). Postural muscles: BB, TB and AD, prime mover FDS. Data were collected from the whole population, in the last 5 min of 1 mA Transcranial Direct Current Stimulation (tDCS) application (DUR) and 20 min after its end (POST). Amplitude data are plotted on the left (expressed as percentage of the amplitude measured before tDCS, % of PRE), latencies referred to movement onset on the right (mean ± SE). Repeated measures *stimulation* × *time* ANOVA, and Tukey *post hoc* (see asterisks), found a significant increase in the amplitude of BB and TB APAs under ANODAL vs. CATHODAL and SHAM stimulation, while the APA in AD was unaffected. No effect of *time* or *interaction* was observed, thus

(*Continued*)

FIGURE 6 | (Continued)
ANODAL stimulation enhanced APAs in TB and BB with an effect lasting at least 20 min. No significant changes were observed in APAs latency. Note also that tDCS had no effect on the amplitude and latency of FDS activity, witnessing that the increase in BB and TB APAs should not be ascribed to a stronger recruitment of the prime mover. *Reproduced from* Bolzoni et al. (2015), *© 2015 Elsevier B.V., with permission of Elsevier*.

metria comes from Bruttini et al. (2015), who demonstrated that when performing a brisk index-finger flexion, cerebellar subjects showed a timing-disruption of *intra-limb* APAs (**Figure 4**), while their pattern (excitation in TB; inhibition in BB and AD) was unmodified. These data open the question whether cerebellar dysmetria may stem from an erroneous timing of APAs.

Moreover, considering that a disruption of the APA chain may lead to movement inaccuracy and taking into account that Moisello et al. (2008) demonstrated that 12-h of immobilization are already sufficient in affecting the inter-joint coordination by interfering with the feed-forward mechanisms, Bolzoni et al. (2012) investigated the effect of a short-term immobilization on the *intra-limb* postural control accompanying index-finger flexion. In this article it was shown that 12-h of wrist and finger immobilization effectively modified APAs on elbow and shoulder muscles, without altering the prime mover activation (**Figure 5**). The APA modifications were also paralleled by a less efficient stabilization of the elbow joint. Therefore, these results may shed light on some of the mechanisms underlying the feeling of motor awkwardness and the reduction of the voluntary movement precision that are commonly experienced after the removal of a cast or a splint.

A last apparent evidence in favor of the importance of APAs in movement precision has been recently provided by Bruttini et al. (2016), who illustrated that the different precision observed when comparing pointing movements performed with the preferred vs. non-preferred hand partly stems from changes in the temporal organization of APAs in the two sides. Indeed, APAs were delayed when moving the non-preferred side. This delay was associated to an impaired stability of the elbow joint during the wrist pointing movement. As a result, the focal movement perturbation caused an increased elbow excursion in the non-preferred hand, eventually leading to the diminished movement precision on that side.

Surely, APAs are not the only determinant of movement precision. In fact, it is well known that when a healthy subject points to a target cross, an eventual error in reaching the target derives from an incorrect sensorimotor transformation, from the visual representation of the target to the kinematics representation of the planned trajectory (Soechting and Flanders, 1989a,b; for a review see also Massion, 1992). Indeed, these authors showed that when subjects have to reach a position which has been previously appreciated kinesthetically (thus after having empirically built up the exact transformation), pointing errors dramatically reduce. In particular, several studies showed that the parietal cortices play a critical role in integrating visual and somatic inputs for building up this sensorimotor transformation. Such transformation seems also assisted by the skin receptors, which detect the torsion forces that act on the skin of the feet

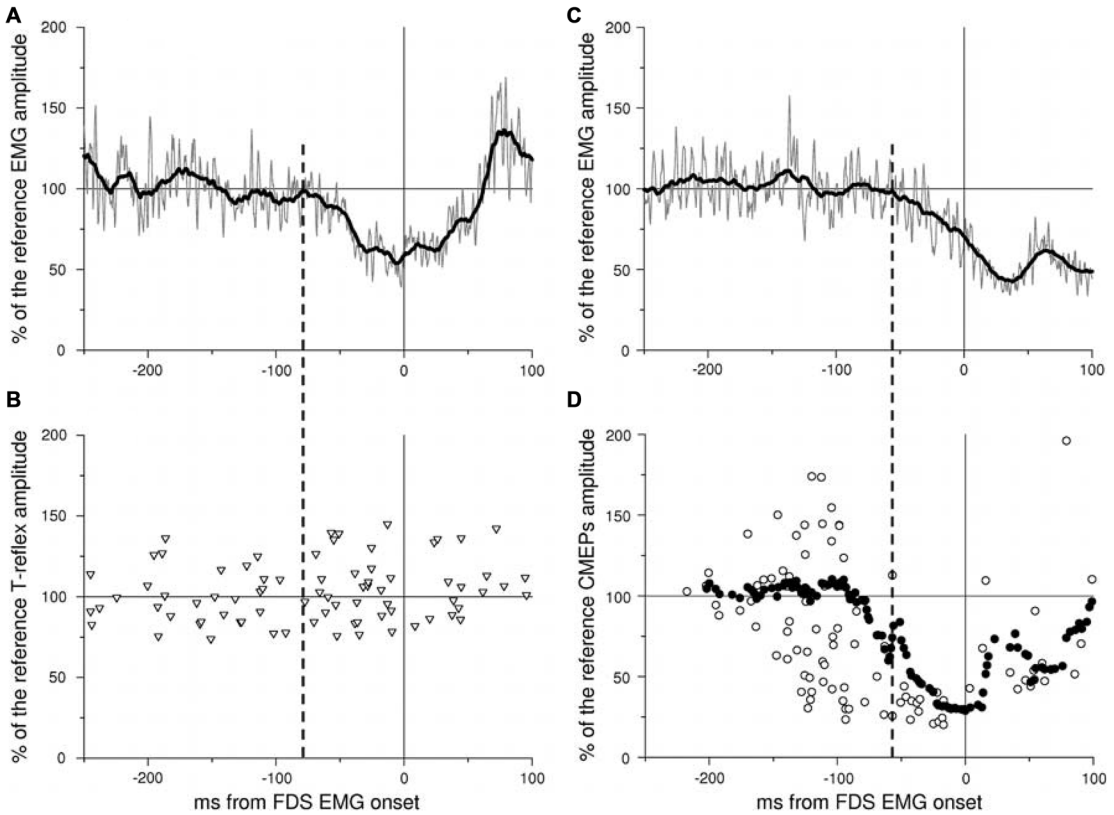

FIGURE 7 | Time course of spinal and cortico-spinal excitability in the resting BB before an index finger flexion. An inhibitory APA (iAPA) occurs in the BB EMG in two representative subjects **(A,C)**: in both cases rectified (gray trace) and integrated (black trace) EMG activity (average of 40 trials) is strongly reduced well in advance to the onset of FDS, taken as time 0. The time course of BB spinal excitability has been tested by means of tendon tap reflexes **(**T-reflex, triangles in **B)**, while that of BB cortico-spinal excitability by Transcranial Magnetic Stimulation (TMS)-elicited cortical motor-evoked potentials **(**CMEPs, open circles in **D)**. Each symbol marks amplitude and latency of one single evoked potential. Note that T-reflexes are un-modulated in size in the iAPA window, edged by the iAPA onset (vertical dashed line) and prime mover onset (vertical continuous line), whereas CMEPs are strongly inhibited. To better identify the onset of this inhibitory effect, the CMEPs time course has been integrated with the same time constant used for the EMG (filled circles). Both EMG and evoked potential amplitude are expressed as a percentage of their mean reference amplitude, i.e., that measured before the acoustic go signal. *Reproduced from Caronni and Cavallari (2009b), © Springer-Verlag 2009, with permission of Springer*.

in contact with the soil (for a review see Kalaska et al., 1997). In this context, it has been also observed (Esposti et al., "APAs associated to reaching movements are programmed according to the availability of visual information", submitted manuscript) that once the target position has been acquired, both visually and kinesthetically, reaching the target while gazing it or in a *blind* condition resulted in similar levels of pointing accuracy; pointing precision was instead significantly impaired in absence of visual information. Finally, these authors suggested that the visuospatial memory may play a key role in movement accuracy, while "active vision" seems to be more engaged in movement precision.

CENTRAL ORGANIZATION OF APAs

Anatomical and Physiological Data

Several studies support the idea that *Supplementary Motor Area* (SMA) is involved in APAs generation. Severe APA impairments were observed in the bimanual load lifting (the so called *barman task*) when the load was held with the forearm contralateral to the lesioned SMA while no APA changes were observed in a patient with normal SMA, but suffering a complete callosal section (Massion et al., 1989; Viallet et al., 1992). This finding supports the idea that coordination between the posture and movement travels through subcortical level. Moreover, a 1-Hz repetitive Transcranial Magnetic Stimulation (TMS) on SMA, which induces an inhibitory effect, reduces the duration of APAs prior to stepping, without affecting their peak amplitude (Jacobs et al., 2009). More recently, Transcranial Direct Current Stimulation (tDCS) over the SMA has been shown to elicit a differential effect on the postural and the focal component of the movement (**Figure 6**), supporting the involvement of SMA in APA programming (Bolzoni et al., 2015).

The role of the *Primary Motor Cortex* in generating APAs has been shown by both human and animal studies. The stimulation of the primary motor cortex in the intact cats was indeed able

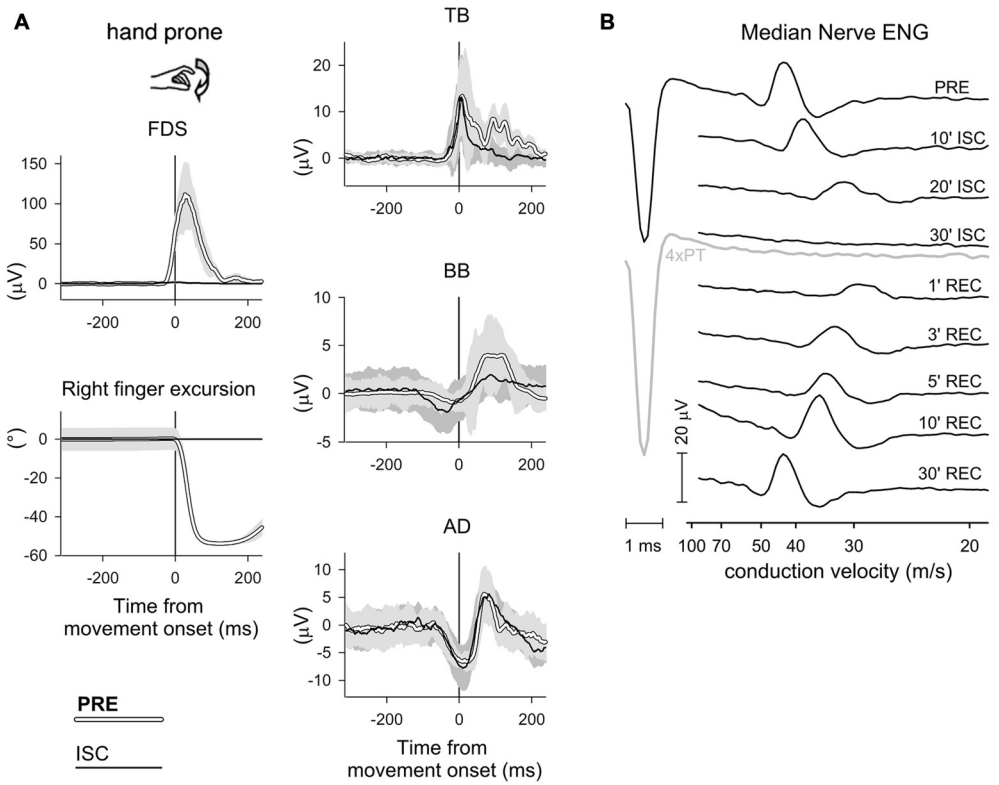

FIGURE 8 | APA persistence under ischemia. (A) Rectified and integrated average recordings of index-finger prime mover EMG and of intra-limb APAs, before and during ischemic block of the median nerve at the forearm. One representative subject. Time 0: movement onset of the left index-finger. When rapidly flexing both index-fingers before ischemia (PRE, white traces, SD in light gray), the right prime mover FDS was activated and the right arm equilibrium was preserved, thanks to an excitatory APA in TB and inhibitory APAs in BB and AD. Under ischemia of the right forearm (ISC, black traces, SD in dark gray), FDS activation and index-finger movement were both suppressed, while excitatory APAs in TB and inhibitory APAs in BB and AD were still evident and qualitatively similar to those recorded in PRE. **(B)** Electroneurogram (ENG) of the right median nerve of one representative subject, showing the effect of ischemia, induced by a pressure cuff, on the afferent volley elicited by electrical stimulation of the index-finger skin (3 × perception threshold, PT). Ischemia progressively reduced the volley amplitude until reaching complete suppression after 30 min (even increasing stimulation to 4 × PT, gray trace, did not elicit a response). After removing the pressure cuff, the effect of ischemia completely recovered in 30 min. *Reproduced from* Bruttini et al. (2014), *© Springer-Verlag Berlin Heidelberg 2014, with permission of Springer*.

to evoke movement in the contralateral side and APAs in the supporting limbs (Gahéry and Nieoullon, 1978), suggesting that the primary motor cortex in cats is able to control both the voluntary prime mover and the associated postural adjustments. Moreover, in cats, the dynamic of the discharge frequency in pyramidal neurons is time locked and directly proportional with the center of pressure displacement, a key parameter associated to APAs preserving the whole body equilibrium (Yakovenko and Drew, 2009). The role of the primary motor cortex in the anticipatory postural control was also observed in human studies. Indeed, Palmer et al. (1994) used the TMS to induce a silent period in either the left or the right M1 while the subject abducted his left arm, a movement which is known to be preceded by APAs in the contralateral Latissimus Dorsi muscle. Left M1 stimulation produced a delay of the APA onset, while the prime mover timing was unmodified; instead, right M1 stimulation just delayed the prime mover activation. Moreover, it has been shown for both *inter-* (Petersen et al., 2009) and *intra-limb* APAs (Caronni and Cavallari, 2009b) that when a postural muscle is at rest the spinal excitability is un-modulated during the whole period of motor preparation, while when that muscle is recruited in a postural chain the cortical motor action potentials are modulated according to the time course of APAs (**Figure 7**). From one perspective, this indicates that APAs processing involves M1 level, and from another this suggests that APAs and voluntary commands cannot be decoupled, since the former remains subliminal, i.e., it does not produce a mechanical effect, when the muscle is at rest. Although this may appear uneconomical, this result corroborates two previous observations in which the cortical excitability of hand movers has been shown to fluctuate under the threshold for motoneuronal firing when the ipsilateral foot was voluntarily oscillated (Baldissera et al., 2002) and in which the *hidden effect* developed in an overt APA when the hand was recruited in a postural act (Baldissera and Esposti, 2005).

Regarding *Basal Ganglia*, severe APAs impairment in patients with Parkinson's disease were already observed by Viallet et al. (1987). More recently, anticipatory brain activity associated to a bimanual load-lifting task was localized in basal ganglia,

SMA and thalamus, contra lateral to the load-bearing arm (Ng et al., 2013). It is worth noting that these areas are component nodes of the basal ganglia-thalamo-cortical motor network, which is known to be implicated in well-learned finger movements (Boecker et al., 1998). This indicates a superposition of the neural structures for APAs and those for voluntary motor command, and indirectly supports the view of a oneness of the motor command for both posture and primary movement.

The *Cerebellum* is deeply involved in APA regulation. Babinski (1899) reported that a cerebellar lesion disrupted the coordination between voluntary movement and equilibrium stabilization, indicating that the cerebellum is involved in postural control. This view agrees with the idea that the cerebellum contains forward internal models that could predict the consequences of an action (according to the perceived postural context) and can be used to overcome time delays associated with feedback control (Wolpert et al., 1998; Imamizu et al., 2000). Several studies on patients positively concluded for such an involvement. Indeed, patients suffering cerebellar lesions failed to show a normal anticipatory adjustment in grip force when lifting or moving an object (Müller and Dichgans, 1994; Babin-Ratté et al., 1999) and cerebellar lesions abolished APAs plasticity in a bimanual unloading task (Diedrichsen et al., 2005). Congruently, Diener et al. (1992) reported that cerebellar patients produce a normal pattern of APAs, but with abnormalities in their timing relationship with the onset of the prime mover. Finally, as shown in **Figure 4**, Bruttini et al. (2015) demonstrated that when performing a brisk index-finger flexion, cerebellar subjects showed a timing-disruption of *intra-limb* APAs, while their pattern was unmodified. Using functional magnetic resonance imaging, Schmitz et al. (2005) reported that APAs were associated with activation of sensorimotor areas, SMA and the cerebellum. On the contrary, Ng et al. (2013) found no evidence of cerebellar involvement during APAs using magnetoencephalography in a bimanual coordination task. Further support on the role of cerebellum in timing APAs come from animal studies. When reaching a water flask with the mouth, wild type mice showed a clear APA in hind-limb muscles, synchronous to neck muscles, while in transgenic mice with defective cerebellar Purkinje cells the hind-limb activity occurred markedly later than that in neck muscles (Yamaura et al., 2013).

Finally, Schepens and colleagues (Schepens and Drew, 2004; Schepens et al., 2008) emphasized the role of pontomedullary reticular formation (PMRF) in the coordination of posture and movement. In particular, they suggested that PMRF is a site of integration of signals from both cortical and subcortical structures, and that these signals ensure that APAs are appropriately scaled in time and magnitude to the intended movement, contributing to integrate the control of posture and movement, as also illustrated by Toussaint et al. (1998).

In summary, these anatomical and physiological studies show a large superimposition between neural structures governing the voluntary and the postural components of the movement, leaving the question open on whether these two processes are implemented separately or they are an expression of a unique *posturo-focal* command.

Dual vs. Shared Command Hypothesis

According to the classical view, the prime mover activity and the associated postural adjustments result from two different central commands *(dual command hypothesis)*, which are independently dispatched to the prime mover and to the muscles generating the postural chain (Babinski, 1899; Hess, 1943; Cordo and Nashner, 1982; Brown and Frank, 1987). Conversely, a growing body of evidences favors the view that APAs and prime mover recruitment are both controlled by a *shared motor command* (Aruin and Latash, 1995; Stapley et al., 1998, 1999; Caronni and Cavallari, 2009b; Petersen et al., 2009). In this regard, it is interesting to mention the studies of Gritsenko et al. (2009) and Leonard et al. (2011), showing that when correcting an ongoing arm pointing movement, the CNS employs a predictive mode of postural control and consistently adapts the postural muscle activities before modifying the prime mover recruitment. These authors concluded that the postural corrections could be described as being a component of the voluntary movement, rather than ensuring the maintenance of equilibrium. Further, Bruttini et al. (2014) demonstrated that the APA chain associated to a voluntary movement cannot be decoupled from the command driving the focal movement. Indeed, when repeatedly trying to flex the index-finger under forearm ischemia, so that the voluntary command was normally dispatched but the prime mover not able to receive it, significant anticipatory adjustments were clearly visible in BB, TB and AD (**Figure 8**).

In this peculiar condition, in which no postural perturbation is generated, one would have expected that APAs were suppressed since unnecessary and uneconomical, unless the postural and the prime mover muscles obey a "shared" motor command. It is of course apparent that "ischemia" results does not allow to discern whether: (i) one specific neural structure generates both the postural and the voluntary commands; or (ii) two neural structures exist, one for the voluntary and the other for the postural commands, and one of the two acts as a master on the other; or (iii) a third neural structure exists, which simultaneously triggers the two slave "postural" and "voluntary" neural structures. However, from the point of view of the muscles (i.e., the only aspect that such experimental approach allowed to observe), these three ways of organizing the posturo-focal integration are all identical. Given this neural organization, it may be conceived that the system prefers an *economy* in computational terms, rather than in diminishing the number of activated neurons. In this case, one may imagine that any given voluntary command is associated with an arborized pattern of postural commands, forwarded to a number of possible fixation points. Thus, the most useful arborization for providing the actual support would be supraliminarly recruited, while the leftover branches would be still present but kept silent, i.e., under threshold. The amplification of APA transmission to certain targets, and the parallel attenuation towards other targets, could be automatically accomplished by servo-systems like PMRF neurons. This would effectively free the upper centers from the computational demand of adapting the APAs to the postural context. This view is also corroborated by the already cited works of Baldissera et al. (2002) and Baldissera and Esposti (2005), who showed that subliminal *inter-limb* APAs in a resting

arm during foot movements become supraliminal when that segment is actively used for postural stabilization. Similar results were also shown for *intra-limb* APAs by Caronni and Cavallari (2009b).

The oneness of postural and voluntary command is also supported by the finding that the APA latency depends on the movement instruction, not on its actual velocity (Esposti et al., 2015). This conclusion was based on two observations. First, no correlation was found between APA latency and movement speed when subjects had to follow a *go fast* instruction (i.e., to move as fast as possible), nor when they had to *go slow* (at half their maximal speed). Second, the maximal speed was variable among subjects, so that minimum movement speeds within the range of *go fast* trials intermingled with maximal movement speeds within the range of *go slow* trials. Despite similar velocities, APAs were earlier in the former and less anticipated in the latter. Thus, APAs looked much more tailored on the expected perturbation than on the real one, favoring the idea of a functionally unique postural and focal command.

CONCLUSIONS

This review shows that *intra-limb* APAs and *inter-limb* APAs share the same organizational and behavioral principles. The simplicity and flexibility of the *finger tap* experimental model has also allowed to shed light on a new general characteristic of the postural control. In fact, APAs not only deal with whole-body equilibrium, segmental posture and movement initiation, but are also involved in providing the correct postural set necessary to obtain precise movements. Finally, this approach has been useful in inspecting the central organization of APAs. In particular, the persistence of APAs after the ischemic block of the prime movers provides a principal piece of evidence in assessing the oneness of the focal and postural commands.

AUTHOR CONTRIBUTIONS

All authors contributed in collecting the literature, critically analyzing it and writing the manuscript. All authors approved the final version and agree to be accountable for all aspects of this work.

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Higher Precision in Pointing Movements of the Preferred vs. Non-Preferred Hand Is Associated with an Earlier Occurrence of Anticipatory Postural Adjustments

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It is a common experience to exhibit a greater dexterity when performing a pointing movement with the preferred limb (PREF) vs. the non-preferred (NON-PREF) one. Here we provide evidence that the higher precision in pointing movements of the PREF vs. NON-PREF hand is associated with an earlier occurrence of the anticipatory postural adjustments (APAs). In this aim, we compared the APAs which stabilize the left or the right arm when performing a pen-pointing movement (prime mover flexor carpi radialis (FCR)). Moreover, we analyzed the elbow and wrist kinematics as well as the precision of the pointing movement. The mean kinematics of wrist movement and its latency, with respect to prime mover recruitment, were similar in the two sides, while APAs in triceps brachii (TB), biceps brachii (BB) and anterior deltoid (AD) were more anticipated when movements were performed with the PREF than with the NON-PREF hand (60–70 vs. 20–30 ms). APAs amplitudes were comparable in the muscles of the two sides. Earlier APAs in the preferred limb were associated with a better fixation of the elbow, which showed a lower excursion, and with a less scattered pointing error (PREF: 10.1 ± 0.8 mm; NON-PREF: 16.3 ± 1.7). Present results suggest that, by securing the more proximal joints dynamics, an appropriate timing of the intra-limb APAs is necessary for refining the voluntary movement precision, which is known to be scarce on the NON-PREF side.

Keywords: motor control, posture, APAs, handedness, precision, human

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INTRODUCTION

Anticipatory postural adjustments (APAs) are commonly defined as unconscious muscular activities aimed to counterbalance the perturbation caused by the primary movement. In this respect, they have been shown to ensure whole-body balance (Massion, 1992; Bouisset and Do, 2008) and to stabilize body segments (Patla et al., 2002). They are also involved in initiating the displacement of the body center of mass when starting gait (Brenière et al., 1987) and forward reaching (Stapley et al., 1998, 1999). The APAs originate from a feed-forward command (Belen'kiĭ et al., 1967; Aruin and Latash, 1995), tailored on several kinematical aspects of the primary movement. Within a few trials, the central nervous system (CNS) is able to adapt APAs to

changes in the desired movement speed (Shiratori and Aruin, 2007; Esposti et al., 2015), amplitude of motor action (Aruin and Shiratori, 2004) and the expected mass of the moving segment (Friedli et al., 1984; Toussaint et al., 1998). APAs have been first illustrated in movements that involve a relatively large mass, such as a shoulder flexion, that would produce a backward displacement of the center of mass projection on the ground (Bouisset and Zattara, 1987). Such perturbation may lead to the loss of the whole body equilibrium (Hess, 1943; Bouisset and Zattara, 1987); therefore, in order to counteract it, the recruitment of the prime mover muscles is normally preceded by *inter-limb APAs* in lower limbs, hips and trunk, which in turn induce a forward displacement of the center of mass, preventing falling.

More recently, Aoki (1991) reported that a pattern of postural activity in arm muscles also precedes voluntary wrist movements (*intra-limb APAs*), and that this pattern is related to the movement direction in space, just as similar to the inter-limb APAs described above. In this path, Caronni and Cavallari (2009) reported that also when voluntarily flexing a single segment of tiny mass, such as the index-finger, an intra-limb APA chain develops in several upper-limb muscles, to stabilize the *segmental* equilibrium of the whole arm. Similarly to the APAs preceding wrist flexion, the APA pattern associated to a finger flexion changes according to the direction of the focal movement. Indeed, with the prone hand, both wrist and index-finger flexions are preceded by an excitatory burst in triceps brachii (TB), while biceps brachii (BB) and anterior deltoid (AD) show a concomitant inhibition. Instead, with the hand supine, the opposite occurs: BB and AD show excitatory APAs, while TB undergoes a concomitant inhibition. From these last data, an additional role of APAs may be envisaged: besides maintaining the whole-body equilibrium, it seems that APAs may be important in refining voluntary movement precision. In fact, according to the results obtained in a four-joint software mechanical model and confirmed by an electrical stimulation of the median nerve, Caronni and Cavallari (2009) suggested that intra-limb APAs not only guarantee the maintenance of the arm posture, but may be also very important in controlling the trajectory and the final position of the moving segment. However, up to now, no direct evidence of such a conclusion has been reached when dispatching a voluntary motor command.

To shed further light on the relationship between APAs and movement precision, we studied pointing movements performed by flexing the wrist while holding a digitizer pen, so as to ascertain whether the well known imprecision of the non-preferred (NON-PREF) vs. preferred (PREF) arm (Woodworth, 1899) leading to smaller pointing errors with the PREF limb (Roy et al., 1994; Ypsilanti et al., 2009), may be correlated to a worse control of APAs. Considering that APAs are scaled according to the mass of the moving segment and given that the two hands have a similar mass, it would be surprising to observe differently structured APAs accompanying similar movements of the two sides. On the other hand, a different APAs programming between the two sides, e.g., in timing and/or amplitude, would demonstrate that APAs are essential in refining movement precision.

MATERIALS AND METHODS

Experiments were carried out in 13 adult healthy volunteers (4 females); mean age 31.7 ± 9.4 years. All subjects were right-handed, as confirmed by their scores on the 10-item version of the Edinburgh Handedness Inventory (Oldfield, 1971). The procedure was conducted in accordance to the Declaration of Helsinki. All subjects provided written informed consent; none of them had any history of orthopedic or neurological diseases. No ethical approval was required because the experimental procedure was non-invasive, did not require any drug administration and was carried out on healthy volunteers.

Experimental Procedure

Subjects sat on a chair with both arms along the body, elbows flexed at 90°, the wrists prone and in axis with the forearm. The moving wrist was kept unsupported and slightly extended, with the dorsum of the first metacarpo-phalangeal joint in contact with a proximity switch (CJ10–30GK-E2, Pepperl+Fuchs®, Mannheim, Germany). Subjects were explicitly asked to keep their back supported, the arm/forearm still and to look at the target during the experiment, to be aware of their movement performance. Subjects were asked to hold a digitizer pen with the most natural pinch grip and to briskly flex their wrist so as to point to the target with the pen tip as quick and precise as possible (pen-pointing). The target consisted in two orthogonal lines drawn on a white paper, taped on the pen tablet (Intuos Pen and Touch small, Wacom®, Saitama, Japan; active tablet area 152 × 95 mm; pen weight 12.5 g). The lines were 1 mm thick × 2 cm long, so that the target center was clearly visible. The chair was height adjustable, while the proximity switch and the pen tablet were screwed on articulated arms (Manfrotto 143 MAGIC ARM® + 035 Superclamp Kit, Manfrotto®, Cassola, Italy), so as to adapt to the different body dimensions of the subjects. In the initial position, the pen tip was held approximately 6–7 cm above the cross.

Each pen-pointing movement was self-paced and performed after an acoustic signal. The time between the beep and the movement onset varied according to the subject will; this procedure was adopted to exclude any reaction time.

In each experiment, two sessions of 60 pen-pointing movements were performed, one with each hand (PREF vs. NON-PREF); each session was divided into four sequences of 15 movement trials. The 15 trials were accomplished in a temporal window of about 2 min, and then the subject had time to rest (about 3 min) before undergoing a new sequence. Subjects never complained about fatigue.

At the end of each session, the EMGs of the BB, TB and AD muscles of each side were separately evaluated during a maximal press against a fixed support, which changed according to the tested muscle. The upper limb was kept in the same posture adopted during the pen-pointing experiments, so as not to alter the positioning of the recording electrodes with respect to the muscles. Subjects were thus asked to push as hard as possible upon a fixation point and maintain the push for 5 s. When testing

the AD, the fixation point was positioned in front of the arm, at the level of the cubital fossa, and subjects had to push forward against it by trying to flex the arm at the shoulder. When testing the TB, the fixation point was positioned under the wrist and subjects had to push downward against it by trying to extend the forearm at the elbow. When testing the BB, the fixation point was positioned over the wrist and subjects had to push upward against it by trying to flex the forearm at the elbow.

Movement and EMG Recordings

The onset of the wrist flexion was monitored by the proximity switch. Flexion-extension of wrist and elbow joints was recorded by strain-gauge goniometers (mod. SG65 and SG110 respectively, Biometrics Ltd®, Newport, UK) taped to the skin over the respective joint. Angular displacements were DC amplified (P122, Grass Technologies®, West Warwick, RI, USA), A/D converted at 2 KHz with 12 bit resolution (PCI-6024E, National Instruments®, Austin, TX, USA) and stored. Goniometer calibration was undertaken before each experimental session.

Pairs of pre-gelled surface electrodes, 24 mm apart, (H124SG, Kendall ARBO, Tyco Healthcare, Neustadt/Donau, Germany) were used to record the EMG signal from the prime mover flexor carpi radialis (FCR) and from some of the ipsilateral postural muscles: BB, TB and AD. A good selectivity of the EMG recordings was achieved both by a careful positioning of the electrodes over the skin covering the muscle belly and by checking that the activity from the recorded muscle, during its phasic contraction, was not contaminated by signals from other sources. EMG was AC amplified (IP511, Grass Technologies®, West Warwick, RI, USA; gain 2–10 k) and band-pass filtered (30–1000 Hz, to minimize both movement artifacts and high frequency noise). Goniometric and EMG signals were A/D converted at 2 kHz with 12-bit resolution (PCI-6024E, National Instruments®, Austin, TX, USA), visualized online and stored for further analysis.

The position of the subject was always visually controlled by the experimenter, who also evaluated the amplitude and duration of each pointing movement by looking at the wrist angle trace on the computer screen, so as to remind the subject to speed-up the movement, if necessary.

Data Analysis

For each tested hand, the 60 EMG traces of the prime mover and those simultaneously recorded from the postural muscles were digitally rectified and integrated (time constant: 25 ms). All the EMG and goniometric traces were then averaged in a fixed temporal window: from −1000 to +300 ms with respect to the onset of the FCR EMG, identified by a software threshold set at +2 SD of the initial excitation level (from 1000 to 500 ms prior to movement onset).

On each experiment, latency and amplitude of the postural activity was measured off-line on the averaged traces, after subtracting from them the initial excitation level. Since the initial EMG level represented the tonic activity required to keep the upper limb in the experimental position, the APAs superimposed on it and should therefore be measured as changes (either positive or negative) in postural muscles activity. Also the peak-to-peak amplitude of wrist and elbow movements were measured off-line on the averaged traces, after subtracting their initial level for illustration purposes. The EMG onset in each postural muscle was identified by a software threshold set at ±2 SD of the initial excitation level, and visually validated. Latency of the APA was referred to the FCR EMG onset, with negative values indicating a time-advance. In order to measure the amplitude of each APA, the rectified EMG was first integrated from the APA onset to the movement onset. The resulting value was then normalized to the corresponding reference value, which was calculated as the mean value of the rectified EMG during the 5 s maximal press multiplied by the APA duration. APA amplitudes (normalized EMGi) were thus expressed in % of the reference value.

The peak-to-peak angular displacement of the elbow joint was measured from the onset of wrist flexion, signaled by the proximity switch, to the moment when flexion started to be braked, i.e., when wrist acceleration zeroed. The time of first contact between the pen tip and the tablet signaled the movement end; the distance between the pen-tip position and the target center at that moment being the pointing error. APA latencies and APA amplitudes (absolute values) were compared by a repeated measures analysis of variance (ANOVA) with factors *muscle* (BB vs. TB vs. AD) and *side* (PREF vs. NON-PREF). All other PREF vs. NON-PREF comparisons were performed by using paired *t*-tests. Statistical significance was set at $p < 0.05$.

RESULTS

When pointing while holding a pen with the PREF hand the FCR muscle activation was preceded by clear inhibitory postural adjustments in BB and AD muscles, and by an excitatory postural adjustment in TB (**Figure 1**, representative subject). This APA pattern preceded wrist flexion of about 60 ms. Instead, when the same subject pointed with the NON-PREF hand, APAs showed a similar pattern (excitation in TB and inhibition in BB and AD), but were clearly less anticipated. This change in the APA timing was associated to an increased elbow angular displacement during the movement, with respect to the PREF side. Thus, thanks to a better stabilization of the proximal joint, the representative subject was more precise in PREF than in NON-PREF. Indeed, this is apparent when comparing the final position of the pen-tip in the two sides.

Figure 2 illustrates the mean latency and amplitudes of APAs, the average latency, duration and amplitude of the wrist movement, as well as the average elbow displacement and pointing error in the whole sample. Note that the latency, amplitude and duration of wrist movement were at all similar in the PREF vs. NON-PREF hand (latency: $t_{(12)} = 0.19$, $p = 0.84$; duration: $t_{(12)} = 0.32$, $p = 0.75$; amplitude: $t_{(12)} = 0.17$, $p = 0.86$). Despite the invariance of average kinematics of the focal movement, the excitatory APA in TB and inhibitory APAs in BB and AD were delayed of about 20–30 ms in NON-PREF

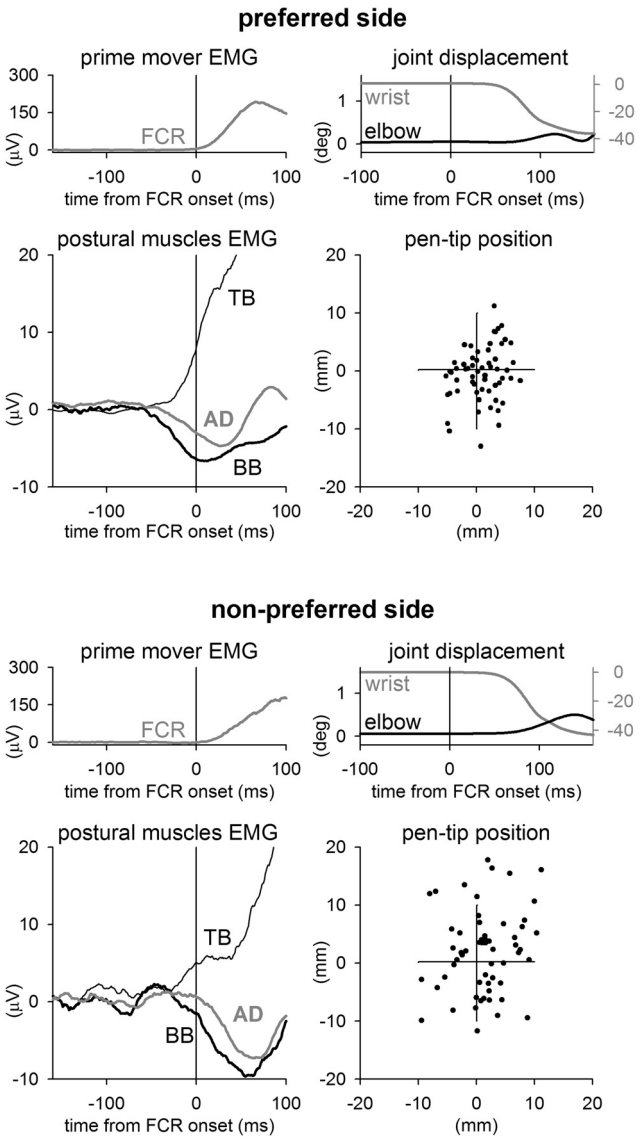

FIGURE 1 | Sample recordings from a representative subject. Rectified and integrated average recordings of EMG in Flexor Carpi Radialis (FCR, prime mover), Biceps Brachii (BB), Triceps Brachii (TB), Anterior Deltoid (AD), together with wrist flexion, elbow excursion and ensuing final position of pen-tip. Time 0 = FCR onset. When pointing with the preferred wrist (upper panels), the right elbow equilibrium was preserved thanks to excitatory APAs in TB and inhibitory APAs in BB and AD, which precede the FCR activation by about 65 ms. In the non-preferred side (lower panels) APAs were delayed, indeed they advanced the prime mover onset by just 20–30 ms. This was associated with an increase of the elbow excursion during the wrist movement. The effect that the different APA timing and the associated elbow stabilization had on the pen-tip final position is shown on the right-lowermost panels.

with respect to PREF, the time shift being similar in all muscles. Indeed, two-way ANOVA only found a main effect of *side* ($F_{(1,12)} = 18.43$, $p = 0.001$), with no effect of *muscles* ($F_{(2,24)} = 2.90$, $p = 0.075$), nor *interaction* ($F_{(2,24)} = 0.71$, $p = 0.50$). The absolute values of APA amplitude were different in the three muscles but did not show any significant PREF vs. NON-PREF difference. Indeed, two-way ANOVA only found a main effect of *muscle* ($F_{(2,24)} = 16.65$, $p < 0.0001$; Tukey *post hoc* revealed that APA was lower in BB than in TB and AD, with no difference among the latter two), with no effect of *side* ($F_{(1,12)} = 1.23$, $p = 0.29$) nor *interaction* ($F_{(2,24)} = 2.05$, $p = 0.15$).

When pointing with the NON-PREF hand, the delay of the APA chain was associated to a greater displacement of the elbow joint with respect to the PREF side ($t_{(12)} = 3.68$, $p = 0.0035$) and to a larger and more scattered pointing error ($t_{(12)} = 5.18$, $p < 0.0002$).

DISCUSSION

This article illustrates an asymmetry in the temporal organization of the intra-limb APAs that stabilize the arm when producing a pen-pointing movement, performed by flexing one or the other wrist. Indeed, when pointing with the NON-PREF side, the APA chain in BB, TB and AD was less anticipated with respect to FCR recruitment. Considering that the mechanical perturbations induced by the focal movements were similar in the two sides, as witnessed by the similarities of wrist kinematics, the change in the APA timing was associated to the less efficient fixation of the elbow joint, which led to the reduced precision of the pointing movement. Therefore, we propose that the increased precision of the PREF hand stems from a more precise tailoring of APAs timing in that side.

Considerations About APA Amplitude Measurements

Given the difference in APA latency, statistics about APA amplitude should be interpreted carefully. In fact, they are based on data which do not represent comparable portions of the feedforward postural commands in the two sides. The onset of this command clearly produces the APA onset, but its end may occur either before or after the movement onset. As an example, the AD inhibitory APA, illustrated in **Figure 1**, seems to decay before wrist flexion in the PREF side while it decays after such movement in the NON-PREF side. Therefore, the APA amplitude in the PREF side fully quantifies the expression of the feedforward command, but it represents only a fraction of it in the NON-PREF side. In other words, the feedforward postural command does not necessarily end within the APA but may as well continue during the movement, when the simultaneous postural adjustments (SPAs) occur. In this case, SPAs become expression of a compound feedforward-feedback signal, in which it is impossible to identify the end of the feedforward component.

To overcome this problem, it could have been possible to choose a fixed time-window, ending before the movement onset. However, amplitude measurements would have been again inconclusive. Indeed, if the time window had ended before the APA peak, the measurement would have approximated the slope (rate of change) of the feedforward command, not its real

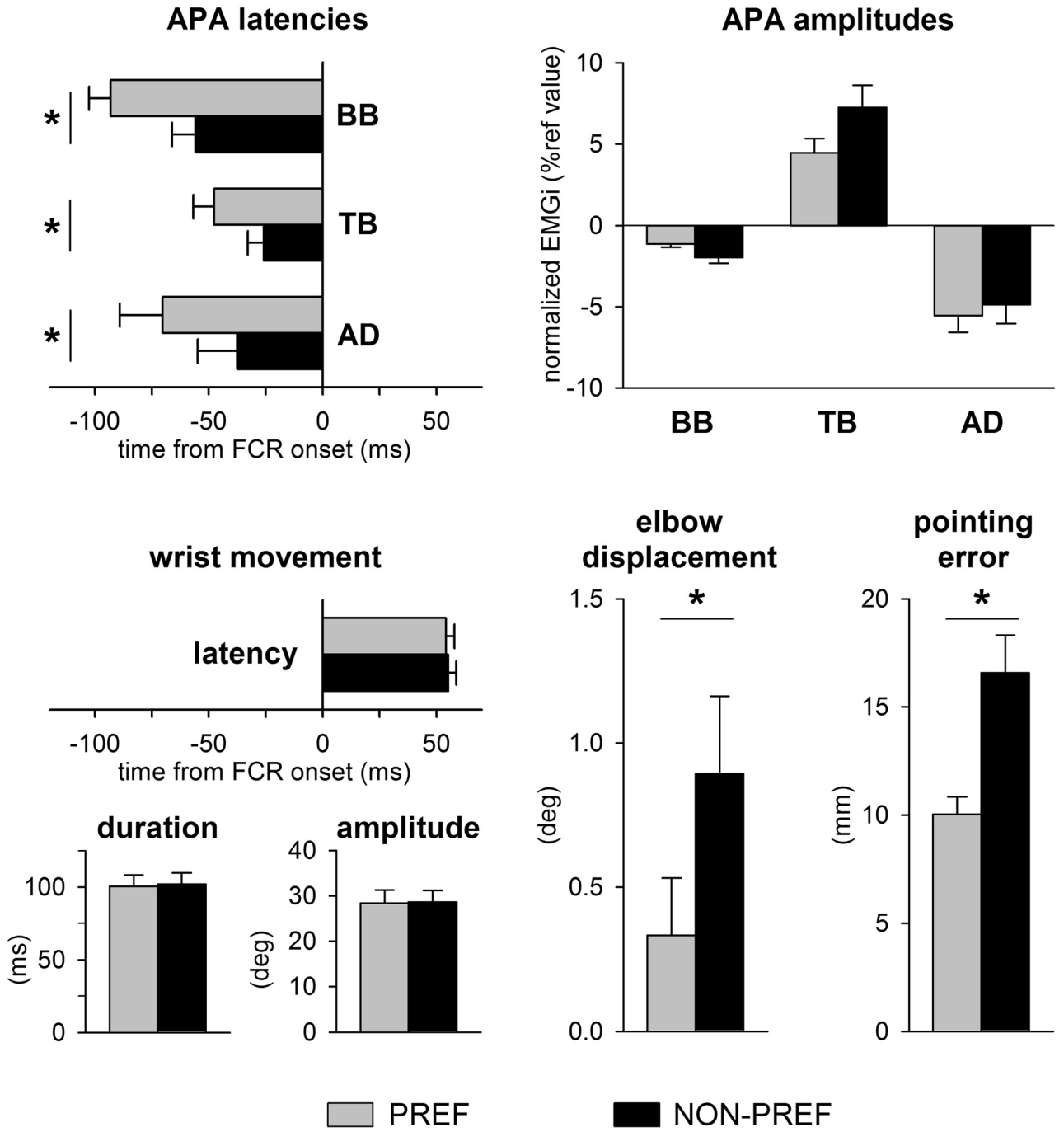

FIGURE 2 | Data from all subjects. Top panels show APAs latencies and amplitudes in TB, BB and AD of the preferred (PREF, gray) and of the non-preferred (NON-PREF, black) sides. Bottom panels report the latency, duration and amplitude of the wrist movement, as well as the elbow displacement and the pointing error on each side. Changes in APA latency were associated to a significant increase of the elbow displacement and pointing error. Time 0 = EMG onset in the prime mover Flexor Carpi Radialis (FCR). Mean values ± SEM. $*p < 0.05$.

amplitude. If instead the time-window had included the APA peak but not its decay, the measurement would have mixed-up amplitude and slope, in variable proportions.

In conclusion, the absence of statistical differences between the APAs amplitudes in the two sides does not grant that the respective feedforward commands were also comparable. Instead, since the APAs onset is the direct expression of the onset of the feedforward command, the observed change in latency grants for a different the temporal organization of the APAs.

APAs Accompanying Preferred and Non-Preferred Limb Movements

Literature about *lateralization* of motor control shows a greater skill in the PREF vs. NON-PREF side for arm, wrist and finger movements (Todor et al., 1982). Substantial differences were illustrated in the coordination of muscular recruitment and intersegmental torques in the two sides, which in turn implied a more efficient strategy for the dominant (PREF) arm (Sainburg and Kalakanis, 2000; Sainburg, 2014) as well as a right-hand superiority in task such as throwing (Watson and Kimura, 1989), and a superiority in control of body stabilization during rapid step initiation with the PREF-leg (Yiou and Do, 2010). In particular, Bagesteiro and Sainburg (2002) illustrated that the more efficient strategy for the dominant arm was associated to different EMG profiles and therefore, they suggested that manual asymmetries result from differences between the two sides in controlling the effects of limb dynamics (see also Oliveira and Sanders, 2015).

Little is known instead about APAs and lateralization, since the large majority of studies on APAs have been conducted on voluntary movements performed with the PREF hand/side. Only a few studies have addressed the lateralization question (e.g., Teyssèdre et al., 2000; Mezaour et al., 2009; Yiou and Do, 2010). Teyssèdre et al. (2000), as an example, investigated whether lateral preference for one upper limb could involve side differences in APAs of postural muscles, showing an earlier occurrence of APAs for pointing movements performed with the PREF upper limb, and concluding that lateral preference is associated with postural laterality.

On the other hand, with regard to the central organization of the postural control, it has been recently shown that the left hemisphere in right-handers was more involved in the predictive control of the body and the consequent environmental dynamics. Instead, the right hemisphere of the same subjects was more involved during the deceleration phase of motion, as an impedance control mechanism to terminate the movement (Yadav and Sainburg, 2014). Consequently, it could be argued that the enhanced predictive control of body and environmental dynamics, driven by the left hemisphere, led to the more efficient anticipatory postural strategy, as we observed in the PREF side of our right-handed subjects. Recently, by studying long-latency stretch reflexes as a mechanism that permits the postural control, it has been suggested that handedness affects more the feedforward strategies than those based on sensory feed-back (Walker and Perreault, 2015).

In summary, the *lateralization* of APAs observed in the present study is in accordance with all the above described articles and provides novel evidence in favor of a functional linkage between the timing of intra-limb APAs, the resulting stability of elbow joint and the ensuing precision of pen-pointing movements.

APAs and Precision

According to shooting coaches and athletes, good postural balance is a vital component of a successful shooting performance. During bipedal standing, top-level rifle shooters stabilized their whole body balance better than naive shooters (Aalto et al., 1990); the capability to reduce the oscillation, especially in the last few seconds before pulling the trigger, expresses the better control of posture in athletes and was associated with a better shooting performance (Era et al., 1996; Mononen et al., 2007). Ypsilanti et al. (2009) illustrated a better stabilization of the center of pressure (CoP) and an improvement in the movement precision for pointing movements performed with the PREF than NON-PREF upper-limb, but did not provide results regarding the APAs chain. More recently, Furuya et al. (2011) demonstrated that professional pianists tended to play using less muscular activity and to take greater advantage of shoulder joint rotation during a keystroke than did novice.

The idea that the precision of a voluntary movement relies on proper APAs was first proposed for what concerns the *inter-limb* APAs. To the best of our knowledge, this idea was forwarded by studies that analyzed the linkage between APAs and movement precision in pointing to targets of different sizes (Nana-Ibrahim et al., 2008; Bertucco and Cesari, 2010). However, these results might be an outcome of the relationship between APAs and intended movement speed (Shiratori and Aruin, 2007; Esposti et al., 2015), since the speed of voluntary movements varies as a function of the target width, according to the Fitts (1954) law. In order to get rid of the possible bias due to changes in movement speed, Caronni et al. (2013) studied inter-limb APAs during an upper limb pointing movement before and after donning prismatic lenses, which are known to shift the binocular eye field and cause the subject to miss the target (Redding et al., 2005). By using this experimental paradigm, these authors showed that, despite similar kinematics of the focal movement, pointing errors occurred when lower limb APAs were out of proportion with respect to the recruitment of prime mover muscles in the shoulder. It has been also recently demonstrated that training induce improvement in the correct tailoring of the APA chain with respect to the prime mover recruitment, both in young adults (Kanekar and Aruin, 2015) and elderly (Kubicki et al., 2012; Aruin et al., 2015). Thus, the increased precision of voluntary movement observed after training (Hamman et al., 1995; Yang et al., 2013) might be partly due to a more appropriate tuning of APAs on the prime mover recruitment. The linkage between APAs and movement precision was also suggested for *intra-limb* APAs by Caronni and Cavallari (2009). Indeed, these authors showed that when simulating an index-finger flexion using a software mechanical model of the arm, a clear disturbance of both focal movement and upper-limb posture was observed, with relevant changes at wrist and elbow level. In the model, the only way to prevent these effects was to block all segments but the finger, preventing the proximal joints from rotating (*fictive* APAs). Since this observation derived from a very simplified system, Caronni and Cavallari (2009) also looked for a more realistic model: a finger tap was thus evoked in a real arm by electrical stimulation of the median nerve. This experiment showed similar recordings to those predicted by the software mechanical model. However, both the software stimulation and the electrically evoked tap did

not faithfully represent the physiological pointing movement, since in the two cases no voluntary command was generated. Thus, considering that the experimental paradigm used in the present article involved subjects who voluntarily performed a pointing movement, present results are helpful for completing the framework originally proposed by Caronni and Cavallari (2009).

Further Considerations on the Motor Program for APAs and Prime Mover Recruitment

Present data should be discussed in the framework of the suggestion of a *shared motor command* for both APAs and prime mover recruitment (Aruin and Latash, 1995; Stapley et al., 1999; Leonard et al., 2011; Caronni et al., 2013). In particular, it was recently demonstrated that the intra-limb APAs stabilizing the arm when producing a brisk index-finger flexion were still present under an ischemic block of the forearm that suppressed the prime mover EMG, the finger movement and the related mechanical perturbation. Indeed, APAs remained tailored to the intended movement, i.e., to the expected perturbation, even after 60 movement trials in which that perturbation did not occur (Bruttini et al., 2014). Furthermore, in the same article, it was illustrated that intra-limb APAs were strongly attenuated when adding a fixation point to the wrist, i.e., closer to the voluntary moving segment (index-finger), a result that agrees with arm-pull experiments in standing subjects (Cordo and Nashner, 1982; Dietz and Colombo, 1996). Altogether, those results support the idea that the recruitment of postural and prime mover muscles should be driven by a *shared motor command*, according to a well-acquired pattern, which drives the muscular chain starting from the fixation point(s) and including the moving segment. Indeed, the shared motor command theory states that the central command to postural muscles and prime movers is "unique", so that the postural and voluntary components cannot be decoupled. However, this does not imply that a given voluntary command is always coupled to the same postural command. Thus, the observed time difference in postural commands between the PREF and NON-PREF limb can simply be the expression of a *badly* matched timing within the shared motor command (postural vs. focal components) in the NON-PREF side, which in turn may simply result from the reduced motor experience in that side. This latter interpretation seems the one to be PREF, also considering that a similar timing disruption was observed in some pathological studies, in particular for what concerns cerebellar dysfunction. Indeed ataxic patients, who typically display dysmetria (i.e., the inability to precisely reach a given target), showed a temporal disruption of intra-limb APAs both during finger flexions (Bruttini et al., 2015) and in the bimanual unloading task (Diedrichsen et al., 2005). Data from these pathological studies further strengthen the linkage between APA timing and movement precision we observed in the present study. Considering that physical exercise enhances APAs (Kubicki et al., 2012; Aruin et al., 2015; Kanekar and Aruin, 2015) and movement precision (Aalto et al., 1990; Era et al., 1996; Mononen et al., 2007), while a short-term immobilization alters the APAs control (Bolzoni et al., 2012), it is more than probable that training the NON-PREF side would effectively improve APAs timing and movement precision.

Taking into account all these considerations, the classical definition of APA (Massion, 1992) might be extended, for instance, to: motor activities *starting from a fixation point*, aiming to *produce the necessary dynamics* so as to *refine the precision and accuracy of a voluntary movement*, thus implicitly taking into account the perturbation induced by the primary movement.

CONCLUSION

Present results showed a lateralization of the intra-limb APAs stabilizing the arm when producing a pen-pointing movement. The APAs delay in movements performed with the NON-PREF hand, in comparison to the recordings of the preferred side, were associated to an impaired stability of the elbow joint, with similar kinematics of the focal movement in the two sides. As a result, the focal movement perturbation caused an increased elbow excursion in the NON-PREF upper-limb, eventually leading to the diminished movement precision on that side. These data strengthen the idea that the APA chain is essential for an appropriate stabilization of the joints involved in the posture-focal chain and therefore, allows refining the precision of the focal movement.

AUTHOR CONTRIBUTIONS

All authors contributed in conceptualizing and designing the experiment, acquiring and analyzing the data, interpreting the results and writing the article. All authors approved the final version and agree to be accountable for all aspects of this work.

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frontiers in Human Neuroscience

REVIEW
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APAs Constraints to Voluntary Movements: The Case for Limb Movements Coupling

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When rhythmically moving two limbs in either the same or in opposite directions, one coupling mode meets constraints that are absent in the other mode. Isodirectional (ISO) flexion-extensions of the ipsilateral hand and foot can be easily performed with either the hand prone or supine. Instead, antidirectional (ANTI) movements require attentive effort and irresistibly tend to reverse into ISO when frequency increases. Experimental evidence indicates that the direction dependent easy-difficult dichotomy is caused by interference of the anticipatory postural commands associated to movements of one limb with voluntary commands to the other limb. Excitability of the resting wrist muscles is subliminally modulated at the period of ipsilateral foot oscillations, being phase-opposite in the antagonists and distributed so as to facilitate ISO and obstacle ANTI coupling of the hand (either prone or supine) with the foot. Modulation is driven by cortical signals dispatched to the forearm simultaneously with the voluntary commands moving the foot. If right foot oscillations are performed when standing on the left foot with the right hand touching a fixed support, the subliminal excitability modulation is replaced by overt contractions of forearm muscles conforming the APAs features. This suggests that during hand-foot ANTI coupling the voluntary commands to forearm muscles are contrasted by APAs commands of opposite sign linked to foot oscillations. Correlation between the easy-difficult dichotomy and the APAs distribution is also found in coupled adduction-abduction of the arms or hands in the transverse plane and in coupled flexion-extension of the arms in the parasagittal plane. In all these movements, APAs commands linked to the movement of each limb reach the motor pathways to the contralateral muscles homologous to the prime movers and can interfere during coupling with their voluntary activation. APAs are also generated in postural muscles of trunk and lower limbs and size-increase when the movement frequency is incremented. The related increase in postural effort apparently contributes in destabilizing the difficult coupling mode. Motor learning may rely upon more effective APAs. APAs and focal contraction are entangled within the same voluntary action. Yet, neural diseases may selectively impair APAs, which represent a potential target for rehabilitation.

Keywords: APAs, limb movements coupling, in phase and antiphase coupling, direction principle, APAs destabilizing effects on coupling, coupled movements synchronization, motor learning/training

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INTRODUCTION

This review is concerned with a so far neglected aspect of the interaction between Anticipatory Postural Adjustments, APAs, and voluntary movements. Beside the APAs main function of assisting the execution of voluntary movements of any particular body segment, under defined circumstances APAs may result in the impairment of body movements. In particular, this occurs during coupled movements of the limbs and is especially apparent in rhythmic cyclic movements.

In many gestures of everyday life, e.g., handiworks, sport activities or music playing, the voluntary movements of different limb segments may be coupled into a variety of combinations. It is common experience that when oscillating a given couple of limbs in either the same or in opposite directions (in external coordinates), movements are easily performed in one coupling mode whereas coupling in the other mode is hampered. The evidence summarized here strongly suggests that the constraints selectively hindering one specific coupling mode, either the iso- or the antidirectional one, are generated by the APAs associated with the same voluntary limb movements.

The review is structured as follows. Sections *The "Direction Principle" in Coupling Flexion-Extension of the Ipsilateral Hand and Foot. Easy vs. Difficult Coupling Modes* and *Role of Kinesthetic Afferents from the Moving Segments in Controlling the Hand-Foot Synchronism during Coupled Movements: An Interlimb or Intralimb Feedback?* will describe the features of the hand-foot coupled movements and the mechanisms providing the control of movements synchronization. In turn, Sections *Neural Mechanisms Underlying the "Direction Principle" in Hand-Foot Coupling* and *Role of APAs in Differentiating ISO vs. ANTI Coupling Modes in Other Types of Limb Movements* will discuss experimental evidence of the selective APAs effects on coupling coordination in the above as well as in other couples of limbs. Section *Postural Constraints from Neuroscience to Sports and Rehabilitation Medicine* will discuss some potential implications of this knowledge in motor learning, force training, and rehabilitation.

Direction-Dependent Differential Coordination of Coupled Movements of the Limbs

The early observations on limb movements coupling [Müller, 1840; Meige, 1901; Noica (Bucarest), 1912] report that, when performing mirror movements like drawing circles in the air with the two hands in the parasagittal plane, it is quite easy to rotate the hands in the same direction, whereas circling the hands in opposite directions is difficult or even impossible.

For several decades this phenomenon did not attract further interest. On occasion of a seminar held by the first author over 30 years ago, Pietro Civaschi, a physiatrist at the Neurological Institute Carlo Besta in Milan, asked for some explanation about the striking preference of normal individuals to move two ipsilateral body segments together (for instance, the ipsilateral hand and foot in the parasagittal plane) in the same rather than in opposite directions. Having no explanation at that moment, the answer was to analyze the matter together, in the hope of gaining a deeper insight.

This review will summarize the results of the experimental series stemmed from that proposal. The successive steps of this research entered different fields of motor neurosciences and were reported in an irregular series of separate papers. Because of the time dispersion of the reports and the variety of methodological and conceptual approaches utilized, it seemed convenient to facilitate the interested reader by tracing in one review the logic route connecting the successive experiments, interpretations and hypotheses.

Three different combinations of coupled limb movements were studied (**Figure 1**): (1) coupled flexion-extension of ipsilateral hand and foot in the parasagittal plane; (2) coupled

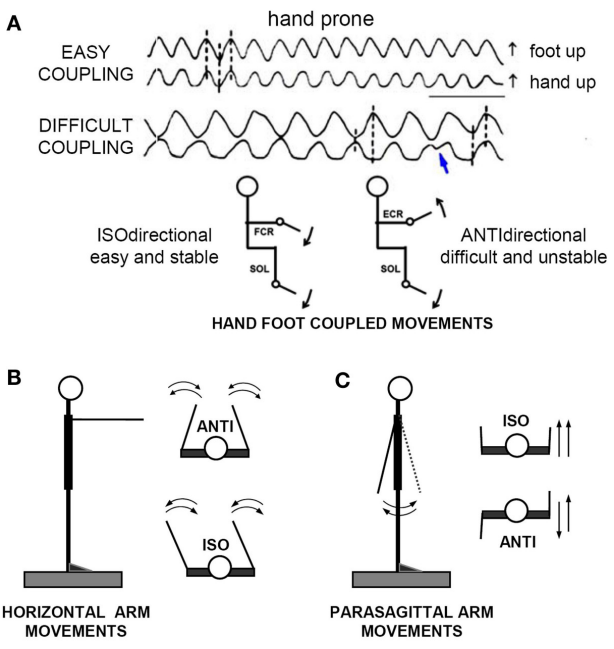

FIGURE 1 | The "direction principle" in hand-foot coupling. (A) Subjects seated on an armchair, with the forearms supported in horizontal position, either prone, or supine. The right hand and foot were fixed to basculating supports, free to cover full-range flexion-extensions of the wrist and ankle. Despite their lower frequency, the ANTIdirectional (difficult) oscillations spontaneously reverse (blue arrow) to the easier ISOdirectional coupling. Time calibration, 1 s. **(B,C)** Schematic illustration of ISO and ANTI coupling of the arm cyclic movements in the horizontal and parasagittal plane, respectively. Reproduced from Baldissera et al. (1982) © Elsevier 1982, with permission of Elsevier.

Abbreviations: Muscles: ECR, Extensor Carpi Radialis; FCR, Flexor Carpi Radialis; RPM, right Pectoralis Major; LPM, left Pectoralis Major; LFCR, right Infraspinatus; LIS, left Infraspinatus; RAD, right Anterior Deltoid; LAD, left Anterior Deltoid; RPD, right Posterior Deltoid; RLD, right Latissimus Dorsi; LPD, left Latissimus Dorsi; RES, right Erector Spinae; LES, left Erector Spinae; RIC, right Ischiocruralis; LIC, left Ischiocruralis; SOL, Soleus; TA, Tibialis Anterior. Neurophysiologic and mechanical variables: CMAPs, Compound Muscle Action Potentials; TMS, Transcranial Magnetic Stimulation; CoP, Center of Pressure; $\Delta\dot{V}O_2$, oxygen uptake; $\Delta\Phi$, interlimb relative phase; SD$\Delta\Phi$, Standard Deviation of the $\Delta\Phi$ variability.

adduction-abduction movements of the arms in the horizontal (transverse) plane and (3) coupled flexion-extension movements of the arms in the parasagittal plane.

The preferred coupling mode is isodirectional in movement types 1 and 3, and antidirectional in type 2. Substantial evidence was found that in all three movement types the direction-dependent dichotomy between preferred and non-preferred modes correlates with the distribution of the Anticipatory Postural Adjustments associated with the same movements.

For methodological, technical, and statistical details the original papers should be consulted.

THE "DIRECTION PRINCIPLE" IN COUPLING FLEXION-EXTENSION OF THE IPSILATERAL HAND AND FOOT. EASY vs. DIFFICULT COUPLING MODES

When asked to perform simultaneous rhythmic flexions-extension movements of the extremities in the parasagittal plane, in the way they feel the most easy and spontaneous, all subjects normally choose to keep the forearm prone and to rotate the extremities in the same angular direction[1] (isodirectional coupling, ISO), by synchronizing hand extension with foot dorsal flexion and hand flexion with foot plantar flexion (**Figure 1A**, uppermost traces).

If asked to increase the oscillations rate, all subjects are able to maintain the ISO coupling for more than 1 min even at the maximal possible rate (3–4 Hz). When requested to reverse the phase between the limbs (antidirectional coupling, ANTI, lower traces), the subjects generally stop briefly, restore the movements with some initial hesitation and/or errors, and are afterwards compelled to pay continuous attention to maintain the phase opposition. Any attention release, as well as any attempt to increase the movement frequency, eventually leads to a breaking point, beyond which the association reverses to the isodirectional pattern (blue arrow). Transitions is abrupt or preceded by a progressive shift of the interlimb phase difference, and occurs after a time that progressively shortens as the movement frequency increases: continuing for more than 10 s is impossible beyond a critical frequency that ranges between 1.2 and 2.5 Hz in different individuals.

Finally, when invited to repeat the task with the hand supine, all subjects confirm their preference for ISO coupling, now associating hand flexion to foot dorsal flexion and hand extension to foot plantar flexion. The determinant factor of coupling preference seems therefore to be the movements reciprocal direction (*direction principle*, Baldissera et al., 1982) and not a stable pattern of parallel innervation of specific muscles in the forearm and the leg.

Coupling Coordination: Accuracy and Stability of the Interlimb Relative Phase

In the following years studies on limb coupled movements increased in number and the "direction principle" was found to hold in many other types of coupled movements of ipsilateral limbs (cfr Baldissera et al., 1982, 1991, 1994, 2000; Baldissera and Cavallari, 2001; Kelso and Jeka, 1992; Carson et al., 1995; Jeka and Kelso, 1995; Swinnen et al., 1995; Serrien and Swinnen, 1998), bilateral limbs (cfr. Kelso, 1984; Carson, 1993; Swinnen et al., 1995; Serrien and Swinnen, 1998; Swinnen, 2002) and also different segments within one limb (for instance flexion-extension of the wrist with flexion-extension of the elbow, as earlier recognized by Kots et al., 1971). As a general rule, one given coupling mode, in some occasions ISO and in others ANTI, is easily performed, subjectively preferred and better co-ordinated; whereas the opposite mode is difficult to perform (thus, non-preferred) and less coordinated. *Easy* and *preferred*, as well as *difficult* and *non-preferred* will be used hereafter as synonyms.

Kelso's theoretical elaboration (Haken et al., 1985, see Presentation 1 in the Supplementary Material) assimilates the coupled oscillations of two limbs to those of a system of non-linear oscillators moving in one of two stable states (in phase or in phase opposition) with different levels of stability. This model stresses the centrality of the *interlimb relative phase*, $\Delta\Phi$, as being the collective variable that describes the qualitative changes in pattern coordination. In real movements the $\Delta\Phi$ variability, i.e., the coupling instability, is expressed by its standard deviation, $SD\Delta\Phi$. The latter is positively related to the oscillation frequency and it is higher in the difficult (non-preferred) compared to the easy (preferred) coupling mode. Based on this observation, when the movement frequency, and thus $SD\Delta\Phi$, reaches to a critical level, the model shifts by 180° from the unstable to the stable state. Accordingly, the values of $SD\Delta\Phi$ indicate for each value of the movement frequency the degree of coupling instability, and thus the difficulty in contrasting the phase reversal.

Mechanical Differences between the Limbs and Neural Compensation for Their Desynchronizing Effect on Coupled Movements

In order to understand the mechanistic origin of the differences in coordination stability between the two coupling modes, two interlaced aspects needed to be analyzed. First, how synchronization between the limbs is achieved and how this is influenced by the limb mechanical properties; second, why the interlimb coordination varies when the coupling mode is reversed. A response to the first question is proposed in Section *Role of Kinesthetic Afferents from the Moving Segments in Controlling the Hand-Foot Synchronism during Coupled Movements: An Interlimb or Intralimb Feedback?*. In Sections *Neural Mechanisms Underlying the "Direction Principle" in Hand-Foot Coupling and Role of APAs in Differentiating ISO vs. ANTI Coupling Modes in Other Types of Limb Movements* evidence will be presented suggesting that the constraints to the "difficult" mode depend on the directional distribution of the anticipatory postural adjustments associated with the primary movements.

Mechanical Characteristics of the Hand and Foot Oscillations

The oscillations of the hand (Stark, 1968; Stiles et al., 1983; Lakie et al., 1984; Lehman and Calhoun, 1990) and foot

[1]Throughout this review the movement direction will always be referred to external coordinates.

(Hunter and Kearney, 1982) can be satisfactorily modeled by a 2nd-order system (a pendulum) with lumped parameters (mass, stiffness, and viscosity). During passive oscillations, the unloaded hand behaves like a simple mass (negligible elastic and viscous momenta) but when the wrist is pre-loaded it behaves like a mass-spring system (Lehman and Calhoun, 1990). Also during voluntary cyclic flexion-extension of the wrist (Bobet and Norman, 1990) and elbow (Viviani et al., 1976), the phase relationships between the movers EMGs and the joint position approximate those of an ideal pendulum.

Accordingly, should two limbs share identical mechanical properties and be moved by homologous muscles (e.g., flexion-extension of the two hands), a common rhythm generator sending one and the same motor command in parallel to both segments (Schmidt et al., 1979; Turvey et al., 1989) would obtain a correct coupling at all frequencies. If instead the two limbs have different mechanical features, as it is the case for the hand and foot, the oscillations of the two limbs induced by a parallel synchronous command will have different phase delays with respect to the command itself. Moreover, the interlimb phase difference would increase as the movement frequency is raised.

Based on the greater mass of the foot compared to the hand, one would predict that, when driven by a common command, the foot oscillations are phase-delayed with respect to the hand by an extent proportionate to the movement frequency. In fact (Baldissera et al., 2000), the hand movements cycle slightly lags the required synchronism with the foot cycle (namely 0° in ISO and 180° in ANTI) by an almost constant value over the entire frequency range (**Figure 2A**). Correspondingly (compare **Figure 2B** and **Figure 2C**), as the frequency is raised the onset of the EMG activity in forearm muscles (*Extensor Carpi Radialis,* ECR) progressively phase-advances the EMG onset in leg muscles (*Tibialis Anterior*, TA). This occurs in both coupling modes.

These findings would indicate that: (1) the mechanical impedance is greater for the hand than for the foot, despite the smaller mass of the hand; and (2) when the movement frequency is raised, the increase of the hand-foot delay is avoided by a progressive phase advance of the EMG burst in ECR with respect to TA, demonstrating that a neural mechanisms has intervened to counteract the desynchronizing effects of the mechanical disparities.

In conformity with the afore mentioned pendulum model (see features and details in Presentation 2 in Supplementary Material), the input-output phase relations of each limb were derived (Baldissera et al., 2000, 2004; Esposti et al., 2005) from the frequency-dependent changes of the phase delay between the onset of the EMG activity in the movement prime movers (input) and the homologous instant of the related movements (output).

The frequency responses of both the hand and the foot fit the pendulum equation. The foot response, however, shows a slower decay and a higher value of the ratio $\sqrt{K/I}$ (the resonant frequency) compared to the corresponding response of the hand, indicating that the larger mass of the foot is naturally associated with an even larger active stiffness. This difference will justify the smaller EMG-movement lag in the foot than the in hand illustrated in **Figure 2C**.

ROLE OF KINESTHETIC AFFERENTS FROM THE MOVING SEGMENTS IN CONTROLLING THE HAND-FOOT SYNCHRONISM DURING COUPLED MOVEMENTS: AN INTERLIMB OR INTRALIMB FEEDBACK?

The neural control mechanisms that compensates for the desynchronizing effects of the mechanical disparities between

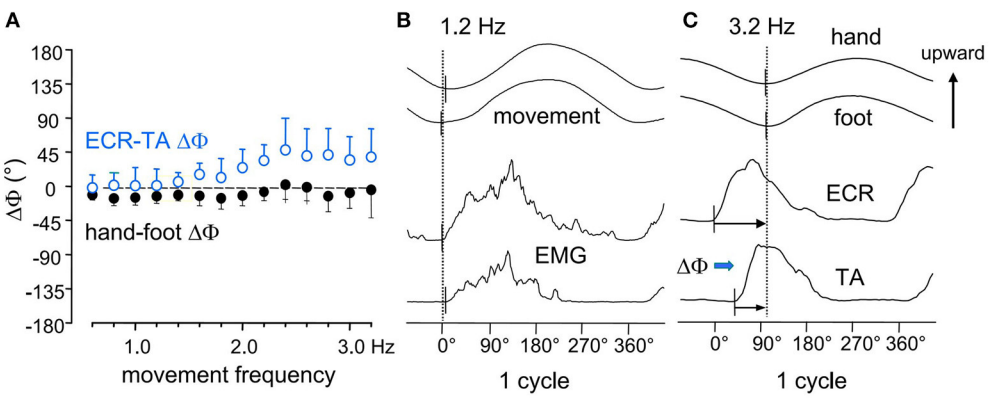

FIGURE 2 | (A) the phase difference between the two movements (*hand-foot* $\Delta\Phi$, filled black circles) remains mostly unmodified over the entire frequency range. **(B)** at 1.2 Hz the upward rotation of the two limbs and the onset of the integrated EMGs in the respective movers *ECR, Extensor Carpi Radialis*; *TA*, *Tibialis Anterior*, all start synchronously. **(C)** at 3.2 Hz, both movements lag the EMG burst onsets, the hand to a larger extent than the foot (black arrows), revealing that the two limbs have different mechanical features. This difference, however, is compensated for by a calibrated advance of the ECR on the TA burst *(ECR-TA* $\Delta\Phi$, blue arrow) which increases with frequency (open circles in A) and maintains the movements synchronism. Reproduced from Baldissera et al. (2000), © Springer-Verlag Berlin Heidelberg 2000, with permission of Springer.

the limbs might theoretically monitor the deviations of the instantaneous hand-foot relative phase, $\Delta\Phi$, from the programmed value (0° or 180°) and use these error signal for recovering the intended synchronism. Alternatively, each oscillating limb might be provided with an independent neural control which monitors the position of that limb and reacts so as to eliminate any phase mismatch between the rhythmic central command and the actual movement. The functional difference between these two mechanisms lies in the fact that the first one would tend to keep the interlimb relative phase constant whilst being unable to control the synchronization of the limbs oscillations with the central rhythm generator; while the second mechanism would simultaneously achieve both results. Distinguishing between these two mechanisms was attempted by two complementary approaches.

First, the existence of a crossed kinesthetic feedback between the limbs was explored by testing whether the afferent signals generated during voluntary oscillations of one limb may induce excitability changes in the motor structures innervating the second, resting limb. Second, the phase synchronization of the hand and foot oscillations with an external clock signal was measured both when the two segments were moved in isolation and when they were coupled, either iso- or antidirectionally. This allowed to test whether the clock-movement phase-delay, measured when one limb is moved alone, changed as the two limbs were coupled, thus proving that one limb can influence the other in controlling the interlimb synchronization.

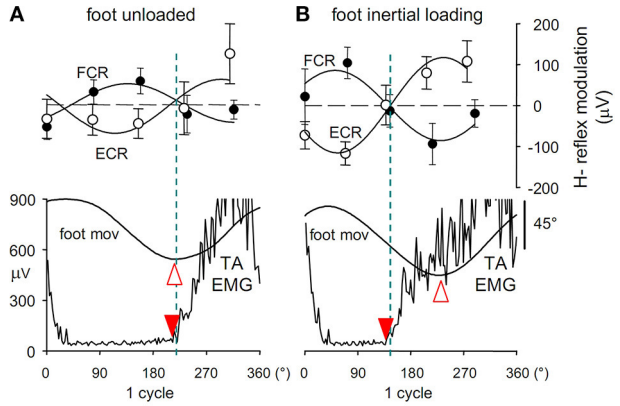

FIGURE 3 | (A) Cyclic modulation the H-reflex size, phase-opposite in the two forearm antagonists *ECR* (open circles) and *FCR* (filled circles), at 5 delays during ipsilateral foot oscillations.Modulation is expressed as the absolute deviation of the reflex size from the cycle mean value and is plotted together with the angular position of the ipsilateral foot (*foot mov*, dorsal flexion up) and the EMG activity in TA muscle (*TA EMG*). Best-fit sinusoidal functions (solid lines) with the same period as movement are superimposed to the H-reflex plots. Crossing between the two H modulation sine waves (dashed blue line) occurs almost synchronously with both the foot flexion peak (open arrowhead) and the onset of TA activation (filled arrowhead). After foot inertial loading **(B)** the foot flexion peak lags the onset of the TA burst by about 90°, while the H-reflex modulation remains phase-linked to the TA activation, showing to be insensitive to the afferent signals monitoring the phase shift of the foot position. Figure assembled with data from Cerri et al. (2003) and Borroni et al. (2004).

Modulation of Motoneuronal Excitability in the Resting Forearm Muscles during Voluntary Oscillations of the Ipsilateral Foot

The excitability of wrist flexor and extensor muscles in the resting forearm was tested during voluntary oscillations of the ipsilateral foot, so as to ascertain whether it was modified by the foot movements (Baldissera et al., 2002).

Indeed, during foot oscillations the size of the H-reflex evoked in the resting *Flexor Carpi Radialis* (FCR) undergoes a sine-wave modulation with the same period as the foot movements (**Figure 3A**). With the forearm in prone position, the FCR H-reflex (filled circles) is facilitated during foot plantar flexion and dis-facilitated during dorsiflexion, while a phase-opposite H-modulation is seen in the antagonist *Extensor Carpi Radialis*, ECR (open circles). Moreover, when the forearm position is changed from prone to supine, the modulation in both ECR and FCR shifts by 180° with respect to the foot movement, thus maintaining the phase opposition in the two antagonists (Borroni et al., 2004; Byblow et al., 2007).

Should these subliminal excitability changes in forearm flexor and extensor motoneurons occur when the hand is moved together with the foot, they would have the same sign (excitatory or inhibitory) as the simultaneous voluntary commands to forearm muscles during ISO coupling; and an opposite sign in ANTI coupling, thus favoring the former and contrasting the latter coupling mode. Moreover, this pattern would hold both when the hand is prone and when it is supine, in agreement with the "direction principle" of hand-foot coupling.

The compound muscle action potentials (CMAPs) evoked in FCR and ECR muscles by transcranial magnetic stimulation (TMS) of the primary motor cortex are also modulated in size during foot oscillations, with the same time course of, but more strongly than, the H-reflex. Finally, interactions between the corticospinal and the Ia afferent effects (Baldissera et al., 2002) convincingly prove that the changes in motoneurons excitability associated with foot oscillations have a cortical origin.

Similar results were also obtained by other investigators in the context of bimanual coupling. In sitting subjects with the hands in semiprone position, Carson et al. (2004) found that the amplitude of the H-reflex and CMAPs in the resting FCR muscle is cyclically modulated during rhythmic oscillations of the contralateral wrist in the horizontal plane. Further, by analysing the EMG spectrogram, Ridderikhoff et al. (2005) found evidence for bursting activity in the resting ECR that occurs in phase with the extension of the contralateral wrist. Also in these cases the excitability modulation would favor the preferred coupling mode, which is mirror symmetrical (ANTI in external coordinates) in these hand movements.

Altogether, these results seemingly supported the working hypothesis that the kinesthetic signals for position (and/or velocity) from one limb cyclically activate the corticospinal projections to the other limb, thereby modulating the motoneuron excitability. Through this mechanism, the afferent

signals from the foot might in fact interfere—either positively or negatively according to the coupling mode—with the generation of the voluntary cortical commands to the hand.

This conclusion was soon falsified, however. Since application of an inertial load to the foot, as well as raising the frequency of foot movements, both increase the phase-delay of the foot oscillations with respect to the motor commands (Section *The "Direction Principle" in Coupling Flexion-Extension of the Ipsilateral Hand and Foot. Easy vs. Difficult Coupling Modes* and Presentation 2 in Supplementary Material), it was argued that if the H-reflex modulation at the forearm was driven by the kinesthetic information from the moving foot, if would remain phase linked to the foot rotation. Instead (Cerri et al., 2003), after both loading (**Figure 3B**) and/or increasing the oscillation frequency, the H-modulation in the forearm muscles remains tightly linked to the voluntary motor command, thus anticipating the foot movement. This finding disproves that the cyclic excitability modulation in forearm motoneurons is elicited by the afferent signals that transduce the foot rotation and suggests that it is instead generated in the forearm area of the primary motor cortex simultaneously with the voluntary commands dispatched to the foot. The view that the interlimb relative phase is controlled through an interlimb afferent feedback is then seriously challenged. The possibility remains, however, that the hypothesized crossed feedback was hidden in this experiment because it is only activated when both limbs are oscillated together.

If this were to be the case, however, the different mechanical properties of the two segments would imply that, when each segment is moved alone, the movement phase delay with respect to an external clock (*clock-mov delay)* is different in each limb, and that such difference increases as the oscillation frequency is raised. Consequently, achieving the movements synchronization during coupling through a crossed kinesthetic feedback would necessarily modify the "intrinsic" *clock mov-delay* of either one of the two limbs or both.

Independent Position Control of Each Limb by a "Private" Kinesthetic Feedback

As depicted in **Figure 4A** (Baldissera et al., 2006), the *clock-mov delay* of both the hand and the foot remains almost constant when the frequency is increased (negative values = movement delay) and is not significantly different when the limbs are moved in isolation (green solid and dashed lines) or when they are isodirectionally coupled (hand: blue circles, foot: red triangles). Enhancing the mechanical difference between the limbs, e.g., by connecting the hand to an inertial load (**Figure 4B**), does increase the hand phase delay with respect to the foot but is ineffective in dividing the phase curves obtained when the hand is moved alone and when it is coupled. All this holds true for antidirectional coupling too. Further details on these measurements are given in Presentation 3 in Supplementary Material.

In conclusion, the phase delay with respect to a common time-giver is apparently controlled in each limb independently from what simultaneously occurs in the other limb, even after artificially enhancing the mechanical disparity between the limbs.

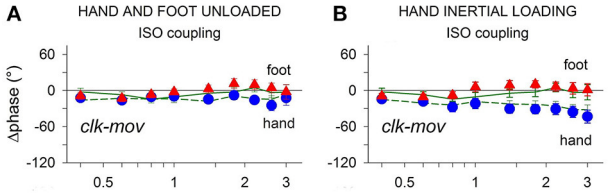

FIGURE 4 | Frequency dependent changes of the *clock-mov* phase-delay during separate oscillations of the hand and foot (green dashed and continuous lines, respectively) and during hand-foot ISO coupling (hand, blue circles; foot, red triangles). (A) When both limbs are unloaded the *clk-mov* delay of each limb, no matter whether isolated or coupled, remains nearly constant over the whole frequency range. **(B)** same relations as in **(A)** but obtained after applying an inertial load to the hand. Loading induced the expected increase of the hand *clk-mov* delay as the frequency is raised but in either limb the frequency relations obtained during separate and coupled movements still superimpose. Reproduced from Baldissera et al. (2006), © 2006 Baldissera et al; licensee BioMed Central Ltd.

The control of the interlimb relative phase will thus directly result from the efficacy of the separate phase controllers of each limb.

The synchronism control of each individual limb may possibly be operated through a "private" kinesthetic feedback which provides matching of the limb movements with the motor commands linked to the central time giver. A neuro-mechanical model that faithfully simulates the operations of such a feedback (Esposti et al., 2007) is illustrated in Presentation 4 in Supplementary Material.

Added to the previously discussed evidence that the excitability changes in forearm motoneurons during foot movements are not generated by afferent signals, these last results should definitely rule out the hypothesis that the coupling coordination is achieved by a crossed kinesthetic feedback between the limbs.

NEURAL MECHANISMS UNDERLYING THE "DIRECTION PRINCIPLE" IN HAND-FOOT COUPLING

Altogether, the results reported in Section *Role of Kinesthetic Afferents from the Moving Segments in Controlling the Hand-Foot Synchronism during Coupled Movements: An Interlimb or Intralimb Feedback?* enlighten both issues presented in Section *Mechanical Differences between the Limbs and Neural Compensation for their Desynchronizing Effect on Coupled Movements*. On one side, they indicate, in a way consistent with basic physical and neurophysiological concepts, that the limbs relative phase results from an independent synchronization of each limb movement with the common clock signal. On the other side, these results also show that during foot voluntary oscillations the commands that move the foot are associated with descending subliminal commands to the "isodirectional" muscles in the resting forearm, distributed so as to facilitate ISO and contrast ANTI coupling both in the prone and supine forearm position.

Once excluded that the effects onto the resting forearm are generated by the kinesthetic afferents that monitor the foot movements, it remained to understand which physiological role these effects may have within the frame of motor control. A survey of the known motor mechanisms led to the idea that they may carry Anticipatory Postural Adjustments, APAs.

Anticipatory Postural Adjustments (APAs) as Possible Candidates for Generating the Subliminal Excitability Modulation in Forearm Muscles during Foot Oscillations

Albeit in different conceptual and experimental contexts, the modulation of motoneuron excitability in one limb during voluntary movements of another limb had been described since several years, and explicitly discussed in many instances as due to APAs (Kasai and Komiyama, 1996; Kawanishi et al., 1999; Hiraoka, 2001).

APAs (Marsden et al., 1978, 1981; Cordo and Nashner, 1982; Bouisset and Zattara, 1987; Zattara and Bouisset, 1988; Bouisset and Do, 2008), are unconscious muscle contractions aimed at preparing fixation chains linking the segment(s) to be consciously moved to one or more firm supports, where the reaction forces to the prime movers contraction can develop (third Newton's principle) without producing any displacement. In this way it is determined which of the body segments connected by the prime movers will actually move. In the absence of a firm support, APAs will produce counter-movements that contrast the postural unbalance produced by the consciously intended movement (also said the "focal" movement). However counterintuitive it may appear, the unconscious APAs are yet a necessary and fundamental component in the generation and control of the "willed" movements.

In EMG recordings, APAs are characterized by the combined activation of muscles in one or more fixation chains, simultaneously with, or in slight advance to, the prime movers contraction. APAs scale in size with the magnitude of the primary movement (Aruin and Latash, 1996), they are influenced by the position and number of the fixation points (Slijper and Latash, 2000) and by tactile and proprioceptive information (Slijper and Latash, 2004). Also, their timing and spatial distribution may vary when the surround conditions or some feature of the movement (e.g., the direction) are changed (Cordo and Nashner, 1982; Nashner and Forssberg, 1986; Aruin and Latash, 1995). Of direct relevance in the present context are the facts that during flexion/extension of the wrist the APAs in proximal arm muscles are directionally organized (Chabran et al., 1999, 2001) and, even more interesting, that they are generated in elbow flexors when the forearm is supine but in elbow extensors when it is prone (Aoki, 1991), showing that APAs action is "isodirectional" with the primary "focal" movement whatever the forearm position.

In the past years, interest for APAs has been mainly focused on their role in stabilizing the body equilibrium, while a minor attention was devoted to their general function of providing firm support to any moving segment. For instance, the interactions between coupled limb movements and the overall body posture have been examined looking at the effects exerted by the coordinated movements on the stability of body balance (Ferry et al., 2004; Ustinova et al., 2004; Forner-Cordero et al., 2007). Here, instead, we will focus on the less investigated effects of postural anticipatory adjustments on coordination of voluntary movements (cfr. Yiou, 2005; Yiou and Schneider, 2007; Yiou et al., 2007, for the interactions between the postural dynamics elicited by arm pointing and the step initiation).

APAs Generated in Forearm Muscles during Movements of the Ipsilateral Foot Reproduce the Same Distribution Pattern as the Subliminal Modulation

Convincing experimental evidence supports the hypothesis that the subliminal excitability changes in forearm muscles linked to the ipsilateral foot oscillation should be recognized as APAs.

When sitting on an armchair, as in the standard experiments on hand-foot coupling, body fixation is mainly obtained through the large contact surface of the posterior aspect of trunk and thighs with the seat. This would strongly attenuate the postural role of the forearm contact with its support, so that only small or subliminal APAs should develop in forearm muscles, perhaps corresponding to the excitability changes described in Section *Neural Mechanisms Underlying the "Direction Principle" in Hand-Foot Coupling*. Enhancing the forearm postural role might then transform those subliminal changes into manifest contractions.

Consider the following experiment. The subject stands upright, with the left foot on a stable surface, the right foot on a pivoting platform and the right arm protracted with the hand contacting a rigid support (inset of **Figure 5**) so as to increase the postural role of the right arm. In this asset, the cyclic flexion-extension of the right foot, which entails the risk of a forward/backward fall, is indeed counteracted by a cyclic activation of the forearm flexor and extensor motoneurons which has the same period as the foot movement (Baldissera and Esposti, 2005). If the hand is prone and in palmar contact with the support (**Figure 5A**), the positive phase of the modulation in FCR is coincident with the contraction of the plantar flexor SOL. Conversely, if the hand contact is dorsal (**Figure 5B**), activity is modulated in ECR and its positive phase coincides with the activation of TA. With the hand supine the above pattern reverses (**Figures 5C,D**).

If cyclic foot oscillations are replaced by fast flexion or extension movements, single EMG bursts fulfilling the APAs requisites develop in the "isodirectional" forearm muscles, together with a simultaneous depression of the background activity (when present) in the antagonists (**Figure 6**).

The strict topographical superimposition of these canonically identified APAs with the cyclic EMG activities and the subliminal excitability modulation observed when sitting would indicate that they share the same nature, even if one cannot exclude that the cyclic effects include reflex components too (see also later).

In summary, during single and cyclic foot movements and irrespective of the movement direction (plantar or dorsal flexion) and forearm position (prone or supine), excitatory burst or cyclic contractions, respectively, arise in those forearm muscles

that rotate the hand isodirectionally with the foot, providing a subsidiary postural support at the hand contact. Matching these overt activities with the subliminal excitability modulation observed in the sitting position suggests that they represent two grades of one and the same event, i.e., the preparation of a fixation chain connecting the moving foot to the firm hand support. It seems therefore apparent that even when a manifest intervention of anticipatory postural adjustments is not required, subthreshold APAs may nevertheless develop, which can only be disclosed by instrumental excitability testing; and that, depending on the body postural needs, the subliminal changes can be transformed into overt APAs and viceversa.

To mechanistically explain this APAs flexibility it was imagined (Baldissera and Esposti, 2005) that any given voluntary movement is associated with the co-activation of an arborized pattern of postural commands directed toward a number of possible fixation points; and that activation of the arborization branches is supraliminal in those directed to the segments providing actual support and subliminal in those not involved at the moment in that function. Within this organization, the control of APAs might consist, from time to time, in amplifying transmission to certain targets and attenuate transmission to others, a task that could be automatically accomplished by low-level mechanisms based on afferent information.

Indeed two experimental observations support this view. On one side, studies on the feline reticulospinal neurons candidate for APA transmission (Schepens and Drew, 2004, 2006; Schepens et al., 2008) disclosed that on occasion of single forelimb movements a widespread postural activity is induced from the motor cortex in reticulospinal neurons. Such activity is then restricted to the motoneurons actually involved in postural support by selectively gating (inhibiting) at the spinal level the transmission of the APA commands to the other motoneurons, so that they remain available for voluntary activation. On the other side, in man, when two supports are available and one of the two fixation chains is voluntarily privileged, activation of the second chain is proportionally attenuated (Esposti and Baldissera, 2011) This shows that gating of the APAs commands does not take place in all-or-none fashion but is modulated in a coordinated way in the different chains.

This organization would create a pattern of subliminal activation of the motor pathways to those body segments that are not (but may potentially be) used for postural support. Even when they are subliminal, the forearm APAs described

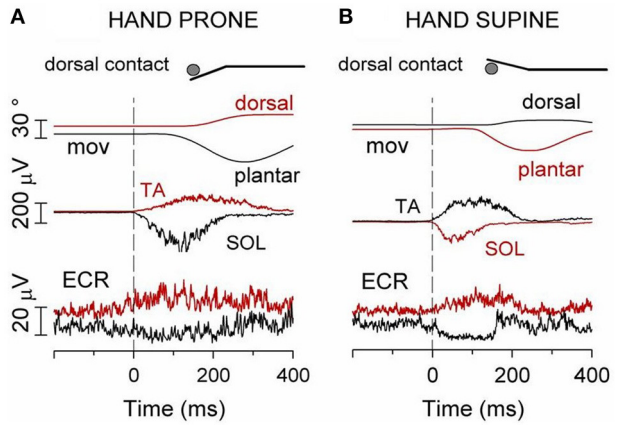

FIGURE 6 | (A) Hand prone, dorsal contact. Red traces: TA contraction and the ensuing foot dorsal flexion are preceded by an excitatory APA in ECR, the "isodirectional" mover of the hand. Black traces: contraction of SOL and foot plantar flexion are preceded by an inhibitory APA in ECR. **(B)** Hand supine, dorsal contact. Red traces: an excitatory APA in ECR precedes contraction of the "isodirectional" SOL and foot plantar flexion. Black traces: when the movement direction is inverted to dorsal, ECR becomes "antidirectional" to SOL and the APA changes to inhibitory. Reproduced from Baldissera and Esposti (2005) © Wolters Kluwer Health, Inc. 2005, with permission of Wolters Kluwer Health, Inc.

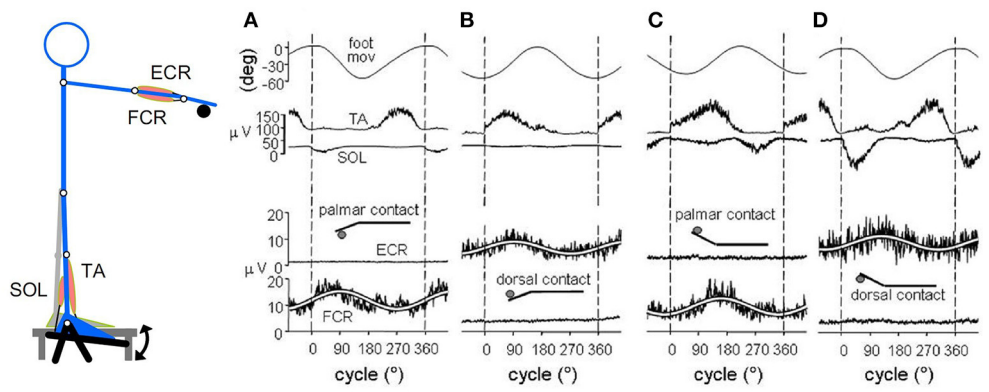

FIGURE 5 | When standing on the left foot, with the right hand touching a fixed support (inset), cyclic oscillations of right foot modulate sinusoidally the EMG activity of ipsilateral wrist muscles at the frequency of the foot movement (1.5 Hz). Soleus (SOL) EMG reversed. **(A)** hand prone, palmar contact; FCR EMG is cyclically modulated, the positive phase coincides with SOL activation. **(B)** dorsal contact; the positive phase of the ECR EMG modulation coincides with TA activation. **(C,D)** hand supination reverses the above pattern. In this and the following figures the white lines superimposed to the EMG recordings are the best fit sine-waves with the same period as the movements. Reproduced from Baldissera and Esposti (2005) © Wolters Kluwer Health, Inc. 2005, with permission of Wolters Kluwer Health, Inc.

above might selectively contrast the voluntary co-activation of "antidirectional" foot and hand movers: hence the necessity of suppressing APAs by gating. In this perspective, the gating mechanism would be central in determining the hand-foot coupling preference since its attenuation or default would selectively hamper the ANTI movements.

Imagine that during flexion-extension of the right foot one needs, or wants, to simultaneously move a body segment—for instance the right hand—that belongs to one of the fixation chains that actually assist the foot movement. Following this decision, the forearm muscles would be simultaneously targeted by both the voluntary command moving the hand and the APAs command linked to the foot movement, thus being called to function as prime movers and as postural muscles at the same time.

Being dispatched to the same target, the voluntary and the APAs commands will converge at some, yet unknown, level of the motor pathways to forearm muscles. When voluntary and APA actions are isodirectional, i.e., when the postural and the voluntary commands have the same sign (either excitatory or inhibitory) this convergence will favor both actions and the previously described double goal will be met. Conversely, when the voluntary and the postural actions have opposite directions, a conflict will be generated, which may be avoided only if either the voluntary command or the APA command is suppressed. An example of voluntary movement suppression is the irresistible transition from the difficult to the easy coupling mode (Section *The "Direction Principle" in Coupling Flexion-Extension of the Ipsilateral Hand and Foot. Easy vs. Difficult Coupling Modes*). The alternative intervention, i.e., the APAs suppression aimed to free the voluntary mobilization, cannot regard a main fixation chain without challenging the steady equilibrium but it might allow voluntary activation of those muscles that actually have a minor postural function (like forearm muscles when sitting on a chair).

In conclusion, in hand-foot coupling a neural conflict between APAs and voluntary commands may occur in the motor pathways to the prime movers when the two segment are moved in opposite angular directions. The entity of the conflict should in turn depend on the APAs size, i.e, on the functional relevance of the fixation chain in which the prime movers are actually included.

ROLE OF APAS IN DIFFERENTIATING ISO vs. ANTI COUPLING MODES IN OTHER TYPES OF LIMB MOVEMENTS

In the practical impossibility of collecting from human experiments more detailed and direct evidence concerning the intimate neuronal mechanisms of the interaction between postural and voluntary actions, it seemed reasonable to search for further indirect evidence supporting the interpretation proposed for hand-foot coupling. Considering that APAs generation is intrinsic to every voluntary movement, it was decided to test whether the correlation between APAs distribution and coupling preference is also observed in other types of coupled limb movements, so as to represent a general rule of motor control.

A suitable experimental model to start exploring the reliability of this idea are the coupled movements of the arms, performed in either the horizontal (transverse) or the vertical (parasagittal) plane. Indeed, in both types of movements the moving masses and the available fixation chains remain the same, but changing the plane of arms motion would produce a topographical re-distribution of the reaction forces and moments and, consequently, of the APAs. Assuming the coupling stability to be correlated with the APAs distribution and size, it would be expected to observe stability to vary in agreement with the intervening changes in the APAs pattern.

Verifying the above idea implied measuring in the four coupling combinations, i.e., horizontal ISO (*hISO*) and ANTI (*hANTI*) and parasagittal ISO (*pISO*) and ANTI (*pANTI*), (1) the variability of the movements relative phase, SD$\Delta\Phi$ (i.e., the reciprocal of coupling stability, see Section *The "Direction Principle" in Coupling Flexion-Extension of the Ipsilateral Hand and Foot. Easy vs. Difficult Coupling Modes*), to be matched, in each coupling combination, with (2) the distribution of the postural adjustments associated with unidirectional and cyclic arm movements.

Coupling Coordination of ISO vs. ANTI Cyclic Movements of the Arms in the Horizontal and Parasagittal Planes

A directional easy-vs.-difficult polarization is found in arm coupled movements performed in either plane of motion, being however opposite in horizontal movements (ANTI vs. ISO) with respect to parasagittal movements (ISO vs. ANTI) (Baldissera et al., 2008b; Baldissera and Esposti, 2013). Indeed SD$\Delta\Phi$ is lower (i.e., coupling stability is higher) in *hANTI* and *pISO* than in both *hISO* and *pANTI*. No significant SD$\Delta\Phi$ difference is found between the two easy modes while SD$\Delta\Phi$ is higher in *hISO* than in *pANTI*. Consequently, the stability loss between easy and difficult coupling is larger in horizontal than in parasagittal movements. Summing up, the instability (difficulty) of the four movement combinations, as evaluated by SD$\Delta\Phi$, increases along the scale $hANTI \neq pISO < pANTI < hISO$.

APAs Associated with Arm Movements in the Horizontal and Parasagittal Plane

The reaction forces to movements of one arm in either the horizontal or parasagittal planes, are discharged by two main fixation chains, to the contralateral arm and to the ground, respectively (cfr. **Figure 7** for horizontal movements).

The relative engagement of each chain varies according to the body asset. In the standing position, the major anticipatory postural activation usually develops in muscles of the chain to the ground, but when the ground surface is slippery (e.g., iced), or when sitting on a turnable chair, the role of APAs in muscles of the contralateral arm becomes relevant.

Distribution of the muscular and mechanical APAs linked to unidirectional movements of one and, more rarely, both arms was already reported by several authors (e.g., Belen'kii et al., 1967; Friedli et al., 1984; Bouisset and Zattara, 1987; Zattara and Bouisset, 1988; Aruin and Latash, 1995; Hodges

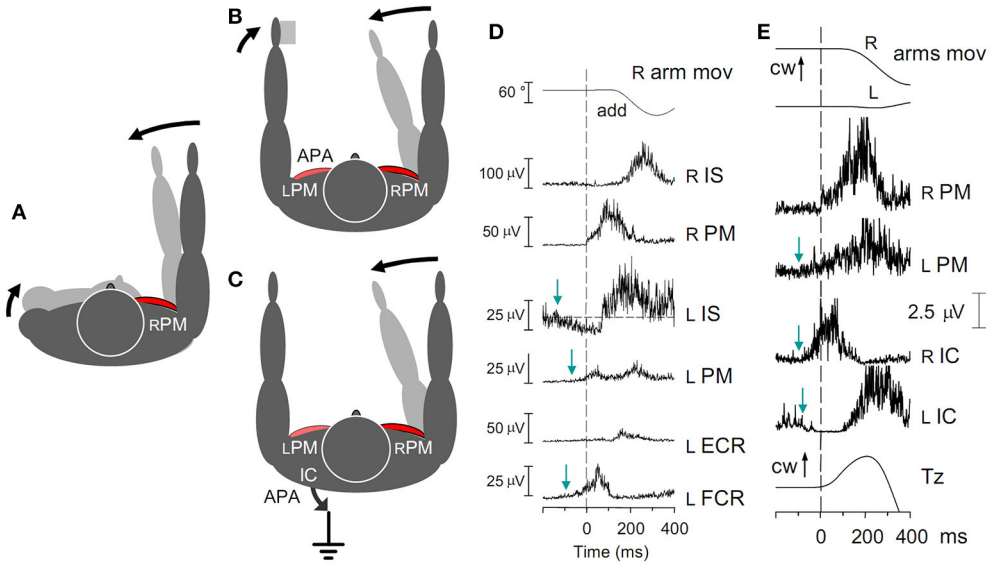

FIGURE 7 | (A) Contraction of the right RPM in the absence of any fixation chain would counter-rotate the right arm and the trunk. A pure arm movement is obtained if the trunk rotation is opposed by APAs in the fixation chain between the arms **(B)** and/or to the ground **(C)**. **(D)** Fast adduction of the right arm in the horizontal plane, prime mover right RPM. Subject sitting on a turnable chair, palmar surface of the left hand touching a fixed support. Excitatory APAs develop in left arm muscles LPM and LFCR, inhibitory APAs in LIS. All APAs precede the prime mover contraction (dashed line). No inhibition is seen in LECR, due to the absence of any background activity. **(E)** Activation of the RPM is preceded by excitatory APAs in both the LPM and the RIC, while LIC is simultaneously inhibited. The related change of Tz starts simultaneously with the RPM activation. cw, clock-wise. Reproduced from Baldissera et al. (2008a,b), © Springer-Verlag Berlin Heidelberg 2008, with permission of Springer.

et al., 1999, 2000; Shiratori and Aruin, 2004; Bouisset and Do, 2008; Tomita et al., 2010). In the perspective discussed here, however, these data had to be supplemented with some further observation.

APAs in Arm Adduction-Abduction in the Horizontal Plane

Fast unidirectional movements of the right arm

When standing upright, the voluntary adduction of the right arm in the horizontal plane (prime mover right *Pectoralis Major*, RPM) exerts at the shoulder a torque that tends to rotate the trunk clockwise (**Figure 7A**). This torque is contrasted by the body inertia and actively counteracted by a counterclockwise torque simultaneously generated by the two fixation chains mentioned above (**Figures 7B,C**), in different proportions in the various contexts (Baldissera et al., 2008a,b).

Fixation chain between the arms. During a fast adduction of the right arm, if a rigid support is available to the left hand (**Figure 7B**) APAs develop in the homologous left-side adductor, LPM, and in the wrist flexor LFCR (**Figure 7D**); meanwhile in the left *Infraspinatus*, LIS, the background EMG activity (if present) is reciprocally depressed. These APAs discharge the primary rotational perturbation onto the support and arrest the clockwise rotation of the trunk. When no support is available, APAs in LPM fixate the left arm to the trunk, thus increasing the overall inertia, or even produce an adduction of the left arm and a mirror reaction torque, in either case attenuating the trunk rotation.

Fixation chain to the ground. A counterclockwise torque is also exerted on the thorax by APAs in the trunk and lower limb muscles (**Figure 7C**), an example of which are the prominent burst in the right *Ischiocruralis* muscle, RIC, and the simultaneous anticipatory depression of LIC (**Figure 7E**). These asymmetric APAs generate at the ground a clockwise reaction torque about the vertical axis, *Tz*, in the direction opposite to the arm acceleration.

When the right arm is cyclically oscillated, in both fixation chains the above APAs are replaced (**Figure 8A**) by a sinusoidal EMG modulation with the same period as the right arm oscillations (Baldissera et al., 2008b). In both arm (LPM) and leg (RIC) muscles, the modulation phase-advances the RPM cyclic activity, its absolute timing being quantitatively congruent with the time-anticipation of the APAs linked to unidirectional movements.

Cyclic coupled adduction-abduction of both arms

During coupled arm movements, APAs in arms muscles cannot be distinguished from the voluntary activation, and only APAs in the fixation chain to the ground can be analyzed.

When cyclic movements are mirror symmetrical (ANTI), EMG modulation in LIC and RIC is absent or marginal over the whole frequency range (1.0–3.0 Hz), justifying the virtual annihilation of *Tz* (**Figure 8B**). Conversely, during arms ISO movements (**Figure 8C**), the amplitude of the phase-opposite modulation of RIC and LIC EMG and the size of *Tz* are much larger than in one-arm movements and this difference steeply

increases when the frequency is raised (see also Section *Effects of APAs in the Fixation Chain to the Ground on Coupling Coordination of Horizontal and Parasagittal Arm Movements*).

The view that the APAs and the sinusoidal EMG modulation share the same nature is not only suggested by the identical distribution and the temporal compatibility of the two events, but it is also supported by the observation (Leonard et al., 2011) that when the target of a pointing task is unexpectedly shifted after the movement had started, the correction movement is preceded by legs postural adjustments in the same way as at the movement initiation, showing that the online correction of voluntary finalized movements includes both the conscious and the associated APA commands. If one considers that cyclic movements are continuously changing in velocity and direction so as to require uninterrupted control of trajectory and timing, it is reasonable that the related APA commands are continuously updated over the entire sinusoidal course of movements. Thus, although the possibility exists that these cyclic postural activities may include reflex components too, we will continue hereafter to name the cyclic postural activities as APAs.

APAs in Arm Flexion-Extension in the Parasagittal Plane

Fast unidirectional flexion or extension

The reaction forces to arm movements in the parasagittal plane are discharged by APAs in the same two fixation chains as horizontal movements, but with a different topographical distribution. For a mechanical analysis of these effects, see Esposti and Baldissera (2013).

APAs in the fixation chain between the arms

Supplementing the scanty data available in the literature (Zattara and Bouisset, 1988) it was disclosed (Esposti and Baldissera, 2013) that a fast flexion (**Figures 9A,B**) or extension of the right arm (prime movers right *Anterior Deltoid*, RAD, and *Posterior Deltoid* RPD, respectively) elicits APAs in the left side homologous LAD and LPD so as to replicate the excitation and inhibition pattern of RAD and RPD. In the left extensor

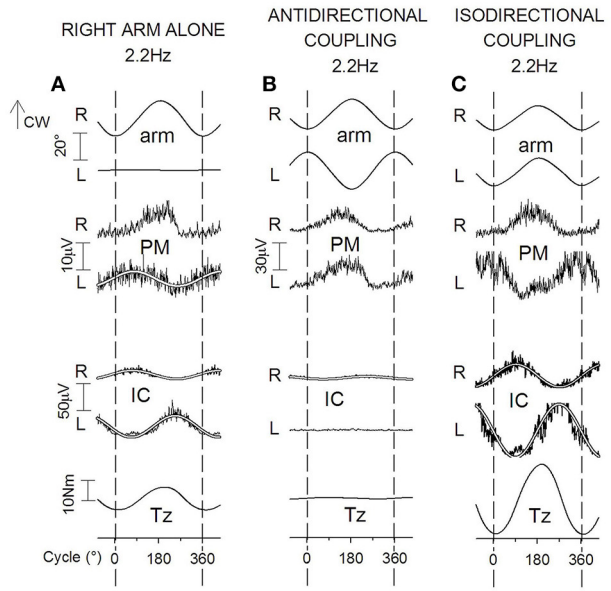

FIGURE 8 | Cyclic postural adjustments during rhythmic oscillations in the horizontal plane of the right arm alone (A) and of both arms in ANTI and ISO coupling **(B,C)**. Prime movers, RPM in **(A)**, RPM and LPM in **(B,C)**. During one arm movements, cyclic APAs develop both in LPM and, phase-opposite, in RIC andLIC. This same pattern of EMG modulation, but doubled in size, is present in IC muscles during ISO (difficult) coupling **(C)**. During ANTI coupling, instead, activity is absent in LIC and minimal in RIC **(B)**. In all coupling modes, *Tz* undergoes changes parallel to the IC activities; cw, clock-wise. Reproduced from Baldissera et al. (2008b), © Springer-Verlag Berlin Heidelberg 2008, with permission of Springer.

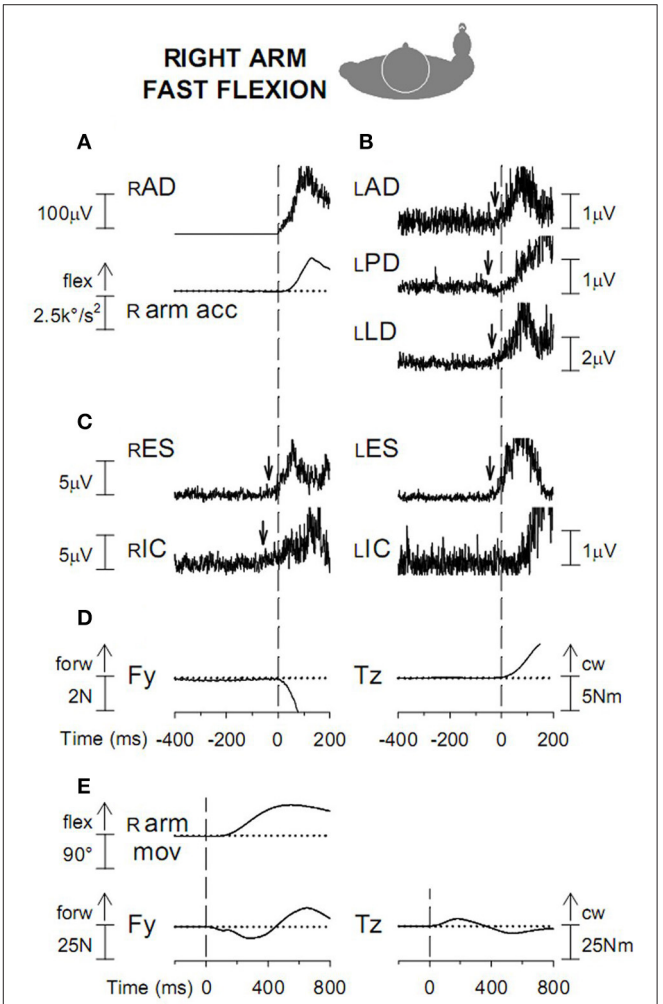

FIGURE 9 | (A) Voluntary activation of RAD and acceleration (R arm acc) of the ensuing arm flexion. Vertical dashed line: onset of the RAD EMG burst. **(B)** APAs in the left arm muscles, excitatory in LAD and LLD and inhibitory in LPD. **(C)** excitatory APAs in trunk muscles RES and LES and in the right leg muscle RIC. **(D)** anterior-posterior force *Fy* and clockwise moment about the body vertical axis *Tz*, discharged to the ground. **(E)**. *Fy* and *Tz* changes are displayed on a longer time base. Dashed line: onset of prime mover burst; cw, clock-wise. Reproduced from Esposti and Baldissera (2013), © Springer-Verlag Berlin Heidelberg 2013, with permission of Springer.

Latissimus Dorsi, LLD, APAs are instead opposite to the voluntary actions in RLD.

APAs in the fixation chain to the ground

Many details of the APAs in trunk and legs associated with flexion-extension of one or both arms had been previously reported (see above for references, cfr. also Zattara and Bouisset, 1988; Shiratori and Aruin, 2004; Bleuse et al., 2005; Bouisset and Do, 2008; Morris et al., 2013) and some were confirmed. Fast flexion of the right arm (**Figure 9C**) is associated with symmetric APAs in the right and left *Erector Spinae* (RES and LES) and asymmetric APAs in RIC and LIC, excitatory on the right side during arm flexion (cfr. Zattara and Bouisset, 1988; Bleuse et al., 2005) and on the left side during extension. An anticipatory change of the anterior-posterior force *Fy* and of the torque *Tz* are meanwhile discharged to the ground (**Figures 9D,E**). During single arm oscillations all the above APAs are replaced by EMG modulation cycles with the same period as the arm movement and increasing in size when the movement frequency is raised (Baldissera and Esposti, 2013).

Cyclic coupled flexion-extension of both arms

During ISO arms oscillations (**Figure 10A**) cyclic APAs develop symmetrically both in RES and LES and in RIC and LIC (**Figure 10B**), as requested to cope with the anterior-posterior perturbation. When frequency is raised, APAs in both muscles pairs increase in size remaining synchronous on the two sides. The anterior-posterior reaction force *Fy* undergoes a sinusoidal modulation with the same period as the arm movements (**Figure 10C**) and significantly increases in size when the frequency increases. Conversely, the size of *Tz* remains negligible throughout the whole frequency range.

During ANTI coupling (**Figures 10D–F**) the APAs modulation in RES and LES is significantly smaller than in ISO, but it increases in either mode as the frequency is raised. The phase difference between the two sides is highly variable among subjects and, on the average, half-way between 0° and −180°. Cyclic APAs activation is phase-opposite in RIC and LIC and, when the frequency is raised, it increases in size to a greater extent than in ISO. Concerning the ground reactions, the sinusoidal modulation of *Fy* remains very low over all the frequency range, while the torque *Tz* significantly increases between 1.0 and 2.2 Hz but progressively decreases by about the same amount between 2.2 and 3.4 Hz (see later). The phase of *Tz* oscillations during ANTI is opposite to that of the right arm movements and is not significantly affected by frequency.

In summary, the coupled arm oscillations in the horizontal and parasagittal plane are distinguished because the preferred (more stable) coupling mode is ANTI in horizontal and ISO in parasagittal movements. Both movement types, however, share the common feature that the unstable coupling mode is the one in which: (1) in the motor pathways to the prime movers of each arm the voluntary commands have opposite sign with respect of the APAs commands linked to the voluntary activation of the contralateral arm (cfr. Section *APAs Associated with Arm Movements in the Horizontal and Parasagittal Plane*); and, (2)

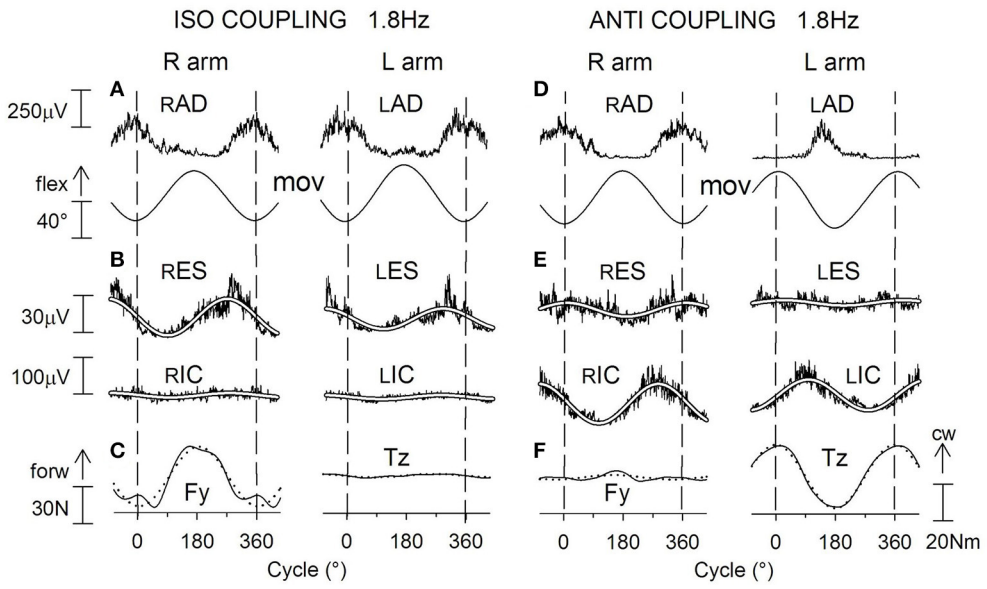

FIGURE 10 | Voluntary oscillations of both arms in the parasagittal plane. ISO and ANTI coupling. Same labels as in **Figure 9**. **(A,D)**: cyclic voluntary EMG activity in RAD and LAD muscles and ensuing oscillations of the right and left arms. In ISO coupling the activation of both trunk (ES) and thigh (IC) postural muscles is synchronous on the two sides **(B)** and corresponds **(C)** to a clear-cut anterior-posterior ground reaction *Fy* while the torque *Tz* is marginal. **(E)** in ANTI coupling, the EMG modulation in RES and LES remains synchronous but consistently lower with respect to ISO, whereas the IC activation is increased in size and is phase-opposite in RIC and LIC. Correspondingly **(F)**, a large reaction torque *Tz* is generated while *Fy* is strongly reduced. Reproduced from Baldissera and Esposti (2013), © Springer-Verlag Berlin Heidelberg 2013, with permission of Springer.

the prime movers generate torsional perturbations, which are discharged by APAs to the ground by producing a reactive torque *Tz*.

Interactions betweeen APAs and Voluntary Commands during Coupled Arm Movements

Combining the results presented in Sections *Coupling Coordination of ISO vs. ANTI Cyclic Movements of the Arms in the Horizontal and Parasagittal Planes and APAs Associated with Arm Movements in the Horizontal and Parasagittal Plane* suggests that the selective constraints affecting the two difficult modes, *hISO* and *pANTI*, may be related to the APAs that occur in both the fixation chains, between the arms and to the ground.

In the following, the two mechanisms will be discussed separately.

Neural Interference between APAs and Voluntary Commands in the Motor Pathways to the Prime Movers in Horizontal and Parasagittal Arm Movements

Horizontal movements

During ANTI (mirror symmetrical) coupling, voluntary, and postural commands to the prime movers have the same sign (i.e., both excitatory or inhibitory). Accordingly, they should potentiate each other. However, it should be noted that in ANTI coupling the two arms exert on the trunk opposite torques that physically cancel each other, so that no postural adjustment is needed. Indeed, no APAs are generated during ANTI in the fixation chain to the ground (**Figure 8B**) and, reasonably, APAs should be absent in the contralateral arm too, thus leaving movement coupling unaffected.

During ISO coupling the APAs elicited in the prime movers of either arm are opposite in sign with respect to the voluntary commands. Hence, maintaining the movement amplitude, as done in the experiments described here, would require that either the voluntary commands are increased or APAs are actively suppressed (gated). The former intervention, however, would be doomed to fail since when the frequency (velocity) of the arm movements increases, the size of APAs also increases (Baldissera et al., 2008b, see also Shiratori and Aruin, 2007).

Parasagittal arm movements

The interaction between voluntary and APAs commands is somewhat more complex in parasagittal than in horizontal oscillations (cfr. discussion in Baldissera and Esposti, 2013).

In the motor pathways to *Anterior* and *Posterior Deltoid*, the voluntary commands and the APAs linked to the movement of the contralateral arm have the same sign during ISO, thus facilitating or leaving unaffected (see above) the coupled movements. Conversely, during ANTI coupling, voluntary commands and APAs have opposite sign and maintaining the movement amplitude requires APAs to be actively suppressed (gated).

In the motor pathways to *Latissimus Dorsi*, instead, APAs and voluntary commands have opposite sign during ISO (see Section *APAs in Arm Flexion-Extension in the Parasagittal Plane*), thus creating a local neural conflict during the preferred mode.

Escape from APAs suppression

As discussed in Section *Anticipatory Postural Adjustments (APAs) as Possible Candidates for Generating the Subliminal Excitability Modulation in Forearm Muscles during Foot Oscillations for hand-foot coupling,* the conflict arising in both horizontal and parasagittal movements when APAs and voluntary commands have opposite signs can be solved with the intervention of the control mechanism that provides gating of transmission of the APAs commands (Schepens and Drew, 2004, 2006; Schepens et al., 2008). One sign of such intervention may be the higher increase of cerebral activation during non-preferential coupling compared to preferential coupling (Sadato et al., 1997; Debaere et al., 2001, 2004; Immisch et al., 2001; Ullen et al., 2003).

However, as the oscillation frequency increases, the size of APAs also increases, implying that the gating mechanism for APAs suppression must be intensified in parallel. Descriptively, the decay in coupling stability observed when either the movement frequency is raised or the exercise duration is prolonged, fits the general description of fatiguing systems. It may therefore be supposed that during "difficult" coupling the gating system undergoes neural "fatigue" (linked to the turnover of synaptic transmitters, adaptation, or potentiation phenomena, etc.) proportionate to the frequency and duration of the exercise, so as to progressively attenuate the suppression of APAs transmission. This, in turn, would increase the coupling instability and favor the transition to the opposite coupling mode.

Effects of APAs in the Fixation Chain to the Ground on Coupling Coordination of Horizontal and Parasagittal Arm Movements

The major clue suggesting that in both movement types APAs in the chain to the ground may exert an indirect influence on coupling coordination is the increase of the chained postural actions observed when passing from the more stable to the less stable coupling mode (Sections *APAs in Arm Adduction-Abduction in the Horizontal Plane and APAs in Arm Flexion-Extension in the Parasagittal Plane*). Evidence for such an effect has also been reported by Van der Woude et al. (2008) for synchronous and alternate hand cycling. Aimed to better elucidate this correlation, the effort sustained by the postural chain to the ground was tentatively quantified (1) by the forces discharged to the ground and (2) by the energy cost of the chain actions.

Ground reactions Fy and Tz

Each of the EMG and mechanical variables pertaining to the fixation chain to the ground is exclusively related to either *Fy* or *Tz* (Esposti et al., 2013). The latter can then be taken as indicators of the overall entity of postural actions occurring in the chain.

In a group of subjects performing both horizontal and parasagittal movements in the same experimental session, no significant *Tz* changes are observed (**Figure 11B**) at any frequency in the two more stable "easy" modes (*pISO* and *hANTI*). Conversely, *Tz* is large and increases with frequency in

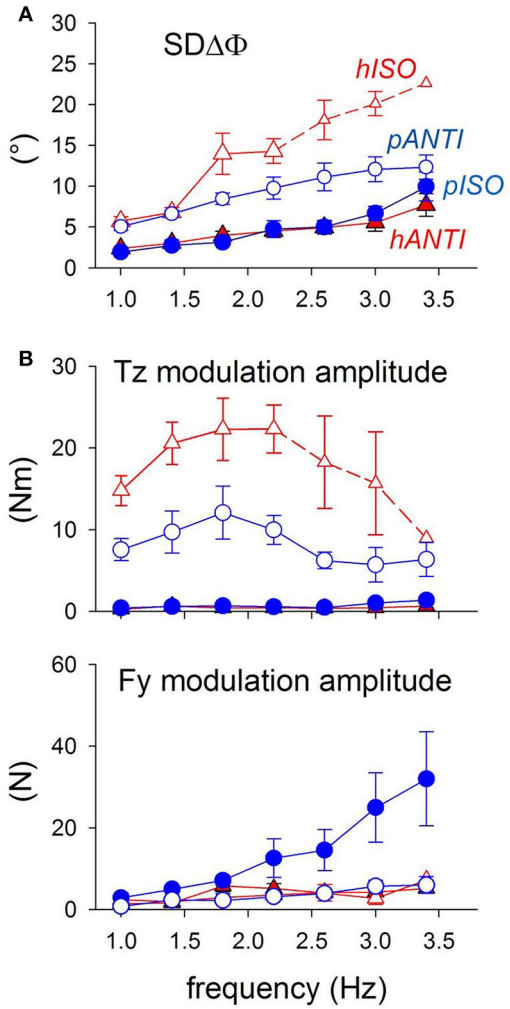

FIGURE 11 | Coordination marker SDΔΦ and postural markers *Fy* and *Tz* recorded during coupled arm movements performed by the same subjects in both the horizontal and parasagittal planes (red triangles and blue circles, respectively). Filled symbols, stable (easy) modes; open symbols, unstable (difficult) modes. **(A)** SDΔφ is identical in the easy modes *pISO* and *hANTI*, larger in *pANTI* and even more so in *hISO*. Small symbols and dashed lines: values obtained in only part of the subjects. **(B)** *Tz* is virtually null in the two easy modes (filled symbols) and not significantly different between the two movement types. Instead, it increases with frequency in the two difficult modes (open symbols), more in *hISO* than in *pANTI*. Above 2.0–2.4 Hz, *Tz* starts however to decrease progressively. Size of *Fy* increases monotonically with frequency up to 3.4 Hz in *pISO* while it remains negligible in the other three movement combination. Reproduced from Baldissera and Esposti (2013), © Springer-Verlag Berlin Heidelberg 2013, with permission of Springer.

both the "difficult" modes, significantly more in *hISO* than in *pANTI*. Thus, the distribution gradient for *Tz* among the four movements combinations is: $hANTI \neq pISO < pANTI < hISO$, i.e., just the same as for SDΔΦ.

The anterior-posterior force *Fy* is appreciable and increases significantly with frequency only during ISO parasagittal movements (**Figure 11B**) thus appearing as unsuitable for discriminating among the four movement conditions.

Note, however, that in both movement types *Tz* decreases above 2.0–2.5 Hz while SDΔΦ continues to grow (compare **Figure 11A** and **Figure 11B**). This discrepancy might disprove the existence of a causal link between postural effort and coupling stability but it may also indicate that in the high frequency range *Tz* does not express all the forces generated for postural aims because part of them are "absorbed" within the different chained segments of the trunk by opposite muscular actions.

Oxygen uptake during coupling of horizontal and parasagittal movements

Theoretically, in both horizontal or parasagittal movements the mechanical work for voluntarily oscillating the two arms together should be equal in ISO and in ANTI, insofar as the movements amplitude and frequency are identical in the two modes. Since these two last conditions were respected in the present experiments, the muscle force and the metabolic consumption for moving the arms should be the same in ISO and ANTI modes. If so, for each movement type, the difference in energy consumption between the stable and unstable coupling modes should represent the cost of the global postural effort in the fixation chain to the ground.

The energy cost of each exercise, $\Delta\dot{V}O_2$ (i.e., the difference between the steady-state oxygen uptake at rest and during the exercise) was evaluated in two groups of subjects during arm oscillations in the horizontal and parasagittal plane, respectively, and normalized for both the body mass and movements amplitude (Esposti et al., 2010, 2013).

In *horizontal movements* (**Figure 12A**, blue triangles) $\Delta\dot{V}O_2$ is quite larger in *hISO* (difficult) than *hANTI* (easy) and increases in both modes when the frequency is raised from 1.4 to 2.0 Hz, to a larger extent in ISO than in ANTI. The related values of SDΔΦ are distributed following the same pattern (**Figure 12B**).

In *parasagittal movements* (**Figure 12A**, black circles), $\Delta\dot{V}O_2$ is higher in *pANTI* (difficult) than in *pISO* (easy) and shows a highly significant linear correlation with frequency in both coupling modes, with a higher slope in ANTI than in ISO. The corresponding changes of SDΔΦ also show a highly significant linear correlation with frequency (**Figure 12B**).

In conclusion, the normalized $\Delta\dot{V}O_2$ varies across the four movement combinations along the gradient: $hANTI \neq pISO > pANTI > hISO$, analogously to the gradient for SDΔΦ measured in these and previous experiments.

Figure 12C relates SDΔΦ with $\Delta\dot{V}O_2$ and shows that in *parasagittal movements* at any given level of $\Delta\dot{V}O_2$, SDΔΦ is definitively higher (i.e., coordination is worse) in *pANTI* than in *pISO*, signaling that a quote of the ISO vs. ANTI stability loss is not related to a change in oxygen uptake, (i.e., to the postural effort), but to some non-metabolic factor(s), presumably to the neural conflict between APAs and voluntary commands.

The metabolic and non-metabolic quotes can be separated from each other. On one side, the quote of the stability loss independent from the oxygen uptake is calculated by subtracting from each other the ISO and ANTI linear relations in plot **Figure 12C**. On the other side, subtraction of the ISO and ANTI linear relations in plot **Figure 12B** measures the total stability loss, due to both the metabolic and the non-metabolic

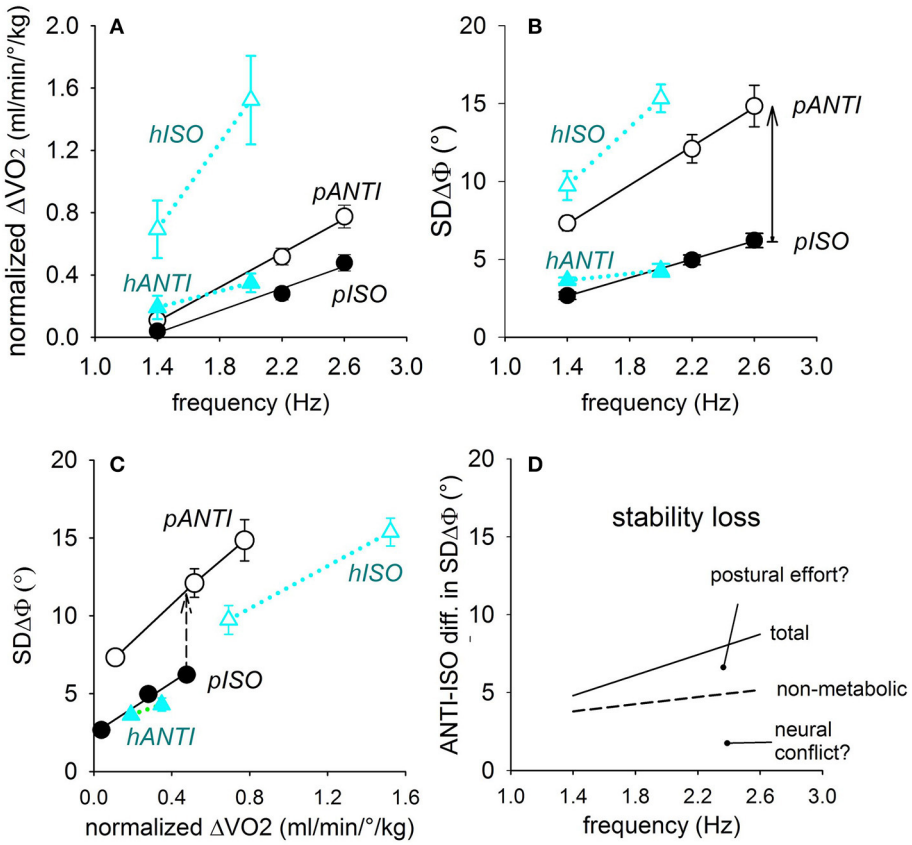

FIGURE 12 | Relations of the oscillation frequency with the normalized oxygen uptake $\Delta\dot{V}O_2$ (A) as well as with the coupling variability SDΔΦ **(B)**, in either coupling mode of the horizontal and parasagittal movements (black and blue symbols, respectively). In **(C)**, direct correlation between SDΔΦ and $\Delta\dot{V}O_2$. The SDΔΦ-$\Delta\dot{V}O_2$ relation in the two difficult modes (*pANTI* and *hISO*) runs higher and has a higher slope than in the respective easy modes (*pISO* and *hANTI*). Continuous arrow in **(B)**: total ISO-vs.-ANTI stability loss; dashed arrow in **(C)**: stability loss independent from $\Delta\dot{V}O_2$. Both are marked at 2.6 Hz. In **(D)** the total and the non-metabolic stability losses in parasagittal movements are plotted by a continuous and dashed lines, respectively, so as to separate the two components of the stability loss, namely the *neural conflict* and the *postural effort*. Reproduced from Esposti et al. (2013), © Springer-Verlag Berlin Heidelberg 2013, with permission of Springer.

components. The total and the non-metabolic losses are shown in plot **Figure 12D** (continuous and dashed lines, respectively) over the range of the frequencies tested, allowing to identify the quote of the stability loss linked to the increase of $\Delta\dot{V}O_2$, i.e., to the postural effort of the fixation chain to the ground.

Mechanism for the coupling destabilizing effect of the postural effort

Hypothesizing a causal relationships between SDΔΦ and the oxygen uptake is possibly supported by the repeated observation that fatigue of either postural or focal muscles modifies APAs timing and size (Morris and Allison, 2006; Strang and Berg, 2007; Kanekar et al., 2008; Strang et al., 2008, 2009). Even if the fatigue levels attained in the cited experiments were not reached in the present exercises, one might argue that the intensified recruitment of both the prime and the postural muscles of trunk and legs during the non-preferred coupling may tend to alter the phase relationships of APAs with respect to the prime movers activity. A control mechanism for maintaining the synchronization between the voluntary and postural components of the movements should then be required, which would progressively become more expensive as the movement frequency increases, giving rise to fatigue phenomena similar to those proposed for the decay of APAs gating in the motor pathways to arm muscles (Baldissera et al., 2008b; Baldissera and Esposti, 2013). If this were to be the case, the stability loss in the less-coordinated coupling mode may result from a unique phenomenon, i.e., the exhaustion of the control mechanisms that govern the interferences arising at different neuronal levels between postural and conscious voluntary commands.

Flexion-Extension Movements of the Hand in the Horizontal Plane

In a group of subjects whose horizontal movements of the arms had been previously analyzed, the same experimental scheme was followed to investigate coupled flexion-extension movements of the hands in the horizontal plane (Baldissera et al., 2008b). As

for arm horizontal movements, SD$\Delta\Phi$ of the hand oscillations is significantly higher (i.e., coupling stability is lower) in ISO than in ANTI coupling, in conformity with the APAs distribution in the two modes.

Rules of Interlimb Coupling: A Special Case of APAs Physiology

The ensemble of the above results demonstrates that the easiness/difficulty of coupled limb movements does not depend on the associated muscles, neither on the ISO or ANTI modality *per se,* nor on the limbs being ipsilateral or symmetric. It strongly suggests, instead, that the coupling preference depends, for each type of coupled movements, on the distribution and size of the anticipatory postural adjustments that assist those movements. While performing their fundamental function of body fixation and stabilization during voluntary movements, APAs fatally generate some undesired "side effect" too. This happens when, during a certain focal movement, one simultaneously wants to move another body segment, belonging to a fixation chain, in the direction opposite to the APAs actions on that same segment. If a main chain reaching the ground is involved, where APAs are strong, performing the voluntary movement would require the APAs to be suppressed (gated) but, in this way, the static equilibrium would be lost. If instead the chain is a secondary one, APAs can be reduced via gating to a weak or subliminal level so that coupling of the two movements becomes possible while the movements are slow. Increasing the movement frequency, then coupling becomes unstable, difficult or even impossible, supposedly due to the exhaustion of the gating mechanism (Section *Neural Interference between APAs and Voluntary Commands in the Motor Pathways to the Prime Movers in Horizontal and Parasagittal Arm Movements*) and to the increased postural effort (Section *Effects of APAs in the Fixation Chain to the Ground on Coupling Coordination of Horizontal and Parasagittal Arm Movements*).

Since APAs are excitatory or inhibitory depending on the direction (in extrinsic coordinates) of the focal movement, this would explain why a "direction principle" rules the dichotomy of easy vs. difficult coupling.

Finally, it has to be expected that any factor that modifies the generation, execution, and organization of the APAs (for instance factors depending on the individual variability, on changes in the sensory context or in the body attitude, on training or on pathological events, see Section *Postural Constraints from Neuroscience to Sports and Rehabilitation Medicine*), will affect the coordination of limb coupled movements too. It cannot of course be excluded that other yet unknown factors may add to the APAs in destabilizing limbs coupling.

POSTURAL CONSTRAINTS FROM NEUROSCIENCE TO SPORTS AND REHABILITATION MEDICINE

In the above Chapters some of the rules of the anticipatory postural control were elucidated, with special reference to the APAs interference with interlimb coordination. Which is the potential translation of this knowledge beyond theoretical neuroscience?

"Will" Develops by Entangling Focal and Postural Movements

APA control is an intrinsic component of voluntary movement, not an "external" phenomenon: by definition, APAs exist as far as a movement is voluntary. Yet, APA develop quite independently and much later with respect to the capacity to imagine a voluntary movement. APA control is only primitively organized in the newborn (see Girolami et al., 2010 for references), consistently with the immature myelination of the central nervous system at birth. Once their neurobiological substrate is mature, focal, and postural movements remain entangled during further motor learning.

The APA component of learning is more relevant the more the movement involves long chains of muscles for within-body and body-ground stabilization.

APA as a Candidate "Neural Factor" in Force Development and Loss

The APA physiology provides a promising model for the explanation of the well-known, yet not entirely understood, "neural" mechanisms underlying the effect of resistance/power training. "Resistance" training, aimed at improving force and power in voluntary movements through muscle hypertrophy, is most commonly based on exercises of heavy lifting efforts which, despite high risk to destabilize the body system, are usually perceived as rather simple to learn and perform. Yet, unspecified "neural" factors (Sale, 1988) have long been postulated to explain (a) why force gains anticipate (even by many weeks) muscle hypertrophy (Clark et al., 2008) and (b) why, although the focal main muscles may stay the same in different exercises, the force gain is higher for the trained and very similar movements (Wirth et al., 2016). Consistently enough, force training with fast movements entails the highest force gain in movements performed at the trained speed; unilateral training allows higher unilateral force gains, compared to bilateral training, etc. (Jones and Rutherford, 1987). Unspecified "neural" factors, supported by TMS (Pearce et al., 2013) and fMRI (Farthing et al., 2011) findings, have also been claimed to subtend cross-education, i.e., force gains on the same movement of the untrained side, or force maintenance after immobilization, thanks to force training of the opposite side, as well as force gains achievable after pure mental practice (Yue and Cole, 1992; Reiser et al., 2011). In all cases, results may depend on the specific postural chains engaged, and thus unconsciously trained or not, in different exercises. De-training leads to force loss higher than the loss in muscle mass (Narici et al., 1989).

APA as a Candidate Ingredient of Skill Acquisition and Loss and Motor Learning

Recent studies evidenced that APA efficiency actually subtends also skill, and not only force, of voluntary movements. For instance, earlier APAs in shoulder muscles have been shown to be associated with higher accuracy in pointing tasks (Caronni et al.,

2013), and in the greater accuracy of pointing with the dominant, compared to the non-dominant upper limb (Bruttini et al., 2016).

De-training also conceals a loss of APAs efficiency. After only a 12 h wrist and fingers immobilization a simple finger tapping task is altered, due to insufficient stabilization of the elbow, reflecting delayed activation or inhibition of proximal muscles (Bolzoni et al., 2012). In general, an improvement of APAs has long been suspected as a potential component of learning of voluntary movements (Rutherford and Jones, 1986).

Yet the relationships between APAs and learning were not extensively investigated in the subsequent literature. It was shown, however, that exercises requiring high motor skills rapidly lead to improvements in balance (Aruin et al., 2015; Kanekar and Aruin, 2015) and in a reaching task while standing (Saito et al., 2014). Improvements were invariably associated with an earlier recruitment of the APAs in lower limb muscles.

APA Can be Specifically Affected in Neural Diseases: Hints to Clinical Diagnostics

Postural and focal movements can be de-coupled in case of nervous diseases. There seems to be no single "APA organ" within the central nervous system: rather, many CNS structures are involved. These include hemispheric cortex, cerebellum, basal ganglia, brain stem, and spinal cord (for a quick overview, see Discussion in Ioffe et al., 2007).

The cerebellum is certainly a key node of the network of postural control (Ioffe et al., 2007). The fact that cerebellar damage entails "postural" consequences was already acknowledged, as shown in **Figure 13** by a famous Babinski's example of a "postural" alteration after cerebellar lesion leaving the "focal" movement unaffected (Babinski, 1899). Cerebellar lesions may selectively impair also the APAs subtending within-limb movements. For instance, in patients with cerebellar ataxia, simple brisk movements of the finger are associated with alterations of the APAs engaging proximal arm muscles (Bruttini et al., 2015; Cavallari et al., 2016).

Recent research also showed that the lesion of many other cerebral structures (e.g., of the supplementary motor area (Viallet et al., 1992) or of the basal ganglia (Viallet et al., 1987) can lead to selective alterations of APAs, thus affecting within-limb and/or body-ground chaining. With respect to the "easy" and "difficult" hand-foot coupling described above, it has been shown that after hemispheric stroke, the "difficult" coupling is selectively impaired (or even impossible) on the unaffected side, which retains an otherwise skilled motricity (Baldissera et al., 1994). The frame of APAs physiology offers an explanation.

As illustrated in Section Role of APAs in Differentiating ISO vs. ANTI Coupling Modes in Other Types of Limb Movements, APAs may well-spread contralaterally to a focal movement; further, the successful completion of the APA "arborization" is a pre-requisite for the subsequent contraction of focal muscles (Cordo and Nashner, 1982; Brown and Frank, 1987). Hence, any impairment of APA commands on the paretic side may impair or even prevent a focal movement on the unaffected side. Not surprisingly, in hemiparetic patients, strength and coordination are affected on the "healthy" side, too (Santos et al., 2016). While overt postural disturbances may not appear, yet the hand-foot coupling test may reveal that they stand subliminal in the background. Therefore, asking for anti-phase coupling of the unimpaired hand and foot can be proposed as a simple, yet highly sensitive bedside test of hemispheric damage. The test is not specific to hemispheric lesions, however. All of the above considerations stimulate clinical reasoning. The studies on APAs in cerebellar patients suggest that ataxia can be seen as a typical consequence of APAs disorders, not less than of the programming of focal movements. Limb ataxia (commonly evidenced by dismetry in the classic index-to-nose or heel-to-knee tests), the incapacity to maintain a stable level of isometric force ("dys-stenia," Tesio, 2010), as well as trunk ataxia with balance deficits can all be interpreted as primarily caused by APAs disturbances. The subject knows what the focal movement should be but is unable to avoid position and/or force errors due to altered APAs.

The capacity of disease to affect selectively focal rather than postural movements is demonstrated by the case of survival of APAs after loss of its related focal movement. This observation is common in clinical practice but only exceptionally reported in the literature. For instance, ischemic or anesthetic block of the hand does not abolish APAs in proximal muscles (Bruttini et al., 2014). Brachial plexus lesions may entail the complete loss of shoulder abduction, yet the "luxury" of a fixation chain crossing the midline during a voluntary effort is preserved. Thus, the very existence of APA warrants the presence of genuine "will," thus providing a useful clinical sign. Fixation chains can only be rarely lost: they may disappear in case of cognitive deficits (e.g., hemineglect or apraxia), chronic "learned non-use" in deep-seated palsies (Taub et al., 2014)

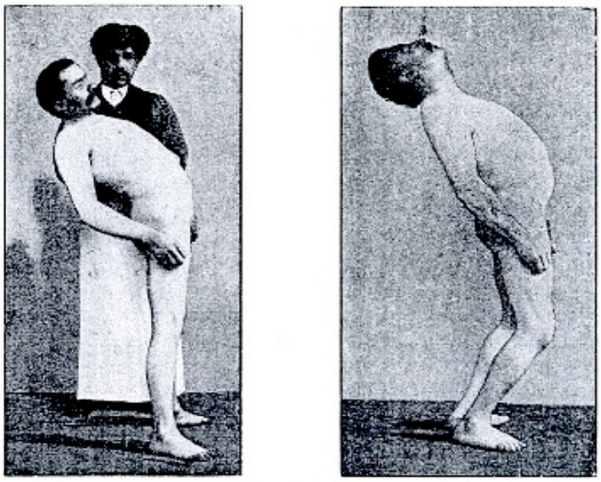

FIGURE 13 | A cerebellar patient (left panel) is requested to lean backward (focal movement) while standing. If not supported by the assistant, he will fall. The right panel shows the correct movement, in which knee flexion (APA) precedes the trunk extension, so that the body center of mass will be projected within the base of support ("cerebellar asynergy," after Babinski, 1899). This established clinical finding was confirmed by later, refined neurophysiologic research. Yet, after nearly 120 years this still remains one of the brightest demonstrations that the postural component of a voluntary moment can be impaired independently from its focal component.

or conditions such as simulation and conversion disorders (Tesio and Colombo, 1992).

APA Can be Selectively Trained in Sports and Rehabilitation Medicine

Motor training science (Magill and Anderson, 2014) has long acknowledged that "coupling" some movements is much more difficult to be trained and learned, compared to other. For instance, teaching how to de-couple the upper limbs in bimanual activities, usually a difficult challenge, is made more effective by dedicated training techniques (Walter and Swinnen, 1994).

Although training a "voluntary" movement is usually explicitly addressed to its focal component, yet it entails an unconscious and indirect training of its postural component (Mouchnino et al., 1992; Ioffe et al., 2007). As a rule, training can be addressed to the desired focal movement (explicit training) or another actual or imagined movement to which the desired one is unconsciously associated (implicit training). This holds also for skilled exercises improperly claimed to directly train the APAs (Aruin et al., 2015; Kanekar and Aruin, 2015). Actually, neither approach targets explicitly the APAs. Specific APA training paradigms are still missing. First, the APA chains subtending the normal voluntary movements must be predicted: although they mostly spread along the plane of the focal movement (Gabbett and Masters, 2011; Bruttini et al., 2014) a detailed "atlas" of expected APAs in various motor tasks is far from being developed. Second, APAs disorders usually consist in incomplete chaining and/or delayed timing/phasing between focal and various postural muscles. The between-muscle delays are in the order of tenths of milliseconds, depending on the muscles involved. In a clinical environment, a very skilled palpation of tendon tension can often succeed in capturing such between-muscle delays. A much easier and sharper temporal discrimination, in the order of few milliseconds, can be reached, both by patient and therapist, by binaural listening of sharp tones generated by transduction of the surface EMG from a focal and a postural muscle, and separately sent to the right and left ears (Tesio et al., 1996). This form of augmented feedback can be said to explicitly target the APAs and to provide a "knowledge of result" fostering the learning of the correct APA (Schmidt and Lee, 2005).

Despite the examples given above, the diagnosis and the treatment of APAs' deficits, both in sports and rehabilitation sciences, is still at the frontiers of physiology and represent a promising field of research.

AUTHOR CONTRIBUTIONS

All authors contributed in collecting the literature, critically analyzing it, and writing the manuscript. All authors approved the final version and agree to be accountable for all aspects of this work.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2017.00152/full#supplementary-material

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An Increase in Postural Load Facilitates an Anterior Shift of Processing Resources to Frontal Executive Function in a Postural-Suprapostural Task

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Increase in postural-demand resources does not necessarily degrade a concurrent motor task, according to the adaptive resource-sharing hypothesis of postural-suprapostural dual-tasking. This study investigated how brain networks are organized to optimize a suprapostural motor task when the postural load increases and shifts postural control into a less automatic process. Fourteen volunteers executed a designated force-matching task from a level surface (a relative automatic process in posture) and from a stabilometer board while maintaining balance at a target angle (a relatively controlled process in posture). Task performance of the postural and suprapostural tasks, synchronization likelihood (SL) of scalp EEG, and graph-theoretical metrics were assessed. Behavioral results showed that the accuracy and reaction time of force-matching from a stabilometer board were not affected, despite a significant increase in postural sway. However, force-matching in the stabilometer condition showed greater local and global efficiencies of the brain networks than force-matching in the level-surface condition. Force-matching from a stabilometer board was also associated with greater frontal cluster coefficients, greater mean SL of the frontal and sensorimotor areas, and smaller mean SL of the parietal-occipital cortex than force-matching from a level surface. The contrast of supra-threshold links in the upper alpha and beta bands between the two stance conditions validated load-induced facilitation of inter-regional connections between the frontal and sensorimotor areas, but that contrast also indicated connection suppression between the right frontal-temporal and the parietal-occipital areas for the stabilometer stance condition. In conclusion, an increase in stance difficulty alters the neurocognitive processes in executing a postural-suprapostural task. Suprapostural performance is not degraded by increase in postural load, due to (1) increased effectiveness of information transfer, (2) an anterior shift of processing resources toward frontal executive function, and (3) cortical dissociation of control hubs in the parietal-occipital cortex for neural economy.

Keywords: dual-task, graph analysis, functional connectivity, event-related potential, network-based statistics

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INTRODUCTION

Postural control is a continuum raging from "controlled to automatic" processing, depending on the level of postural demand and the capacity of attentional resources (Stins et al., 2009; Boisgontier et al., 2013). Maintenance of posture with bilateral stance on a stable surface is an automatic process that requires minimal attentional resources to stabilize the center of gravity of the postural system within the limits of the sway range. When stance difficulty increases, the postural task shifts to a controlled process, manifested with an enhanced postural regularity (Donker et al., 2007; Sarabon et al., 2013). Parallel loading of two component tasks, posture and supraposture tasks, results in an intricate trade-off for central resource allocation (Temprado et al., 2001), depending on the task priority (Levy and Pashler, 2001), response compatibility (Stelzel et al., 2006), relative task difficulty of the two concurrent tasks (Huang and Hwang, 2013), and so on. For some postural-suprapostural dual-tasking, such as golf putting and surgery, withdrawing attention from postural control could help to maximize the precision of the added motor task (Balasubramaniam et al., 2000; Stoffregen et al., 2007). Postural sway is less regular in the dual-task condition than in a single postural task (Donker et al., 2007; Kuczyński et al., 2011). In this context, at least two critical issues with the limited central resource arise. The first issue is that relative cost of postural-suprapostural performance varies with stance difficulty, as differently predicted by the resource-competition model (Woollacott and Shumway-Cook, 2002) and the adaptive resource-sharing model (Mitra, 2004; Mitra and Fraizer, 2004). However, direct neural mechanism regarding to how the brain reorganizes functional networks is largely unknown. Second, most research designed to investigate the neural control of a postural-suprapostural task has employed a concurrent cognitive task as part of the dual-task configuration. Traditional dual-task setups and a postural-suprapostural task with a suprapostural motor goal are very likely to produce different types of resource competition. The reason is that the task quality of a suprapostural motor task must take kinematical advantages of stance stability (Wulf et al., 2004; Stoffregen et al., 2007; Huang and Hwang, 2013), whereas a postural-suprapostural task with a cognitive goal typically has low response compatibility between the two component tasks (Weeks et al., 2003).

The fronto-parietal brain network is a flexible hub of dual-task control (Cole et al., 2013), although the role of the frontal and parietal areas in a dual-task is still debatable. Some neuroimaging studies have reported greater activation of the frontal or prefrontal areas during dual-task trials than during single-task trials (D'Esposito et al., 1995; Collette et al., 2005), whereas others have revealed no specific frontal or prefrontal activation in the dual-task condition (Klingberg, 1998; Adcock et al., 2000; Bunge et al., 2000). In other studies, dual-tasking, as compared to both individual visual and auditory single tasks, activated a predominantly parietal network in the right hemisphere (Deprez et al., 2013), whereas simultaneous car driving and language comprehension suppressed parietal activation in reference to two single tasks (Just et al., 2008). In addition to a paradigm-specific interaction between component tasks (Salo et al., 2015), one of the most appealing explanations to reconcile those seemingly paradoxical results is that a dual-task may not necessarily recruit additional cortical areas; it may instead alter the interactions of the frontal/prefrontal areas with other cortical regions [such as parietal (Gontier et al., 2007) and premotor areas (Marois et al., 2006)]. Consequently, it is more important to examine changes in the inter-regional connectivity than to investigate changes in regional excitability of a dual-task by referencing the baseline activity of a single task.

Recently, graph theoretical analysis has been developed to characterize the topology of inter-regional connectivity and the efficacy of information transmission in brain networks, with important implications for adaptive or pathological changes in brain function (Reijneveld et al., 2007; Bullmore and Sporns, 2012). As postural-suprapostural behaviors involve information mastery potentially contingent upon the fronto-parietal network (Huang and Hwang, 2013), challenging postural sets could affect network connectivity for static stance, compromising the wiring-cost minimization, and postural load increment to achieve a suprapostural goal. Within the brain connectome context, this study aimed to extend the limited previous work by exploring the brain connectome in a particular postural-suprapostural task, when stance difficulty increases. This increase in stance difficulty must be associated with resource allocation of the brain, especially that of the fronto-parietal network, so that suprapostural motor performance and stance stability are jointly optimized. This exploratory study hypothesized that concurrent force-matching from a stabilometer stance would lead to changes in the inter-regional connectivity and the efficacy of information transfer, as compared to force-matching from a level-surface stance.

MATERIALS AND METHODS

Subjects

The study was conducted with 14 healthy right-handed volunteers (7 males, 7 females; mean age: 23.8 $\pm$ 3.8 years) from a university campus. All subjects were asked to abstain from stimulants (such as cigarettes, alcohol, and caffeine) for 24 h before the experiment. All subjects were volunteers naive to the purpose of the experiments and received no reimbursement. The experiment was conducted in accordance with the Declaration of Helsinki and with the approval of the local ethics committee (National Taiwan University Hospital Research Ethics Committee; no. 201312077RINC), and the subjects took part after signing personal consent forms.

Procedures

Before the experiment, the maximum voluntary contraction (MVC) of the right thumb-index precision grip and the maximal anterior tilt angle during stabilometer stance of each participant were determined respectively. For each participant, there were two experimental conditions for concurrent postural and motor tasks with different postural challenges (level-surface stance vs.

Abbreviations: SampEn, sample entropy; SL, synchronization likelihood; C_w, clustering coefficient; E_{glob}, global coefficient; E_{loc}, local coefficient.

stabilometer stance). The participants were required to conduct a thumb-index precision grip to couple a target line of 50% MVC force in response to auditory cues (force-matching task) while standing on a level surface or a tilted stabilometer. The two conditions were varied in a random order. For the level-surface condition, the participants were instructed to execute the force-matching task as accurately as possible while standing on a level surface. Therefore, the participants focused the majority of their attention on the force-matching task and maintained the upright posture automatically. For the stabilometer condition, the participants performed the force-matching task while standing on a stabilometer [a wooden platform (50 × 58 cm) with a curved base (height: 25 cm)]. They were instructed to execute the force-matching task as accurately as possible while maintaining the stabilometer at 50% of the maximal anterior tilt with minimal ankle movement (**Figure 1A**). Therefore, the participants had to pay attention simultaneously to both the force-matching task and postural maintenance. In the stabilometer condition, the subjects were provided with on-line visual feedback regarding the ankle displacement and force output on a computer screen 60 cm in front of them at the participants' eye-level. The target signals for force-matching and posture were presented at the same vertical position of the monitor to reduce the visual load during the concurrent tasking. With visual feedback, the participants could minimize fluctuations of the ankle and force-error in reference to the target angle at all times. In the level-surface condition, only the force-matching related visual feedback was provided. We understood that relative task difficulty could affect the reciprocal effect and task outcome of a postural-suprapostural task. Therefore, the target force for the concurrent motor task and target angle for the postural task were empirically selected based on our previous experiment (Hwang and Huang, 2016; Hung et al., in press). A high target force for force-matching of over 50% MVC and a tilting angle of the stabilometer plate >50% of the maximal anterior tilt were not suitable for repeated measures of event-related potential because of the potential fatigue effect. Moreover, the present combination of tasks was intended to provide a unique dual-task situation that would prevent a marked reduction in force-matching performance due to stabilometer stance for the majority of young healthy adults in the laboratory.

The force-matching act was guided by warning and executive tones, with a total of 14 warning-executive signal pairs in an experimental trial. A warning tone (an 800 Hz tone lasting for 100 ms) was randomly presented at different intervals of 1.5, 1.75, 2, 2.25, 2.5, 2.75, or 3 s before an executive tone (a 500 Hz tone lasting for 100 ms). The interval between the end of the executive tone and the beginning of the next warning tone was 3.5 s. Upon hearing the executive tone, the participants started a quick thumb-index precision grip (force impulse duration <0.5 s) to quickly couple the peak precision-grip force with the force target on the monitor. There were six trials of the postural-suprapostural dual-task for each stance condition, and each trial was composed of 14 precision grips.

Experimental Setting

An electrogoniometer (Model SG110, Biometrics Ltd, UK) was used to record the angular motion of the right (dominant) ankle joint. The electrogoniometer consisted of a 12-bit analog-to-digital converter box and 2 sensors for measuring their relative positions in space. One sensor was placed on the dorsum of the right foot between the second and third metatarsal heads, and the other sensor was fastened along the midline of the middle third of the anterior aspect of the lower leg. The level of force-matching was recorded with a load cell (15-mm diameter × 10-mm thickness, net weight = 7 grams; Model: LCS, Nippon Tokushu Sokki Co., Japan) mounted on the right thumb. The load cell was connected to a distribution box by a thin wire that could not provide stable mechanical support for the postural stance via the grip force apparatus. The auditory stimuli and target signals for conducting the force-matching and postural subtasks were generated with LabVIEW software (National Instruments, Austin, TX, USA). Thirty-two Ag-AgCl scalp electrodes ($Fp_{1/2}$, F_z, $F_{3/4}$, $F_{7/8}$, $FT_{7/8}$, FC_z, $FC_{3/4}$, C_z, $C_{3/4}$, CP_z, $CP_{3/4}$, P_z, $P_{3/4}$, $T_{3/4}$, $T_{5/6}$, $TP_{7/8}$, O_z, $O_{1/2,}$ and $A_{1/2}$) with a NuAmps amplifier (NeuroScan Inc., EI Paso, TX, USA) were used to register scalp voltage fluctuations in accordance with the extended 10–20 system. The ground electrode was placed along the midline ahead of F_z. Electrodes placed above the arch of the left eyebrow and below the eye were used to monitor eye movements and blinks. The impedances of all the electrodes were below 5 kΩ and were referenced to linked mastoids of both sides. All physiological data were synchronized and digitized at a sample rate of 1 kHz.

Data Analyses

Behavior Data

Reaction time (RT) and force error of force-matching was used to represent suprapostural performance in the present study. The RT of force-matching was denoted as the timing interval between the executive tone and the onset of grip force. The onset of grip force was defined as the force impulse profile exceeding the mean plus 3 times the standard deviation of the baseline activity of the force profile (500 ms before and after each warning tone). The RT of each force-matching trial was averaged across trials for each participant in the level-surface and stabilometer conditions. Force error of each force impulse was determined by normalized force-matching error (NFE), denoted as $\frac{|PGF - TF|}{TF} \times 100\%$ (where PGF: peak grip force; TF: target force; **Figure 1B**). The NFEs of all force-matching events were also averaged across trials for each participant in the level-surface and stabilometer conditions. On the other hand, the kinematic properties of ankle movement fluctuations during the interval between the executive tone and the onset of the force impulse profile were used to represent postural performance. The amplitude and regularity of the ankle movement fluctuations were assessed with root mean square and sample entropy (SampEn) after down-sampling of the kinematic data to 125 Hz. SampEn is a popular entropy measure used to characterize the temporal aspects of the variability of biological data, with high consistency and less sensitivity to short data length (Richman and Moorman, 2000; Yentes et al., 2013). A SampEn close to 0 represents greater regularity, while a value near 2 represents higher irregularity. A higher postural irregularity indicates less attentional resources allocated to postural control and thus more autonomous processing (Donker et al., 2007; Kuczyński et al.,

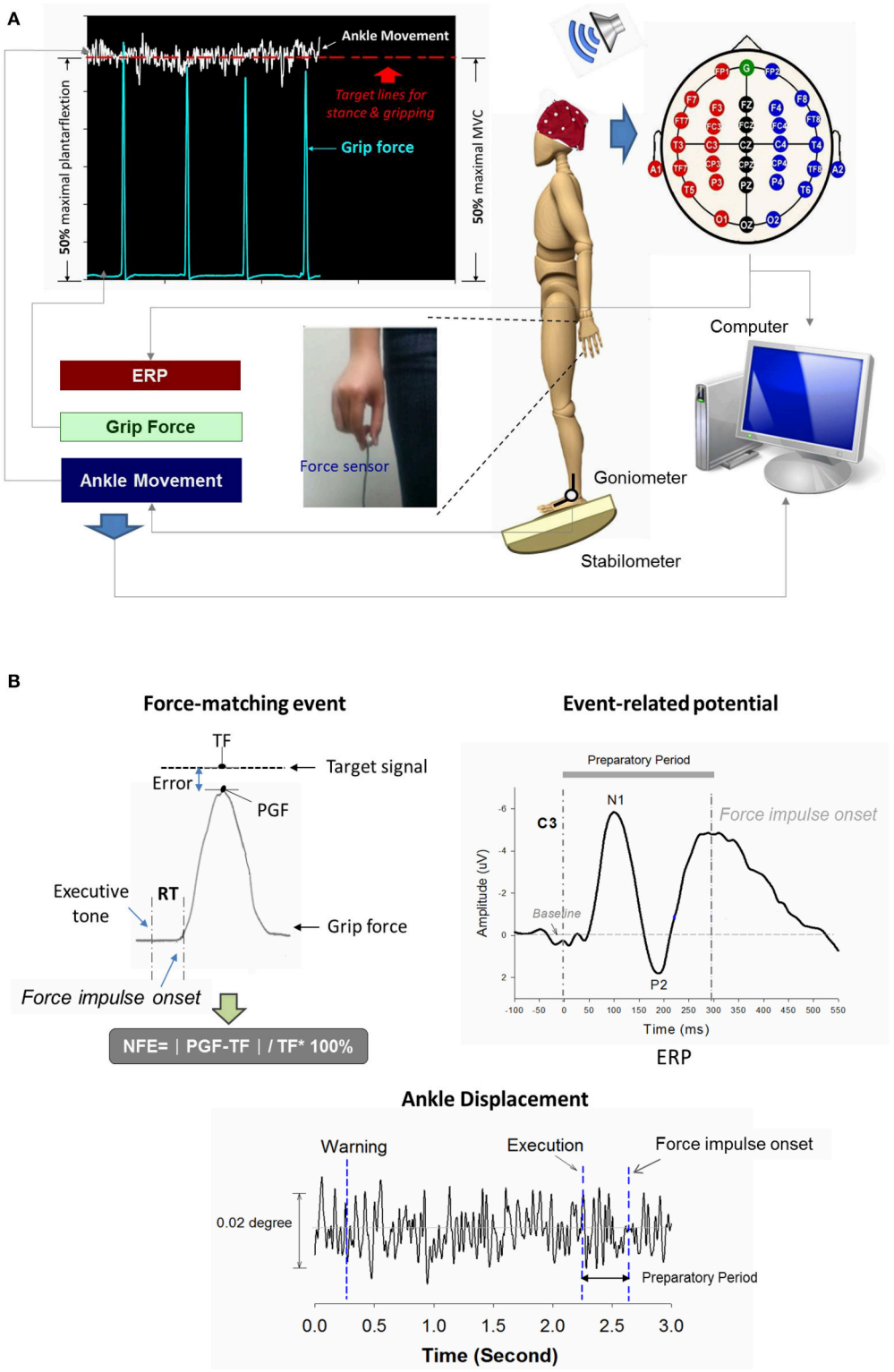

FIGURE 1 | Schematic illustration of experimental setup (A) and physiological data (B). Real-time display of precision grip force, ankle displacement, and target signals for concurrent force-matching and postural tasks. By separate scale-tuning of the manual force target and postural target, the target signals of both postural and force-matching tasks could be displayed in an identical position on the monitor. Suprapostural performance was assessed with the reaction time (RT) and normalized force error (NFE) of a force-matching act. The event-related potential (ERP) of the force-matching act was recorded with scalp electroencephalography. ERP between the executive tone and onset of the force-impulse profile was denoted as preparatory ERP, composed of N1 and P2 components. TF, target force; PGF, peak grip force.

2011). The mathematical formula for *SampEn* was

$$SampEn(m, r, N) = \ln(\frac{\sum_{i=1}^{N-m} n_i^m}{\sum_{i=1}^{N-m-1} n_i^{m+1}}) = \ln(\frac{n_n}{n_d})$$

where N is the total data point number. In this study, m equaled 3 and the tolerance range of r was 0.15 × the standard deviation of the standardized ankle movement fluctuations. For the level-surface condition, the data of the absolute ankle joint angle were used for amplitude and *SampEn* measurement; for the stabilometer condition, the data of the mismatch between the absolute ankle joint angle and the target line were used for amplitude and *SampEn* measurement.

Functional Connectivity Assessment

The DC shift and artifacts of electrical noise of each channel were conditioned with third-order trend correction and a low pass filter (40 Hz/48 dB roll-off) over the entire set of recorded data in off-line analysis. The conditioned EEG data were then segmented into epochs of 700 ms, including 100 ms before the onset of each execution signal. Each epoch was corrected with the NeuroScan 4.3 software program (NeuroScan Inc., EI Paso, TX, USA) to remove artifacts (such as excessive drift, eye movements, or blinks) in reference to baseline activities at the pre-stimulus interval. Poor epochs were also discarded by visual inspection (rejection rate of inappropriate trials: <10%). The remaining artifact-free epochs were averaged for an experimental trial in the level-surface and stabilometer conditions.

Since brain networks can be coupled in a highly non-linear manner (Pijnenburg et al., 2008), the synchronization likelihood (SL) was used to assess the degrees of linear and non-linear dimensions of EEG coupling within cortical networks (Leistedt et al., 2009; Boersma et al., 2011). Theoretically, SL takes into account the recurrences of state space vectors occurring at the same moment that are converted from two time series of interest (Boersma et al., 2011). An SL close to 0 indicates no coupling, whereas an SL of 1 indicates complete coupling. For brevity, detailed descriptions of SL calculation (Stam and van Dijk, 2002; Stam et al., 2003) and parameter settings (Montez et al., 2006) can be found in previous works. Because we were interested in cortical modulation during preparation process for a postural-suprapostural task, we selected the duration of averaged epochs between the executive tone and force-matching onset for SL analysis. A square 30 × 30 SL adjacent matrix was obtained by computing the SL of ERP data from all pairwise combinations of channels in the preparatory period (**Figures 1B**, **2**). In the **Figure 1B**, the 0 of ERP plot represents the onset of the executive signal. Each entry in the SL adjacent matrix represented the connectivity strength within the functional networks. For each participant, the overall SL adjacent matrix from 6 experimental trials in the level-surface or stabilometer condition was averaged. As the choice of the threshold is fairly arbitrary in the literature, we built functional connectomes across various SL thresholds from 0.1 to 0.9. The SL adjacent matrix was rescaled with the proportion of strongest weights, such that all other weights below a given threshold (including SL on the main diagonal) were set to 0. For instance, when the threshold value was 0.1, only the top 10% of the strongest weights in the SL adjacent matrix were considered to determine the network properties of the functional connectome. The mean SL of all the 32 recording sites, frontal (F_z, F_3, F_4, F_7, and F_8), sensorimotor (C_3, C_z, C_4, CP_3, CP_z, and CP_4), and parietal-occipital areas (P_3, P_z, P_4, O_1, O_z, and O_2), were determined for the level-surface and stabilometer conditions.

Using a causal finite impulse response (FIR) filter (24 dB/octave roll-off), we digitally filtered the ERP signal into the classic frequency bands in the theta (4–8 Hz), upper alpha (10–13 Hz), and beta (13–35 Hz) ranges. Spectral connectivity analysis was performed following the construction of theta and beta SL adjacent matrices with the conditioned ERP signal of both specific bands in the preparatory period. As action monitoring and planning for visuomotor tasks are reported to be linked to the mid-frontal theta rhythm (4–8 Hz; Luu et al., 2004; Armbrecht et al., 2012), the SL in the theta band that connected the mid-frontal areas (F_z and FC_z) and other scalp electrodes was used to examine stance-related differences in central executive function (Tanaka et al., 2009). Another research interest was the SL in the upper alpha (10–13 Hz) and beta bands (13–35 Hz) that connected sensorimotor (C_3, C_z, C_4, CP_3, CP_z, and CP_4) or parietal-occipital areas (P_3, P_z, P_4, O_1, O_z, and O_2), as oscillatory changes in these areas are related to preparation for fine motor/postural control (MacKay and Mendonca, 1995; Brovelli et al., 2004; Babiloni et al., 2008) and early perception information processing (Nierhaus et al., 2015). Especially, upper alpha power is more associated with movement performance than low alpha power is (Babiloni et al., 2008). The calculation of SL was accomplished with functions of HERMES for Matlab (Niso et al., 2013).

Graph Theoretical Analysis

Graph theoretical analysis was conducted with weighted network measures to best utilize the weight information. In terms of SL adjacent matrixes at various threshold values, the mean clustering coefficient (C_w), local coefficient (E_{loc}), global coefficient (E_{glob}), and small-world index (*sigma*, σ) of the resulting graphs were determined. Functionally, C_w, E_{loc}, and E_{glob} are metrics of information flow in a brain network. The clustering coefficient (C_w^i) for a vertex i quantifies the proportion of its neighboring vertices j that are connected to each other. The clustering coefficient C_w^i of vertex i was denoted as $C_w^i = \frac{\sum_{j\neq i}\sum_{k\neq i,j} w_{ij}w_{ik}w_{jk}}{\sum_{j\neq i}\sum_{k\neq i,j} w_{ij}w_{ik}}$. Topological mapping of the clustering coefficient was constructed with the clustering coefficients of all nodes. Another network metric, E_{loc} can be defined as $E_{loc} = \frac{1}{N}\sum_{i\in G} E(G_i)$, where G_i is the subgraph of the neighbors of a node i and $E(G_i)$ indicates the efficiency of the subgraph G_i. E_{glob} was calculated with $E_{glob} = \frac{1}{N(N-1)}\sum_{i\neq j\in G}\frac{1}{L_{i,j}}$, where $L_{i,j}$ is the shortest path length from node i to node j. Presuming that cortical regions under different electrodes exchange packets of information concurrently, E_{glob} is a quantitative measure of the efficiency of a parallel information transfer, with greater E_{glob} indicating

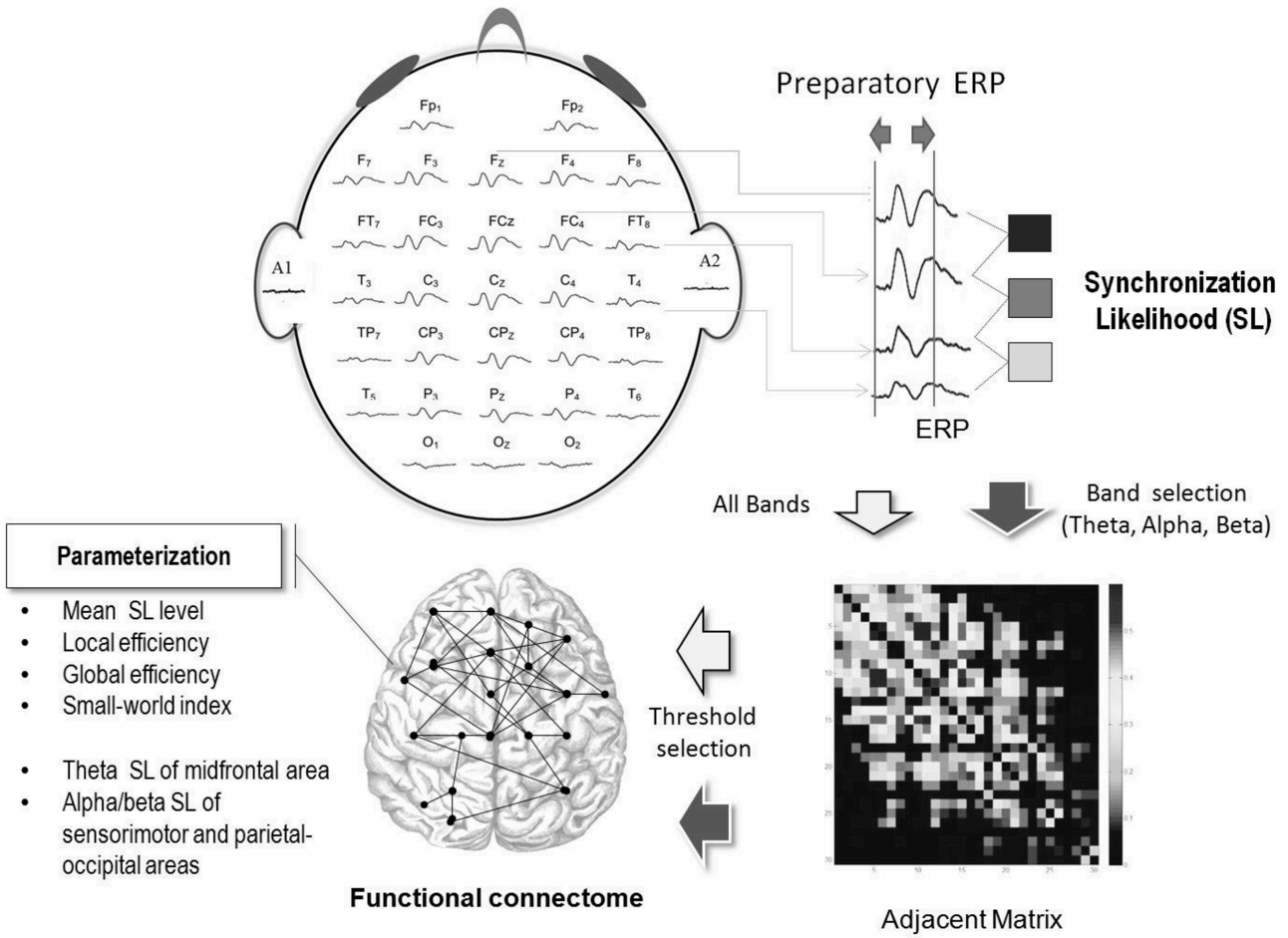

FIGURE 2 | Workflow of cortical network construction with ERP in the preparatory period. Functional connectivity was characterized with the synchronization likelihood (SL) of the paired preparatory ERP of different recording electrodes. The adjacent matrix represents the strengths of inter-electrode synchronization likelihood following appropriate threshold selection. With the adjacent matrix, connectomes in the preparatory period in the level-surface, and stabilometer conditions were established.

better functional integration of brain networks. In contrast to E_{glob}, which indexes a network property of functional integration (Rubinov and Sporns, 2010; Yu et al., 2013), C_w and E_{loc} reflect a network property of functional segregation (Rubinov and Sporns, 2010; Yu et al., 2013). By contrasting the random and regular networks of the same numbers of nodes and edges (Watts and Strogatz, 1998), the small-world index (σ) can provide the network's small-worldness regarding the balance of information flow between local segregation and global integration in a network (Watts and Strogatz, 1998). When σ is >1, the network exhibits small-world properties (Humphries et al., 2006; Stam et al., 2007a). The small-world index (σ) is mathematically formulated as $\sigma = \gamma/\lambda$. Here, $\gamma = C_w/C_{w_rand}$ and $\lambda = L_p/L_{p_rand}$. The C_w and L_p are the clustering coefficient and the characteristic path length of the functional network. The characteristic path length is formulated as $L_p = \frac{1}{n}\sum_{i\in N} L_i = \frac{1}{n}\sum_{i\in N}\frac{\sum j\in N, j\neq i, \wedge d_{i,j}}{n-1}$, where L_i is the average distance between mode i and all other nodes. Both C_{w_rand} and L_{p_rand} were obtained by averaging 50 populations of random networks. The parameterization of network properties was accomplished with functions of the Brain Connectivity Toolbox (Rubinov and Sporns, 2010).

Statistical Analysis

For behavior data, paired *t*-test was used to examine the significance of differences between the level-surface and stabilometer conditions in normalized force-matching error (NFE), reaction time (RT), amplitude of ankle movement fluctuations (AMF_RMS), and sample entropy of ankle movement fluctuations (AMF_SampEn). Since these resemble behavior variables, paired *t*-test was used to contrast all the network parameters [mean SL of all electrode pairs (SL_all), in the frontal (SL_F), sensorimotor (SL_SM), parietal-occipital (SL_PO) areas, E_{glob}, E_{loc}, and small-world index (σ)] of the level-surface and stabilometer conditions across different threshold values. The significance of the stance effect on modulation of clustering coefficients and the mean SL of all electrode pairs was displayed with *t*-values on the basis of a paired difference

TABLE 1 | Means and standard errors of force-matching and postural variables for the concurrent force-matching and postural tasks in the level-surface and stabilometer conditions.

Mean ± SE	Level-surface	Stabilometer	Statistics
NFE (%)	9.89 ± 0.78	10.01 ± 0.79	$t_{(13)} = -0.328$, $p = 0.748$
RT (ms)	304.8 ± 9.6	310.7 ± 9.8	$t_{(13)} = -1.720$, $p = 0.109$
AMF_RMS (degree)	0.012 ± 0.001	0.151 ± 0.023†††	$t_{(13)} = -6.138$, $p < 0.001$
AMF_SampEn	0.514 ± 0.013	0.382 ± 0.006†††	$t_{(13)} = 8.049$, $p < 0.001$

NFE, normalized force-matching error; RT, reaction time for force-matching; AMF_RMS, root mean square value of ankle movement fluctuations; AMF_SampEn, sample entropy of ankle movement fluctuations; †††*, stabilometer > level-surface, p < 0.001.*

test. The level of significance of the above-mentioned statistical analyses was set at $p = 0.05$. Network-based statistics were performed to identify spectral connectivity in the theta, upper alpha, and beta bands of the node pairs that significantly changed with variations in stance configuration. For this purpose, paired *t*-tests were independently performed at each synchronization value of the spectral bands of interest, and t-statistics larger than an uncorrected threshold of $t_{(13)} = 3.012$ ($p = 0.005$) were extracted into a set of supra-threshold connections. Then we identified all connected components in the adjacency matrix of the supra-threshold links and saved the number of links. A permutation test was performed 5000 times to estimate the null distribution of maximal component size, and the corrected *p*-value was calculated as the proportion of permutations for which the most connected components consisted of two or more links. Methodological details of network-based statistics are documented in Zalesky et al. (2010). Statistical analyses were performed in Matlab (Mathworks Inc. Natick, MA, USA) and SPSS v.19.0 (SPSS Inc. Chicago, IL, USA). All data are represented as mean ± standard error.

RESULTS

Force-Matching and Stance Performance

For the suprapostural task, the paired *t*-test revealed that the force-matching error (NFE: level-surface = 9.89 ± 0.78%; stabilometer = 10.01 ± 0.79%) and reaction time (RT: level-surface = 304.8 ± 9.6 ms; stabilometer = 310.7 ± 9.8 ms) of the force-matching task did not change with stance configuration ($p > 0.05$; **Table 1**). For the postural task, the magnitude of ankle movement fluctuations (AMF_RMS) was stance-dependent, for AMF_RMS of the stabilometer condition (0.151 ± 0.023) was greater than that of the level-surface condition (0.012 ± 0.001; $p < 0.001$). The sample entropy of ankle movement fluctuations (AMF_SampEn) was subject to postural load, for AMF_SampEn (0.382 ± 0.006) was lower in the stabilometer condition than in the level-surface condition (0.514 ± 0.013; $p < 0.001$).

Global Network Metrics and Inter-Regional Connectivity

Figure 3 contrasts different network metrics as a function of threshold value between the level-surface and stabilometer conditions. For the majority of the threshold values, the global coefficient (E_{glob}) and the local coefficient (E_{loc}) in the stabilometer condition were significantly larger than those in the level-surface condition ($p < 0.05$), especially for the higher threshold values. However, the small-world index (σ) was stance-invariant for all threshold values ($p > 0.05$). In terms of synchronization likelihood, we found significant stance effects on inter-regional coupling of ERP in the preparatory stage. The mean values of the SL of all the electrode pairs in the frontal and sensorimotor areas (SL_F and SL_SM) were larger in the stabilometer condition than in the level-surface condition ($p < 0.05$). Mean SL in the parietal-occipital area (SL_PO) showed the reverse trend, with lower SL_PO in the stabilometer condition at lower threshold values (threshold = 0.1, 0.2, 0.3, and 0.4; $p < 0.05$). Overall, the mean SL of all the electrode pairs (SL_all) was enhanced in the stabilometer condition ($p < 0.05$). Except for the small-world index, the network parameters were stance-dependent when the threshold was set to 0.3 or 0.4. **Figure 4** displays the population means of adjacent SL matrices in the two different stance conditions (threshold value = 0.3), as well as *t*-values for the examination of the stance effects on the adjacent matrices. In line with the patterned change in the mean level of SL, adjacent SL matrices in the frontal and sensorimotor areas were enhanced, whereas adjacent SL matrices in the parietal-occipital area were suppressed in the stabilometer condition. **Figure 5A** presents the pooled topology of the clustering coefficients (C_w) for the level-surface and stabilometer conditions (threshold value = 0.3), which suggested different functional segregations between the two stance conditions from the standpoint of information flow. The concurrent postural and force-matching tasks in the level-surface condition exhibited a high probability of node connection to neighbors in the parietal lobes and the right fronto-temporal area, in contrast to high frontal C_w in the stabilometer condition. **Figure 5B** is a topological plot of *t*-values for contrasting the spatial distribution of C_w between the level-surface and stabilometer conditions. The stabilometer condition produced a higher C_w in the mid-frontal area but a lower C_w in the parietal area as compared to those in the level-surface condition ($p < 0.05$).

Network-Based Statistics of Spectral Connectivity

Based on the supra-threshold connectivity and permutation test, network-based statistics revealed localized networks (i.e., connected and clustered components) with significantly stance-dependent SL-values in the theta, upper alpha, and beta bands ($p = 0.0002$, corrected). The contrast of stance-related average values of the spectral connectivity in the pairwise connections of interest is displayed in **Figure 6**. Theta connectivity (4–8 Hz) to the mid-frontal area (F_z, FC_z) was stronger in the stabilometer condition than in the level-surface condition (**Figure 6A**). On the other hand, there was a neat dichotomy of stance-related differences in upper alpha (10–13 Hz) and beta (13–35 Hz) connectivity to the sensorimotor (C_3, C_z, C_4, CP_3, CP_z, and

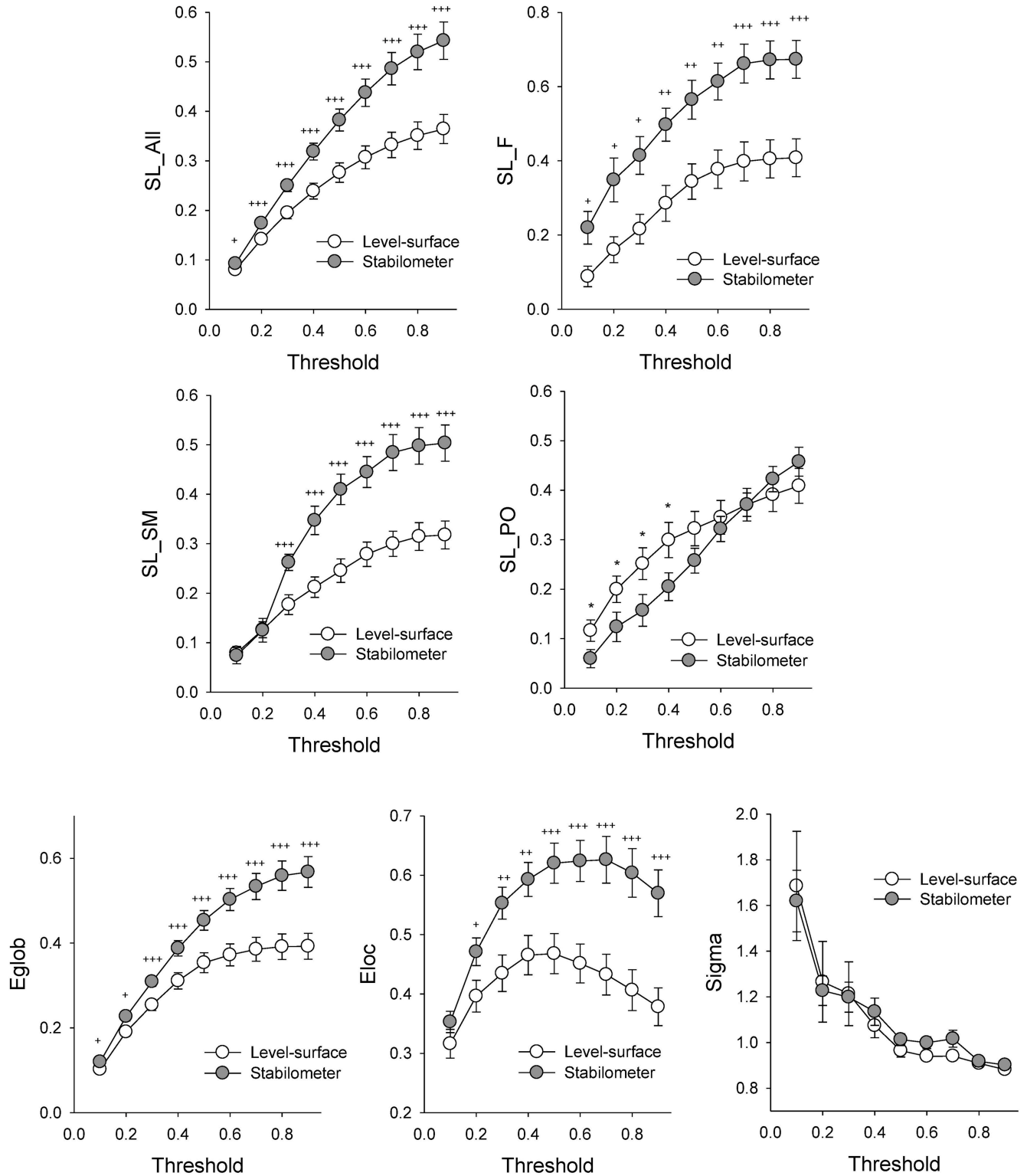

FIGURE 3 | The contrast of network parameters between the concurrent force-matching and postural tasks in the level-surface and stabilometer conditions at different threshold values. E_{glob}, global efficiency; E_{loc}, local efficiency; *Sigma*, small-world index; *, level-surface > stabilometer, $p < 0.05$; †, stabilometer > level-surface, $p < 0.05$; ††, stabilometer > level-surface, $p < 0.01$; †††, stabilometer > level-surface, $p < 0.001$.

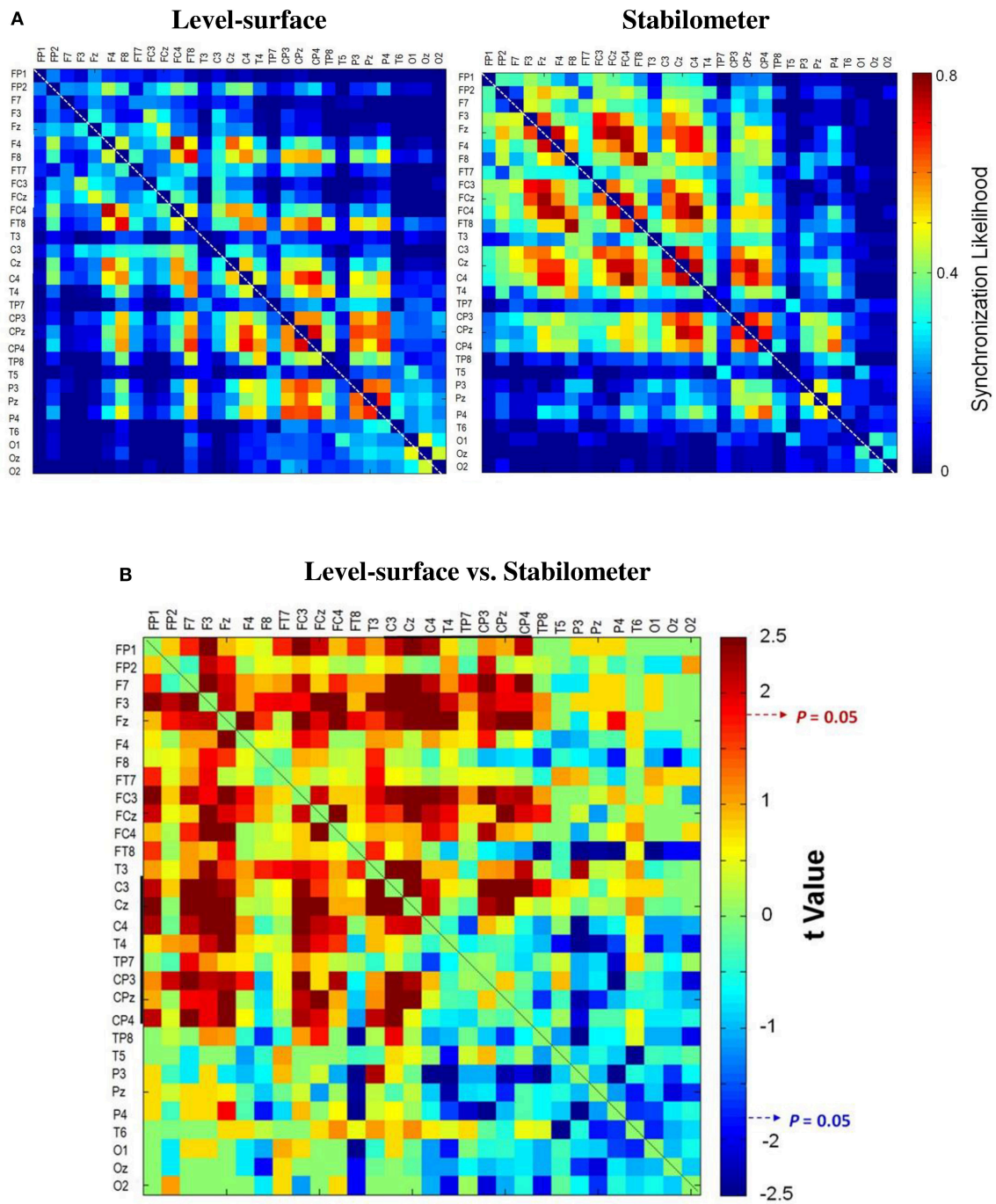

FIGURE 4 | The pooled adjacent matrix of synchronization likelihood (SL) of preparatory ERP for the concurrent force-matching and postural tasks in the level-surface and stabilometer conditions (threshold value = 0.3). (A) Population means of SL adjacent matrix in the surface (left) and stabilometer (right) conditions. **(B)** The adjacent matrix of *t*-values for contrasting SL between the level-surface and stabilometer conditions ($t > 1.771$, stabilometer SL > level-surface SL, $p < 0.05$; $t < -1.771$, level-surface SL > stabilometer SL, $p < 0.05$).

CP_4) and parietal-occipital cortex (P_3, P_z, P_4, O_1, O_z, and O_2; **Figure 6B**). In comparison with the level-surface stance, the upper alpha and beta connectivity to the parietal-occipital cortex, especially the supra-threshold linkages from the right frontal-temporal (FT_8), temporal (TP_8, T_4), and sensorimotor areas (CP_3, CP_z, and CP_4; $p < 0.005$), was significantly suppressed with stabilometer stance ($p < 0.05$). However, the long-distance connectivity of the upper alpha and beta bands to the sensorimotor area (C_3, C_z, C_4, CP_3, CP_z, and CP_4), especially the supra-threshold linkages from the prefrontal and

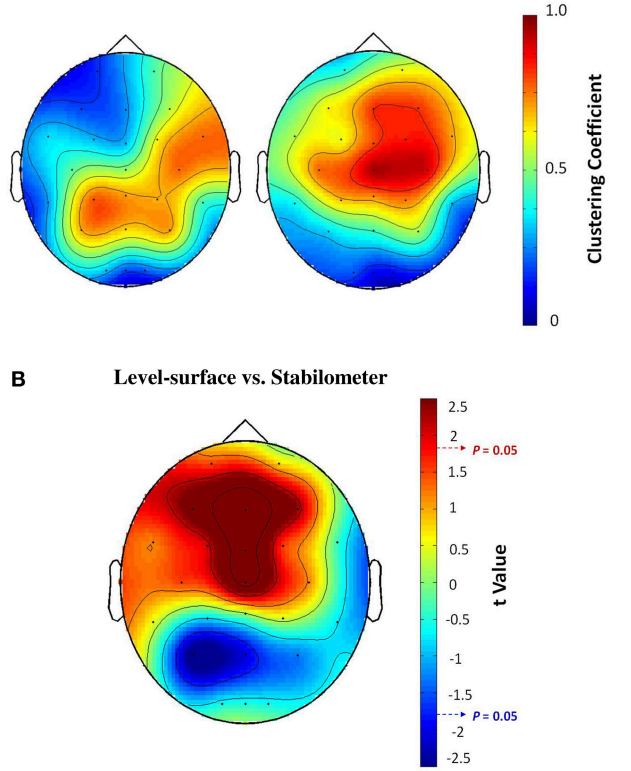

FIGURE 5 | (A) The pooled topological mapping of clustering coefficients (C_W) between concurrent force-matching and postural tasks in the level-surface and stabilometer conditions (threshold value = 0.3). **(B)** The stance-dependent difference in the distribution of clustering coefficients, in terms of the topography of *t*-values plotted on the scalp ($t > 1.771$, stabilometer $C_W >$ level-surface C_W, $p < 0.05$; $t < -1.771$, level-surface $C_W >$ stabilometer C_W, $p < 0.05$).

frontal areas ($p < 0.005$), was enhanced in the stabilometer condition.

DISCUSSION

As expected, the brain adopted a more controlled process for stabilometer stance in respond to increases in the magnitude and regularity of ankle movement. However, the accuracy and reaction time of suprapostural force-matching from stabilometer stance were not significantly affected by increases in postural threats. Our data did not support the facilitation of suprapostural performance by attention withdrawal from the postural task under the framework of resource competition (Cavanaugh et al., 2007; Donker et al., 2007; Derlich et al., 2011; Kuczyński et al., 2011). In fact, the combination of postural and suprapostural tasks of different task loads could result in a variety of performance outcomes, which are not always explainable with behavior contexts. The adaptive resource-sharing hypothesis (Mitra, 2004; Mitra and Fraizer, 2004) seems to be more appropriate for explaining the present observations, for concurrent force-matching was not affected by increasing attentional focus on the postural task. This preliminary study first revealed that brain reorganization under this particular circumstance involved (1) increased efficacy of information transmission, (2) anterior shift of processing resources, and (3) superior network economy in the preparatory period of force-matching.

Enhanced Efficacy of Information Transfer for the Increased Postural Challenge

In light of the global and local efficiencies (E_{loc} and E_{glob}; **Figure 3**, the third row), the information transfer in the brain network was significantly enhanced in the stabilometer condition. Analogous to difficult manipulation of a mathematical task (Klados et al., 2013), the information transfer in brain networks for a postural-suprapostural task consistently increased with stance difficulty for all SL thresholds. The stance-related increase in E_{loc} reflects more short-range connections between neighboring brain regions (particularly in the frontal and premotor areas), by virtue of the high clustering coefficients during concurrent force-matching from stabilometer stance (**Figure 5**). This increasing nodal organization was compelling evidence of context-dependent recruitment of the local frontal area with high postural demands (Mihara et al., 2008; Huang et al., 2014; Mirelman et al., 2014), which allowed the participants to effectively resolve behavioral interference between the component tasks and to plan the timing of force-matching (Pfurtscheller and Berghold, 1989) under the critical posture condition. On the other hand, an enhanced E_{glob} indicates a more optimal network architecture for direct information transfer among distributed regions, commonly seen in skill advancement following motor learning (Sami and Miall, 2013). In the stabilometer condition, the long-distance connectivity between the prefrontal/frontal area and the sensorimotor area (**Figures 4B**, **6B**) facilitates the integration of posture-stabilizing information by selectively gating sensory inputs from multiple sources from the sensorimotor area with the central executive function. However, the small-world property (*sigma*) did not vary with stance configuration (**Figure 3**), indicating a stance-independent balance between local processing specialization and global information propagation.

Anterior Shift in Processing Resources in the Stabilometer Condition

The second major finding of this study was that the increase in stance difficulty caused an anterior shift in processing resources for force-matching from stabilometer stance, in support of several lines of evidence, including increasing frontal emphasis of the SL adjacent matrix (**Figures 3**, **4**), potentiation of frontal clustering coefficients (**Figure 5B**), enhancement of mid-frontal theta connectivity (**Figure 6A**), and increases in inter-regional coupling from frontal to sensorimotor networks in the upper alpha and beta bands (**Figure 6B**). These scenarios jointly suggested a transition of the postural-suprapostural task, which is typically regulated by the frontal-parietal executive

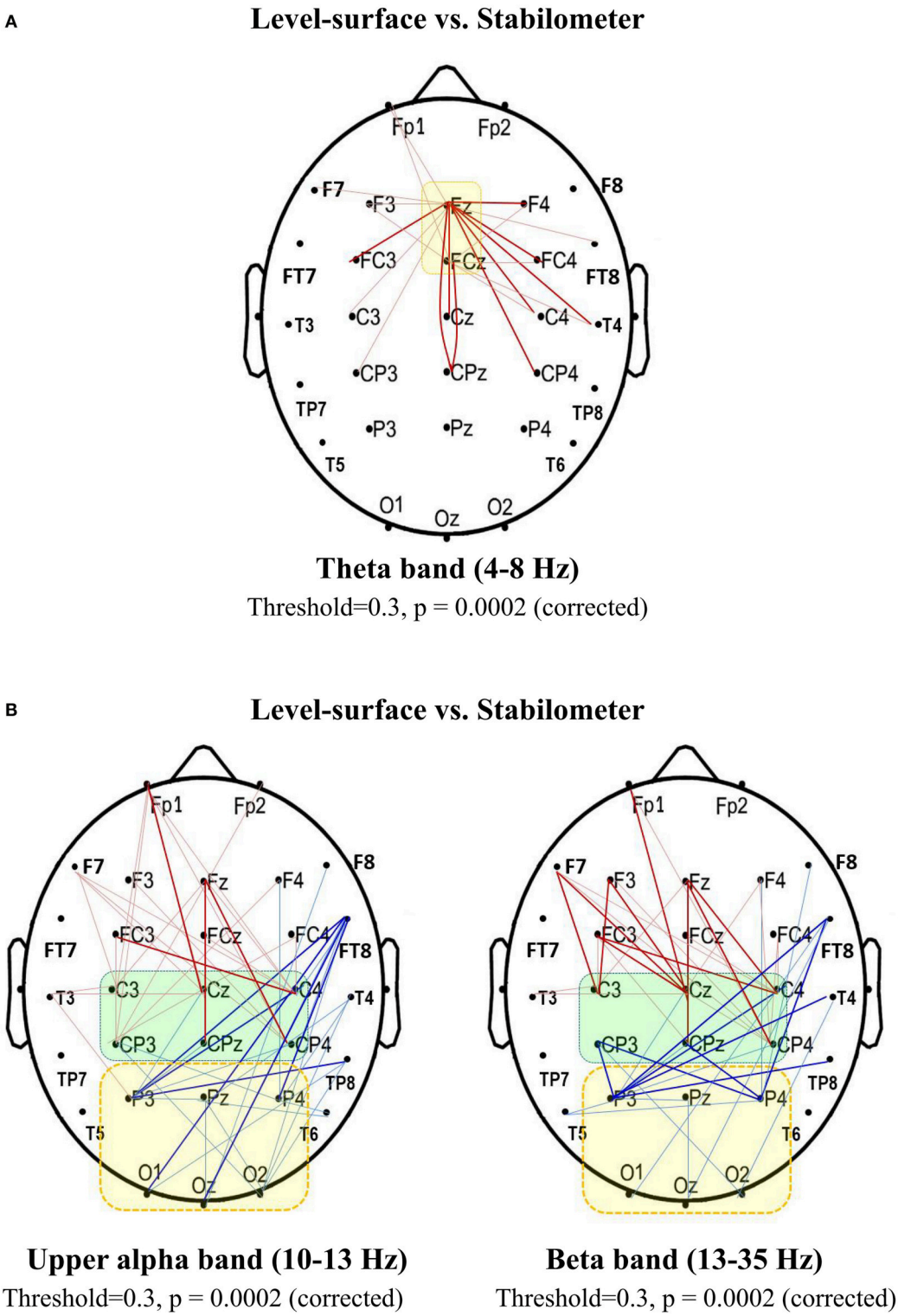

FIGURE 6 | Spectral connectivity analysis for contrasting wiring diagrams between the concurrent force-matching and postural tasks in the level-surface and stabilometer conditions (threshold value = 0.3). (A) Synchronization likelihood in the theta band (4–8 Hz) that connects to the mid-frontal area (F_Z and FC_Z). **(B)** Synchronization likelihood in the upper alpha (10–13 Hz) and beta band (13–35 Hz) of recording electrodes that connect to the sensorimotor (C_3, C_Z, C_4, CP_3, CP_Z, and CP_4) and parietal-occipital (P_3, P_Z, P_4, P_3, O_1, O_Z, and O_2) areas (thin red line, stabilometer connectivity > level-surface connectivity, $p < 0.05$; bold red line, stabilometer connectivity of supra-threshold > level-surface connectivity of supra-threshold, $p < 0.005$; thin blue line, level-surface connectivity > stabilometer connectivity, $p < 0.05$; bold blue line, level-surface connectivity of supra-threshold > stabilometer connectivity of supra-threshold, $p < 0.005$).

system in the level-surface condition, to a state in which the frontal strategic control prevails for concurrent force-matching from the stabilometer stance (Slobounov et al., 2009; Ferraye et al., 2014; Karim et al., 2014). The stabilometer stance altered brain resource reallocation in at least three different aspects: recruitment of resources necessary for dealing with the postural instability, target detection for force-matching, and task-switching associated with the increase in postural load. First, the additional recruitment of frontal executive resources was partly attributable to the attentional focus being shifted to postural destabilization due to variations in stabilometer movement (Dault et al., 2001), as previous studies have found from recording cortical activation in the prefrontal cortex, frontal cortex, and supplementary motor area following posture perturbation (Mihara et al., 2008; Fujimoto et al., 2014). Next, stabilometer movement aggravated externally-induced retinal image motion, adding difficulty to the action monitoring and error detection with visual feedback for force-matching (Sipp et al., 2013; Hülsdünker et al., 2015). Therefore, the enhanced mid-frontal theta activity could also reflect heightened selective attention to improve gaze stability for the detection and prediction of target movements (Mihara et al., 2008). Third, for a postural-suprapostural setup with a suprapostural motor goal, the amplitudes of the N1 and P2 components in the preparation period are related to variations in the task-load of the postural and suprapostural tasks, respectively (Huang and Hwang, 2013). This fact clearly suggests that tasks are scheduled in a sequential order to execute a force-matching act with postural prioritization. Since switch costs are greater when switching from a more difficult task to an easier task (Schneider and Anderson, 2010; Barutchu et al., 2013), the switch cost from the postural task to force-matching in the stabilometer condition was multiplied, entailing an extra computational load on frontal executive function (Liefooghe et al., 2008) in the preparatory period. In addition to increases in the SL_F and frontal clustering coefficients, it was of great significance to observe the increases in the connectivity of functionally specialized regions between the left prefrontal area (Fp_1) and sensorimotor cortex (C_3, C_4, C_z, CP_3, CP_4, and CP_z) in the upper alpha (10–13 Hz) and beta (13–35 Hz) bands (**Figure 6B**). Such long-distance connectivity well explains the greater global coefficient (E_{glob}) for concurrent force-matching and stabilometer stance (**Figure 3**), suggesting underlying cooperative activities within the dorsolateral prefrontal cortex, anterior cingulate cortex, and supplementary motor area (Kondo et al., 2004; Hashimoto et al., 2011). Taxing frontal resources for concurrent postural-suprapostural tasks under high postural threats conceptually supports the previous thinking that the prefrontal or frontal network could be a common bottleneck for dual-tasks (Dux et al., 2006). In addition, the overall increase in functional connectivity (SL_all) with a frontal emphasis is direct neurophysiological evidence of increasing stance-related attentional control over a postural-suprapostural task with increasing postural difficulty, hypothetically indexed with entropy measures of the posture component task (**Table 1**) and previous work (Donker et al., 2007; Stins et al., 2009).

Brain Network Economy for Postural-Suprapostural Task with Increased Postural Challenge

The most interesting finding was a strategic trade-off to avoid a resource ceiling by reducing reliance on the temporal-parietal-occipital network, when the stance difficulty increased for a postural-suprapostural dual-task. In a challenging posture such as the stabilometer condition, stronger inter-dependencies among the temporal-parietal junction (Tachibana et al., 2011; Karim et al., 2013) and parietal-occipital areas (Slobounov et al., 2005, 2009; Pellijeff et al., 2006) are expected, as the subjects needed to depend on an enhanced vestibule-ocular response, visual-proprioceptive control, and motion vision to establish dynamic representations of body schema due to postural destabilization. However, in view of the lower SL_PO (**Figures 3**, **4**) and parietal clustering coefficients (**Figure 5**), the present study conversely exhibited desynchronization of the parietal-occipital network. Moreover, the spectral connectivity of the upper alpha and beta bands in the temporal-parietal-occipital regions (particularly in the right hemisphere) was suppressed during concurrent force-matching from a stabilometer (**Figure 6B**). These facts suggest neural economy to prevent excessive consumption of brain resources, affected by restricting the division of attentional resources toward multisensory information before the force-matching act from the stabilometer stance. It seems that the visuospatial attention to postural control to detect enhanced postural fluctuations could be temporarily disengaged during preparation to execute a force-matching task. We argue that the information inhibition is potentially advantageous in that it increases the resources allocated to frontal executive function, empowering conflict detection, task switching, and facilitation of the suprapostural goal. Due to the flexible resource allocation, the accuracy and responsiveness of force-matching were not affected by postural destabilization (**Table 1**). Supporting the notion of a domain-specific idling of dorsal networks to prevent a resource ceiling, previous neuroimaging studies also reported a comparable neural economy under the condition of relatively high postural threats. Imaged locomotion produced lower activity in the vestibular and somatosensory (right hemisphere preponderance) areas than that during imagined standing (Jahn et al., 2004; Zwergal et al., 2012). However, it should be noted that resource allocation for a dual-task is context dependent. During the concurrent execution of two verbal tasks, Mizuno et al. (2012) found no significant connectivity changes in the parietal and temporal areas with increases in task load. Classic dual task setups (cognitive or verbal tasks) might have very different task compatibilities and reciprocal effects from a postural-suprapostural task (Huang and Hwang, 2013), since a postural subtask is always prioritized naturally, consuming a variety of brain resources.

Methodology Issue

The execution of postural-suprapostural tasks must rely on coordination interactions of neuronal sources across distributed brain regions. Among the several quantitative approaches,

SL was used to characterize the inter-dependences between two cortical activities because it is the most popular index for estimating functional connectivity for neurophysiological data. SL has been widely been used to assess connectivity strength in the graphic based studies using either low-density (Pijnenburg et al., 2004; Smit et al., 2012; Boersma et al., 2013; Liu et al., 2015; Herrera-Díaz et al., 2016) or high-density EEG (Polanía et al., 2011; Cao et al., 2014), because SL is able to account for the repertoire of network states, considering linear and nonlinear interactions between multiple synchronized neural sources in the brain (Stam and van Dijk, 2002). Also, SL can sensitively detect slight and complex variations in the coupling strength (Koenis et al., 2013) and resolve synchronization patterns on a fine time scale (Stam and van Dijk, 2002; Betzel et al., 2012). These advantages were especially helpful in highlighting stance-related differences in rapid dynamic of the ERP with low-frequency oscillations (such frontal theta synchronization and long-stance upper alpha desynchronization; **Figures 6A,B**). However, a few researchers based on stimulation studies to argue that SL is not immune to a volume conduction effect that might cause spurious coupling from common diploe sources (Stam et al., 2005; Tognoli and Kelso, 2009). If the physical synchronization did exist during the experiment, we could not conclusively deny overestimation of the observed differences in local clustering schema, since correlations generated from single diploes tend to be strongest within neighboring electrodes. Despite a potential volume conduction effect, physical synchronization did not rationally explain the patterned changes in network connectivity of the frontal, sensorimotor, and parietal-occipital networks (**Figures 4B**, **5B**), as a global rise or fall of state transition was not influenced by intermittent activity of a single common source. In addition, the stance-dependent changes in network properties of spatially distributed communities was observed across the threshold values (**Figure 3**), which are hard to reconcile with known spatial influences due to volume conduction. To date, there is no perfect mathematical tool to assess inter-regional connectivity. Although some measures of inter-regional connectivity have been proposed to counter common sources like phase lag index (Stam et al., 2007b), yet these phase-based approaches actually measures different inter-dependence properties of regional EEG signals as the SL. In fact, phase-based approaches can be more susceptible to small perturbations (Vinck et al., 2011), raising another validity issue to identify ERP connectivity in the presence of noise and non-stationarities (Cohen, 2015). Therefore, a further study may consider EEG recordings simultaneously with BLOD activation patterns for methodological exactness. However, it is beyond the scope in this study to utterly preclude hypothetical common source with the present setup.

Next, in addition to stimulus-locked ERP used in this study, an alternative analysis is to lock EEG activity with force-matching event (response-locked ERP). The selection of time-lock depends on the experimental design to highlight different information processing underlying response preparation. The response-lock approach is recommended, if the experiment does not change premotor processing (Mordkoff and Gianaros, 2000). When response preparation varies with experimental manipulation, information processing in the time domain is stretched or compressed with the use of response-locked ERP. As reaction time of force-matching was hypothesized to vary with the effect of stance configuration, we favored stimulus-locked ERP to assess dual-task effects in this study. Analysis using response-locked ERP seems to be more popular in those single motor task experiments.

CONCLUSIONS

With brain connectivity analysis, the present work highlights the availability of adaptive resource allocation to explain concurrent suprapostural performance that is insusceptible to increasing postural load. Theoretical graphic analysis validated the hypothesis that brain reorganization would lead to a functional network with superior efficacy and global information transfer to cope with increasing stance difficulty for a postural-suprapostural task. In addition, we have identified fine-grained details regarding cost-effective mechanisms for this particular dual-task condition, involving an anterior shift to frontal processing resources and dorsal idling of the parietal-occipital networks.

AUTHOR CONTRIBUTIONS

Substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data for the work: Conception or design of the work, CH, IH; Acquisition, YT; Analysis, GC, IH; Interpretation of data, CH, IH. Drafting the work or revising it critically for important intellectual content: CH, GC, YT, IH. Final approval of the version to be published: CH, GC, YT, IH. Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved: CH, GC, YT, IH.

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REVIEW
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Effects of Muscle Fatigue, Creep, and Musculoskeletal Pain on Neuromuscular Responses to Unexpected Perturbation of the Trunk: A Systematic Review

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Introduction: Trunk neuromuscular responses have been shown to adapt under the influence of muscle fatigue, as well as spinal tissue creep or even with the presence of low back pain (LBP). Despite a large number of studies exploring how these external perturbations affect the spinal stability, characteristics of such adaptations remains unclear.

Aim: The purpose of this systematic review was to assess the quality of evidence of studies investigating trunk neuromuscular responses to unexpected trunk perturbation. More specifically, the targeted neuromuscular responses were trunk muscle activity reflex and trunk kinematics under the influence of muscle fatigue, spinal creep, and musculoskeletal pain.

Methods: A research of the literature was conducted in Pubmed, Embase, and Sport-Discus databases using terms related to trunk neuromuscular reflex responses, measured by electromyography (baseline activity, reflex latency, and reflex amplitude) and/or trunk kinematic, in context of unexpected external perturbation. Moreover, independent variables must be either trunk muscle fatigue or spinal tissue creep or LBP. All included articles were scored for their electromyography methodology based on the "Surface Electromyography for the Non-Invasive Assessment of Muscles (SENIAM)" and the "International Society of Electrophysiology and Kinesiology (ISEK)" recommendations whereas overall quality of articles was scored using a specific quality checklist modified from the Quality Index. Meta-analysis was performed on reflex latency variable.

Results: A final set of 29 articles underwent quality assessments. The mean quality score was 79%. No effect of muscle fatigue on erector spinae reflex latency following an unexpected perturbation, nor any other distinctive effects was found for back muscle fatigue and reflex parameters. As for spinal tissue creep effects, no alteration was found for any of the trunk reflex variables. Finally, the meta-analysis revealed an increased

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erector spinae reflex latency in patients with chronic LBP in comparison with healthy controls following an unexpected trunk perturbation.

Conclusion: The literature provides some evidence with regard to trunk adaptions in a context of spinal instability. However, most of the evidence was inconclusive due to a high methodological heterogeneity between the studies.

Keywords: electromyography, kinematics, reflex, spinal stability, low back pain, fatigue, ceep

INTRODUCTION

Postural balance is constantly challenged, sometimes unexpectedly, by mechanical forces applied in different directions and continuously triggering postural adjustments. In expected conditions, prior to any movement, the central nervous systems triggers muscles activation/deactivation, and then a movement occurs after a short period of a few milliseconds. These pre-planned adjustments are considered anticipatory postural adjustments (Belen'kii et al., 1967; Bouisset and Do, 2008). For instance, trunk postural adjustments can be represented by early muscle activations (Bouisset and Zattara, 1981; Hodges and Richardson, 1997), as well as increases in muscle activity prior to any external perturbation (Lavender et al., 1993; Cresswell et al., 1994; Moseley et al., 2003) that are believed to contribute to spinal stability. On the other hand, when subjected to unexpected external perturbations of the trunk, muscle activation is delayed (Eriksson Crommert and Thorstensson, 2009), leaving the spine with reduced stability for few milliseconds. Spinal stability is defined as the harmonious cohesion between active muscles surrounding the spine, passive spinal tissues, and neuromuscular control (Panjabi, 1992).

When one or more of these spinal stability components are challenged, adaptations in the trunk system occurs in order to maintain a certain performance level in everyday functional motor tasks. Over the past decades, fundamental research efforts have focused on the quantification of these adaptations through the analysis of trunk muscle activity recordings and trunk kinematic data. Challenges to spinal stability have been commonly investigated using muscle fatigue, spinal tissue creep but also by studying patients with low back pain (LBP). Challenging trunk stability using muscle fatigue has been associated with adaptations in muscle activity recruitment patterns, such as trunk flexor and extensor co-contraction phenomena (Allison and Henry, 2001). Reorganization in spatial low back muscle activity have also been described as a potential strategy to offset muscle fatigue effects (Tucker et al., 2009; Abboud et al., 2014). Moreover, the observation of an altered coordination of trunk muscle activation, a decreased control of trunk movements (Boucher et al., 2012), and alterations in lumbopelvic dynamics have been reported under the influence of muscle fatigue (Descarreaux et al., 2010). Similar trunk neuromuscular adaptations have been observed when passive tissue components of spinal stability are challenged. Active or passive prolonged deep flexions of the trunk, which is believed to generate spinal tissue creep, are usually followed by an increase in trunk flexion range of motion (Rogers and Granata, 2006; Howarth et al., 2013; Olson, 2014). Moreover, an increase in back muscle activity has also been described as a compensating mechanism for the reduced contribution of passive tissues to spinal stability (Olson et al., 2004; Shin et al., 2009; Abboud et al., 2016). Neuromuscular control of the trunk, such as trunk coordination and trunk muscle activation, is commonly altered in patients with chronic LBP (Hodges, 2011; Hodges and Tucker, 2011; Abboud et al., 2014). For example, patients with chronic LBP show longer time-delay of trunk muscle activation during a predictable perturbation (Hodges and Richardson, 1998). Overall, challenges to spinal stability components have been associated with numerous alterations in trunk neuromuscular control.

To investigate neuromuscular adaptations to unexpected trunk perturbations, most studies report adaptations in electromyography (EMG) recordings based on the analysis of baseline activity, reflex latency, and reflex amplitude. However, high heterogeneity in EMG reflex variable analyses led to conflicting results and an incomplete understanding of stabilizing responses to unexpected trunk perturbations. Indeed, most of the studies report different criteria to detect spinal reflex parameters. For instance, baseline activity, also called pre-activation level, is calculated from different time windows ranging from 50-ms to 3-s prior to the onset of an unexpected trunk perturbation (Newcomer et al., 2002; Granata et al., 2004, 2005; Herrmann et al., 2006; Rogers and Granata, 2006; Stokes et al., 2006; Mawston et al., 2007; Grondin and Potvin, 2009; Dupeyron et al., 2010; Lariviere et al., 2010; Ramprasad et al., 2010; Bazrgari et al., 2011; Hendershot et al., 2011; Jacobs et al., 2011; Jones et al., 2012a; Liebetrau et al., 2013; Miller et al., 2013; Muslim et al., 2013; Olson, 2014). The onset of EMG reflex, also called reflex latency, is generally calculated, using the standard deviation method proposed by Hodges and Bui (1996). Although, two standard deviations (SD) seems to be the most used reflex onset detection method (Granata et al., 2004, 2005; Herrmann et al., 2006; Rogers and Granata, 2006; Dupeyron et al., 2010; Lariviere et al., 2010; Ramprasad et al., 2010; Bazrgari et al., 2011; Hendershot et al., 2011; Toosizadeh et al., 2013; Olson, 2014), few others studies used alternate standard deviations values, such as 1.4 SD (Radebold et al., 2000, 2001; Cholewicki et al., 2002), 1.5 SD (Reeves et al., 2005), 3 SD (Stokes et al., 2006; Gao et al., 2014; Akbari et al., 2015), and 4 SD (Liebetrau et al., 2013). Sometimes, the EMG reflex onset is also determined by visual inspection of EMG signals (Newcomer et al., 2002; Mawston et al., 2007; Sanchez-Zuriaga et al., 2010). Maximal amplitude value is usually the predominant method to determine reflex amplitude (Granata et al., 2004, 2005;

Herrmann et al., 2006; Rogers and Granata, 2006; Grondin and Potvin, 2009; Dupeyron et al., 2010; Sanchez-Zuriaga et al., 2010; Liebetrau et al., 2013; Olson, 2014). However, a few studies have also examined reflex amplitude through EMG time windows of various duration (i.e., 10- to 75-ms windows; MacDonald et al., 2010; Ramprasad et al., 2010; Jacobs et al., 2011; Jones et al., 2012a,b; Shenoy et al., 2013). Finally, and perhaps of utmost importance, authors seems to disagree on what should be consider as reflex responses or voluntary movements. Indeed, some authors consider that muscle activity responses longer than 120-ms should be considered non-reflexive (Granata et al., 2005; Herrmann et al., 2006; Rogers and Granata, 2006; Dupeyron et al., 2010; Jacobs et al., 2011) while other authors included responses occurring between the perturbation onset and 150-ms (Lariviere et al., 2010; Bazrgari et al., 2011; Toosizadeh et al., 2013; Olson, 2014), 200-ms (Liebetrau et al., 2013), 250-ms (Cholewicki et al., 2002), and 300-ms (Radebold et al., 2001).

While there is no doubt that spinal reflexes play a major role in spinal stability mechanisms (Moorhouse and Granata, 2007), well-standardized measurement protocols enabling a better understanding of neurophysiological adaptations to unexpected trunk perturbation are still lacking. Consequently, the main purpose of this study was to systematically assess the quality of evidence of studies investigating neuromuscular responses to unexpected trunk perturbation. More specifically, the targeted neuromuscular responses were trunk muscle activity reflex and trunk kinematics under the influence of muscle fatigue, spinal creep, and musculoskeletal pain. This review also addresses two fundamental questions: What are the most relevant EMG and kinematic variables to properly observe and study neuromuscular adaptions to unexpected loading of the trunk? Are neuromuscular adaptations to unexpected perturbations similar under the influence of erector spinae muscle fatigue, musculoskeletal LBP and spinal creep deformation? We believe that the results of this review will guide future research in the field of trunk neuromuscular control. Moreover, this review may have some potential applications in the development of standardized functional spinal evaluation and biomedical engineering diagnostic tools, as well as progress in ergonomic risk assessment strategies.

MATERIALS AND METHODS

Registration

This review protocol was registered in PROSPERO International Prospective Register of Systematic Reviews on May 27, 2016 (CRD42016039374).

Search Strategy

Searches were performed in Pubmed, Embase, and Sport-Discus databases in May 2016 without any time limit. A systematic search of the literature was conducted using the following keywords and search terms alone and in combination: (Perturbation OR Unexpected perturbation OR Postural perturbation OR Sudden release OR Sudden loading OR Quick release OR External load) AND (Back OR Spine OR Spinal OR Trunk OR Lumbar) AND (Muscle fatigue OR Fatigue OR Muscle endurance OR Back pain OR Lumbar impairment OR Stretch OR Creep OR Viscoelastic deformation OR Passive tissue OR Paraspinal tissue OR Prolonged flexion OR Tension–relaxation OR Stiffness OR Static flexion OR Cyclic movement OR Flexion OR Passive movement). Additional data sources included the authors' pre-existing knowledge of the literature, manual review of reference lists of laboratory studies and forward citation tracking. Search strategy is presented in the Appendix A in Supplementary Material.

Eligibility Criteria

Only experimental studies in a controlled environment were selected for this review. Letters, editorials, commentaries, unpublished manuscripts, books and book chapters, conference proceedings, cost analyses, narrative reviews, systematic reviews, clinical practice guidelines were excluded from the study. Studies measuring the effects of any intervention program on trunk stabilization (wearing a lifting belt, rehabilitation, exercise, pharmacology...) were excluded as well. The search strategy was restricted to English and French publications.

Studies were included for subsequent methodological quality assessments if the following criteria were all satisfied: (1) postural perturbation was unexpected; (2) one or more trunk muscle response to postural perturbation was studied; (3) main outcome measure was either trunk muscle reflex recorded with EMG or trunk movement following perturbation; (4) independent variables were erector spinae muscle fatigue or spinal tissue creep or non-specific LBP; (5) human adults participants were tested.

Study Selection

Two independent reviewers (JA, AL) screened citation titles and abstracts to identify the potential eligible articles. A third reviewer (MD) was consulted to resolve any disagreement between the reviewers. Once this first step was done, the relevant full texts were assessed by three independent reviewers (JA, FB, AL) to verify if they could be included in the review according to the five inclusion criteria described previously. In case of disagreement, the two others authors (CD and MD) were consulted. The flowchart of the study has been reported in **Figure 1**. Excluded articles and the reasons for exclusion were explained in this figure.

Tools Used in the Risk of Bias Assessment

To our knowledge, no validated assessments checklists are available to evaluate the quality of laboratory studies including EMG. Therefore, a custom quality checklist adapted from the Quality Index developed by Downs and Black (Downs and Black, 1998) for the first part and based on the "Surface Electromyography for the Non-Invasive Assessment of Muscles (SENIAM)" (Hermens et al., 1999) and the "International Society of Electrophysiology and Kinesiology (ISEK)" (Merletti, 1999) recommendations for the EMG quality assessment for the second part was created in relation to the specific needs of the objectives of this review.

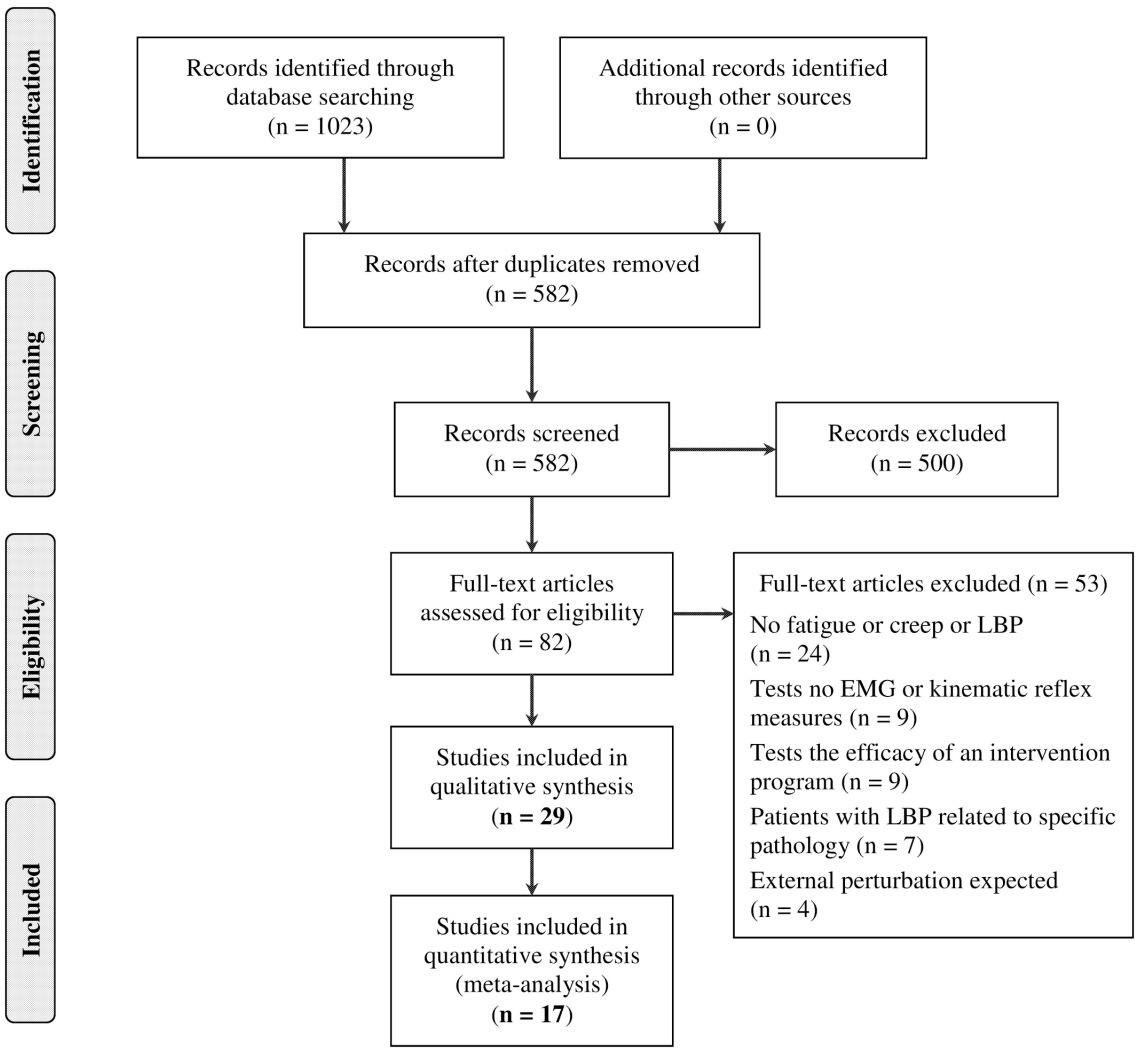

FIGURE 1 | Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flowchart of the literature search.

Quality Index

The Quality Index is a 27-item checklist for assessing the methodological quality of both randomized and non-randomized studies of health care interventions (Downs and Black, 1998). This tool has been extensively used in the literature and presents a good test-retest reliability ($r = 0.88$) as well as a good inter-rater reliability ($r = 0.75$). From the original 27 items, it was decided during a consensus meeting to create a modified version of the Quality Index using 10 items which were deemed relevant in the assessment of the selected studies (for more details of each items, see Appendix B in Supplementary Material). From the initial Quality Index, 7 items were selected from the category "*reporting part*" (Items 1, 2, 3, 4, 6, 7, 10). Those items assessed if the information provided by the authors allow the reader to have an unbiased view of the study findings. Among the "*external validity*" category, which assesses the overall generalizability of the results, only one item was selected (item 12). Finally, 2 of the 6 items (Items 16, 18) for "*Internal validity—Bias*" were also selected. Each item was scored 0 or 1. When applicable, item 4 "*are the interventions of interest clearly described?*" was divided in two subcategories (item 4.1: description of the perturbation protocol and item 4.2: description of either the muscle fatigue protocol, or the spinal creep protocol). Both of these subcategories were also scored 0 or 1 when applicable. The total maximum score was either 10 or 11 for this section of the checklist.

EMG

Electromyography was the main outcome from all the studies included in this review. Based on SENIAM (Hermens et al., 1999) and ISEK (Merletti, 1999) recommendations, the assessment checklist quality was divided in 4 main categories: (1) Surface EMG sensors: 1.1: inter electrode distance, 1.2: material (Ag/AgCl), and 1.3: construction (bipolar). (2) Sensor placement and location: 2.1: Skin preparation, 2.2: placement, and fixation, 2.3: reference electrode and orientation

on muscle. (3) Signal processing: 3.1: Filters (type, kind, bandwidth, and order), 3.2: rectification method (full wave, half wave), 3.3: sampling (manufacturer/type of analogue-to digital (A/D) conversion board, sampling frequency, number of bits, input amplitude range), 3.4: amplitude processing (smoothing, average rectified value, root mean square, integrated EMG), and (4) normalization. Each main categories was scored 0 or 1. For the first three main categories, a score of 1 was only attributed when a minimum of 2 items of each category was reported. On the contrary, a score of 0 was attributed. When normalization item was not applicable (i.e., only reflex latency outcome), the total EMG quality score was 3.

Quality Total Score

Depending of the item 4 and normalization scoring, the total maximum quality score was either 13, 14, or 15. The total quality score for each study was expressed as percentage to facilitate comparison between them.

Risk of Bias Assessment

Three of the authors (JA, AL, FB) independently assessed the quality of included studies. Assessments were then compared during a formal meeting. Two others authors (CD, MD) were involved in resolving any disagreement between the three first authors when a consensus was not reach after the meeting. If additional information was required to complete the assessment, the corresponding authors of the included studies were contacted.

Data Extraction and Synthesis

The first authors (JA) extracted data from the selected studies and completed the evidence table (Appendix C in Supplementary Material).

Statistical Analyses

Inter-rater reliability of the methodological quality checklist was assessed using Fleiss's Kappa statistic with divisions suggested by Landis and Koch (<0.00, poor; 0.00–0.20, slight; 0.21–0.40, fair; 0.41–0.60, moderate; 0.61–0.80, substantial, 0.81–1.00, almost perfect; Landis and Koch, 1977). Meta-analysis could only be performed on reflex latency results because all the authors reported their results with the same unit (ms) while for the other EMG variables, authors reported their results using different units (% of MVC, μV with or without normalization) and it was not possible to pool these outcomes variables together in the same statistical model. To perform the meta-analysis, a random effect model was used since the samples of the included studies did not emanate from the same underlying study population. Meta-analysis were performed using Stata statistical software (College Station, TX: StataCorp LP. 2013). The heterogeneity across the studies was reported as the I^2 (Higgins et al., 2003). It was decided to report a large heterogeneity that was found instead of not reporting the results of the existing evidence.

RESULTS

Search Results

A total of 582 articles were identified from the literature search and 29 articles fulfilled selection criteria. A summary of the search results is presented in **Figure 1**.

Inter-Rater Reliability

The inter-rater reliability, measured by Kappa values, of all items from the quality checklist and EMG quality checklist ranged from moderate to almost perfect (0.52–1.00). As for the % of disagreement, the highest values were found for checklist items 1 (objectives clearly described) and 2 (EMG reflex outcomes clearly described) with 17% of disagreement, item 4a (perturbation protocol clearly described), 6 (EMG reflex response clearly described), and EMG 2.4 (electrode orientation on muscle) with 14% of disagreement (**Table 1**). General agreement among raters was at 90% or more for all other methodological quality checklist items. Item 18 (statistical tests appropriate) was excluded from the inter-rater analysis since, an external assessor helped the three authors (JA, AL, FB) assess this item for most of the included studies. A consensus was reached for each article.

Quality Assessment

Results of the adapted version of the Quality Index are presented in **Table 2**. The mean score obtained from all

TABLE 1 | Inter-rater reliability of quality checklist items [Kappa (95% Confidence interval) and % of disagreement].

	Items	Fleiss's Kappa (95% CI)	% disagreement
Quality index checklist	1	0.66 (0.45–0.87)	17
	2	0.52 (0.31–0.73)	17
	3	0.82 (0.61–1.03)	14
	4a	0.58 (0.37–0.79)	7
	4b	1.00	0
	6	0.55 (0.34–0.76)	14
	7	1.00	0
	10	0.85 (0.64–1.06)	10
	12	0.80 (0.59–1.01)	10
	16	1.00	0
EMG quality checklist	1.1	1.00	0
	1.2	0.94 (0.72–1.15)	3
	1.3	0.91 (0.70–1.12)	3
	2.1	1.00	0
	2.2	0.74 (0.53–0.95)	3
	2.3	1.00	0
	2.4	0.78 (0.57–0.99)	14
	3.1	1.00	0
	3.2	0.91 (0.70–1.12)	3
	3.3	1.00	0
	3.4	0.58 (0.37–0.79)	7
	4	0.86 (0.63–1.09)	7

TABLE 2 | Quality Index assessment scores (*Studies investigated the effect of low back pain were rated using a 10 point scale).

Authors (year)	1	2	3	4a	4b	6	7	10	12	16	18	Score (/10* or /11)	Score (%)
Akbari et al., 2015	0	1	1	1	n/a	1	1	1	0	1	0	7*	70
Bazrgari et al., 2011	1	0	1	1	1	1	1	1	0	1	1	9	81.8
Dupeyron et al., 2010	1	1	0	1	1	1	1	0	0	1	1	8	72.7
Gao et al., 2014	1	0	1	1	n/a	1	1	1	1	1	1	9*	90
Granata et al., 2001	1	0	0	1	1	0	1	0	0	1	1	6	54.6
Granata et al., 2005	1	1	0	1	1	1	1	1	0	1	1	9	81.8
Granata et al., 2004	1	1	0	0	1	1	1	0	0	1	0	6	54.6
Grondin and Potvin, 2009	1	1	0	1	1	1	1	0	0	1	1	8	72.7
Hendershot et al., 2011	1	1	1	1	1	1	1	1	0	1	1	10	90.9
Herrmann et al., 2006	0	1	0	1	1	1	1	1	0	1	1	8	72.7
Jacobs et al., 2011	1	1	1	1	n/a	1	1	1	1	1	1	10*	100
Jones et al., 2012a	1	1	1	1	n/a	1	1	0	1	1	0	8*	80
Jones et al., 2012b	1	1	1	1	n/a	1	1	1	1	1	1	10*	100
Lariviere et al., 2010	1	1	1	1	n/a	1	1	1	0	1	1	9*	90
Liebetrau et al., 2013	0	1	0	1	n/a	1	1	0	0	1	1	6*	60
MacDonald et al., 2010	1	1	1	1	n/a	1	1	1	0	1	1	9*	90
Mawston et al., 2007	1	1	0	1	1	1	1	1	0	1	1	9	81.8
Muslim et al., 2013	1	1	1	1	1	1	1	1	0	1	1	10	90.9
Newcomer et al., 2002	1	1	1	1	n/a	1	1	1	0	1	1	9*	90
Olson, 2014	1	1	0	1	1	1	1	1	0	1	1	9	81.8
Radebold et al., 2000	1	1	0	1	n/a	1	1	0	0	1	0	6*	60
Radebold et al., 2001	1	1	1	1	n/a	1	1	0	0	1	0	7*	70
Ramprasad et al., 2010	1	0	0	1	n/a	0	1	0	1	1	0	5*	50
Reeves et al., 2005	0	1	1	1	n/a	1	1	1	0	1	1	8*	80
Rogers and Granata, 2006	1	1	0	1	1	1	1	1	0	1	1	9	81.8
Sanchez-Zuriaga et al., 2010	1	1	0	1	1	1	1	1	0	1	1	9	81.8
Shenoy et al., 2013	1	0	0	1	n/a	0	1	0	0	0	0	3*	30
Stokes et al., 2006	1	1	0	1	n/a	1	1	0	1	1	0	7*	70
Toosizadeh et al., 2013	1	1	1	1	1	1	1	1	0	1	1	10	90.9

the included studies was 75% (ranging from 30 to 100%). Item 3, which relates to the characteristics of participants generally scored poorly. Only 15 studies were considered to provide sufficient information about the inclusion and/or exclusion criteria of their recruited participants. Item 12 relating to the external validity was the one with the lowest score and in only eight studies, authors have identified the source population or recruitment procedure for their participants.

As for the EMG quality, the assessment yielded a mean score of 86% (express as percentage, obtained from all the included studies ranging from 50 to 100%; **Table 3**).

The total quality score, including the Quality Index and EMG, was 79% (ranging from 43 to 100%; **Table 4**).

Muscle Fatigue

A total of 7 studies investigated the effect of erector spinae muscle fatigue and neuromuscular adaptations following unexpected perturbation of the trunk (Granata et al., 2001, 2004; Herrmann et al., 2006; Mawston et al., 2007; Grondin and Potvin, 2009; Dupeyron et al., 2010; Sanchez-Zuriaga et al., 2010). **Figure 2** provides an overview of results drawn from these studies.

Baseline Activity

Among these studies, results for erector spinae muscle baseline activity prior to an unexpected perturbation was increase after a fatigue task (Granata et al., 2001, 2004; Grondin and Potvin, 2009), while three others studies found no impact on erector spinae baseline activity under the influence of muscle fatigue (Herrmann et al., 2006; Mawston et al., 2007; Dupeyron et al., 2010). As for abdominal muscles, baseline activity results were also mixed. Baseline activity was found to increase after an erector spinae muscle fatigue task for external obliquus in 3 studies (Granata et al., 2001, 2004; Grondin and Potvin, 2009), and for internal obliquus in 2 studies (Granata et al., 2001; Grondin and Potvin, 2009). Conversely 2 other studies found no difference for external obliquus (Mawston et al., 2007; Dupeyron et al., 2010) and internal obliquus muscles (Granata et al., 2004; Mawston et al., 2007). Finally, two studies reported a higher rectus abdominis baseline activity under the

TABLE 3 | EMG quality assessment scores (*When normalization was not necessary, studies were rated on 3 point scale).

Authors (year)	1.1	1.2	1.3	2.1	2.2	2.3	2.4	3.1	3.2	3.3	3.4	4	Score (/3* or /4)
Akbari et al., 2015	1	1	0	1	1	0	1	1	0	1	1	1	4
Bazrgari et al., 2011	0	1	1	0	1	0	0	1	0	1	1	0	2
Dupeyron et al., 2010	0	1	1	1	1	1	1	1	1	1	1	1	4
Gao et al., 2014	0	0	0	1	1	1	1	1	0	1	1	1	3
Granata et al., 2001	0	0	1	1	1	0	1	1	1	1	1	1	3
Granata et al., 2005	0	0	1	0	1	0	0	1	1	1	1	1	2
Granata et al., 2004	0	0	1	0	1	0	1	1	1	1	1	1	3
Grondin and Potvin, 2009	1	1	1	1	1	1	1	1	1	1	0	1	4
Hendershot et al., 2011	0	1	1	1	1	0	0	1	1	1	1	0	3
Herrmann et al., 2006	1	1	0	1	1	0	1	1	1	1	1	1	4
Jacobs et al., 2011	1	1	1	1	1	0	1	1	1	1	1	1	4
Jones et al., 2012a	1	1	1	1	1	0	1	1	1	1	1	1	4
Jones et al., 2012b	1	1	1	1	1	0	1	1	1	1	1	1	4
Lariviere et al., 2010	0	0	0	1	1	1	1	1	1	1	1	1	3
Liebetrau et al., 2013	1	1	1	1	1	1	1	1	1	1	1	0	3
MacDonald et al., 2010	1	1	1	n/a	1	1	1	1	1	1	1	0	3
Mawston et al., 2007	1	1	1	1	1	0	1	1	1	1	1	1	4
Muslim et al., 2013	0	1	1	1	1	0	0	1	0	1	1	0	3
Newcomer et al., 2002	1	0	1	1	1	0	0	1	0	1	1	n/a	3*
Olson, 2014	1	1	1	1	1	1	1	1	1	1	1	1	4
Radebold et al., 2000	1	1	1	1	1	0	1	1	1	1	1	n/a	3*
Radebold et al., 2001	1	1	1	1	1	0	1	1	1	1	1	n/a	3*
Ramprasad et al., 2010	1	1	1	1	1	1	1	1	1	1	1	1	4
Reeves et al., 2005	1	1	1	0	1	0	0	1	1	1	1	n/a	2*
Rogers and Granata, 2006	1	1	1	0	1	1	0	1	1	1	1	1	4
Sanchez-Zuriaga et al., 2010	1	1	0	1	1	1	1	1	1	1	1	0	3
Shenoy et al., 2013	1	0	1	1	1	1	1	1	1	1	1	0	3
Stokes et al., 2006	1	1	1	1	1	1	1	1	1	1	1	1	4
Toosizadeh et al., 2013	0	1	1	0	1	0	0	1	1	1	1	1	3

influence of erector spinae muscle fatigue (Granata et al., 2001, 2004).

Reflex Latency

In the presence of lower back muscle fatigue, reflex latency of erector spinae muscles was not affected in the majority of studies (Granata et al., 2004; Herrmann et al., 2006; Dupeyron et al., 2010; Sanchez-Zuriaga et al., 2010). One study indicated that the reflex latency was significantly decreased after a fatigue protocol involving erector spinae muscles (Mawston et al., 2007). Following an unexpected perturbation, reflex latency of the internal (Granata et al., 2004; Mawston et al., 2007) and external obliquus (Granata et al., 2004; Dupeyron et al., 2010) and rectus abdominis (Granata et al., 2004) was found to be unchanged in the presence of muscle fatigue. In opposition, one study showed a decrease external obliquus reflex latency after erector spinae muscles fatigue (Mawston et al., 2007). Altogether, results of the meta-analysis shows that there is no effect of muscle fatigue on reflex latency of erector spinae muscles [Standardized mean difference (SMD) = 0.54; 95%CI: −0.71, 1.78; I^2 = 86.5%; **Figure 3**].

Reflex Amplitude

In 3 studies, reflex amplitude of the erector spinae was similar with or without muscle fatigue (Granata et al., 2004; Grondin and Potvin, 2009; Sanchez-Zuriaga et al., 2010), while 2 studies found an increased reflex amplitude with fatigue (Herrmann et al., 2006; Dupeyron et al., 2010). External and internal obliquus (Granata et al., 2004; Grondin and Potvin, 2009) and rectus abdominis (Granata et al., 2004) reflex amplitude were not affected by the presence of erector spinae muscle fatigue.

Kinematics

Only 2 studies investigated trunk kinematic behavior in response to a sudden perturbation with erector spinae muscle fatigue. These studies did not observe a difference in kinematics between pre and post fatigue condition (Granata et al., 2004; Mawston et al., 2007).

TABLE 4 | Quality total score (#Studies investigated the effect of low back pain when normalization was not necessary were rated using a 13 point scale; *Studies investigated the effect of low back pain were rated using a 14 point scale).

Authors (year)	Score quality index (/10* or /11)	Score EMG (/3* or /4)	Total score (/13# or /14* or /15)	Note (%)
Akbari et al., 2015	7*	4	11*	78.6
Bazrgari et al., 2011	9	2	11	73.3
Dupeyron et al., 2010	8	4	12	80
Gao et al., 2014	9*	3	12*	85.7
Granata et al., 2001	6	3	9	60
Granata et al., 2005	9	2	11	73.3
Granata et al., 2004	6	3	9	60
Grondin and Potvin, 2009	8	4	12	80
Hendershot et al., 2011	10	3	13	86.7
Herrmann et al., 2006	8	4	12	80
Jacobs et al., 2011	10*	4	14*	100
Jones et al., 2012a	8*	4	12*	85.7
Jones et al., 2012b	10*	4	14*	100
Lariviere et al., 2010	9*	3	12*	85.7
Liebetrau et al., 2013	6*	3	9*	64.3
MacDonald et al., 2010	9*	3	12*	85.7
Mawston et al., 2007	9	4	13	86.7
Muslim et al., 2013	10	3	13	86.7
Newcomer et al., 2002	9*	3*	12#	92.3
Olson, 2014	9	4	13	86.7
Radebold et al., 2000	6*	3*	9#	69.2
Radebold et al., 2001	7*	3*	10#	76.9
Ramprasad et al., 2010	5*	4	9*	64.3
Reeves et al., 2005	8*	2*	10#	76.9
Rogers and Granata, 2006	9	4	13	86.7
Sanchez-Zuriaga et al., 2010	9	3	12	80
Shenoy et al., 2013	3*	3	6*	42.9
Stokes et al., 2006	7*	4	11*	78.6
Toosizadeh et al., 2013	10	3	13	86.7

Spinal Creep

A total of 8 studies reported on the effect of spinal tissue creep and neuromuscular adaptations following unexpected perturbation of the trunk (Granata et al., 2005; Rogers and Granata, 2006; Sanchez-Zuriaga et al., 2010; Bazrgari et al., 2011; Hendershot et al., 2011; Muslim et al., 2013; Toosizadeh et al., 2013; Olson, 2014). **Figure 4** provides an overview of results from these studies.

Baseline Activity

Prior to an unexpected perturbation, baseline activity remained unchanged under the influence of spinal tissue creep for the majority of studies and for all trunk muscles (Granata et al., 2005; Rogers and Granata, 2006; Bazrgari et al., 2011; Hendershot et al., 2011; Muslim et al., 2013; Olson, 2014). Only one study found a decrease in external obliquus baseline activity following creep deformation (Rogers and Granata, 2006).

Reflex Latency

Two studies showed that, under the influence of spinal tissue creep, reflex latency of the erector spinae muscles increased (Sanchez-Zuriaga et al., 2010; Toosizadeh et al., 2013). Conversely, one study reported that erector spinae reflex latency was shorter in the presence of spinal tissue creep (Muslim et al., 2013). Finally, four studies did not observe significant changes in reflex latency between pre- and post-creep conditions for erector spinae muscles (Granata et al., 2005; Bazrgari et al., 2011; Hendershot et al., 2011; Olson, 2014), as well as for the external obliquus and the rectus abdominis muscles (Olson, 2014). Results of the meta-analysis shows that creep does not have an effect on reflex latency (SMD $= -0.26$; 95%CI: $-0.83, 0.31$; $I^2 = 69.1\%$) of erector spinae muscles (**Figure 3**).

Reflex Amplitude

Following an unknown perturbation, erector spinae muscle reflex amplitude are generally unaffected by the presence of creep (Granata et al., 2005; Sanchez-Zuriaga et al., 2010; Olson, 2014). One study also found no impact of spinal tissue creep for the external obliquus and the rectus abdominis muscles reflex amplitude following a sudden perturbation (Olson, 2014). Only one study found lower reflex amplitude values following creep deformation for paraspinal muscles (Rogers and Granata, 2006).

Kinematics

As for trunk kinematics behavior following an unexpected perturbation under spinal creep condition, two studies found no difference between pre- and post-creep conditions (Rogers and Granata, 2006; Olson, 2014), while one study reported decreased trunk kinematic gain following a creep deformation (Granata et al., 2005).

Clinical LBP

A total of 15 studies investigated the effect of LBP and neuromuscular adaptations following unexpected trunk perturbation (Radebold et al., 2000, 2001; Newcomer et al., 2002; Reeves et al., 2005; Stokes et al., 2006; Lariviere et al., 2010; MacDonald et al., 2010; Ramprasad et al., 2010; Jacobs et al., 2011; Jones et al., 2012a,b; Liebetrau et al., 2013; Shenoy et al., 2013; Gao et al., 2014; Akbari et al., 2015). Among these studies, two recruited participants with acute/episodic LBP (Stokes et al., 2006; Jones et al., 2012b) while all other included participants with chronic LBP. **Figure 5** provides an overview of results drawn from these studies.

Baseline Activity

Prior to an unexpected perturbation, patients with chronic LBP demonstrated, in most cases, a significant increase of baseline activity of erector spinae muscles (Lariviere et al., 2010; Jacobs et al., 2011; Jones et al., 2012a). An increase in erector spinae baseline activity was also found in patients with acute LBP (Stokes et al., 2006). Nevertheless, three studies failed to identify differences in back muscle baseline activity between healthy participants and patients with chronic LBP (MacDonald et al., 2010; Liebetrau et al., 2013) or acute LBP (Jones et al., 2012b). As for trunk flexor muscles, three different studies did

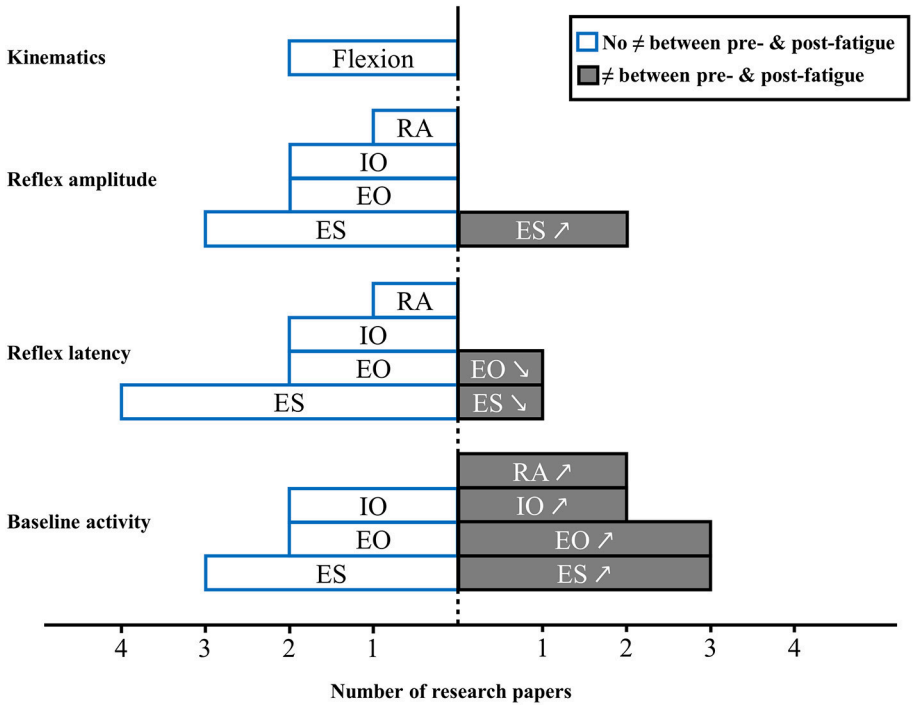

FIGURE 2 | Muscle activity reflex responses to unexpected postural perturbation of the trunk under the influence of muscle fatigue expressed in number of research papers (↗, higher value with muscle fatigue; ↘, lower value with muscle fatigue; RA, rectus abdominis; IO, internal obliquus; EO, external obliquus; ES, erector spinae).

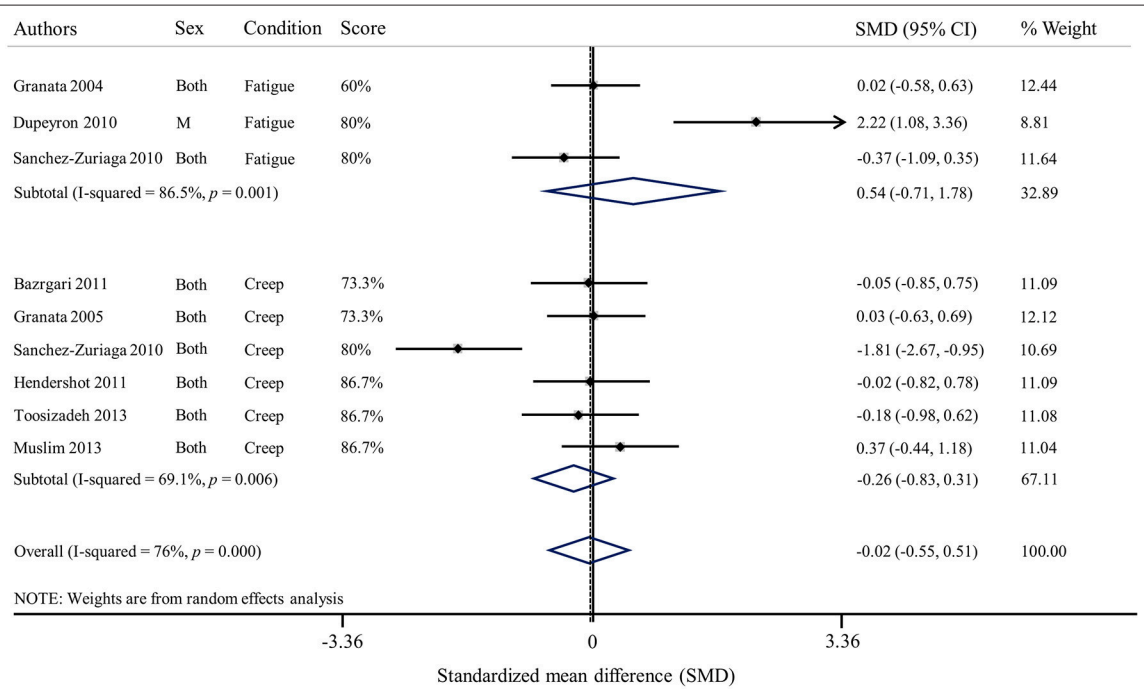

FIGURE 3 | Forest plot of erector spinae reflex latencies under the influence of muscle fatigue and spinal tissue creep (SMD, Standardized mean difference).

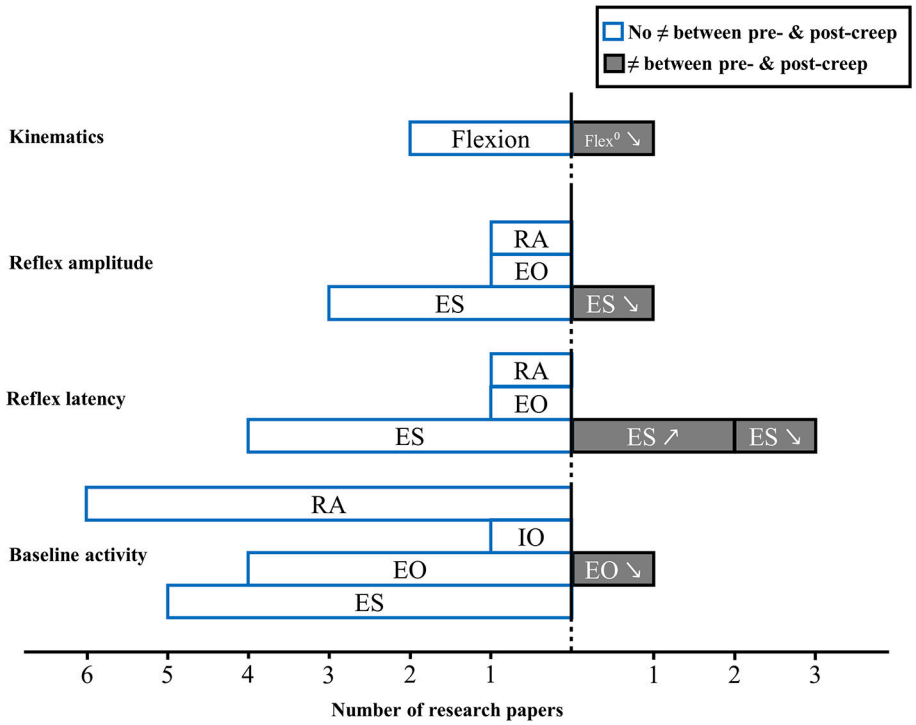

FIGURE 4 | Muscle activity reflex responses to unexpected postural perturbation of the trunk under the influence of spinal tissue creep expressed in number of research papers (↗, higher value with creep; ↘, lower value with creep; RA, rectus abdominis; IO, internal obliquus; EO, external obliquus; ES, erector spinae).

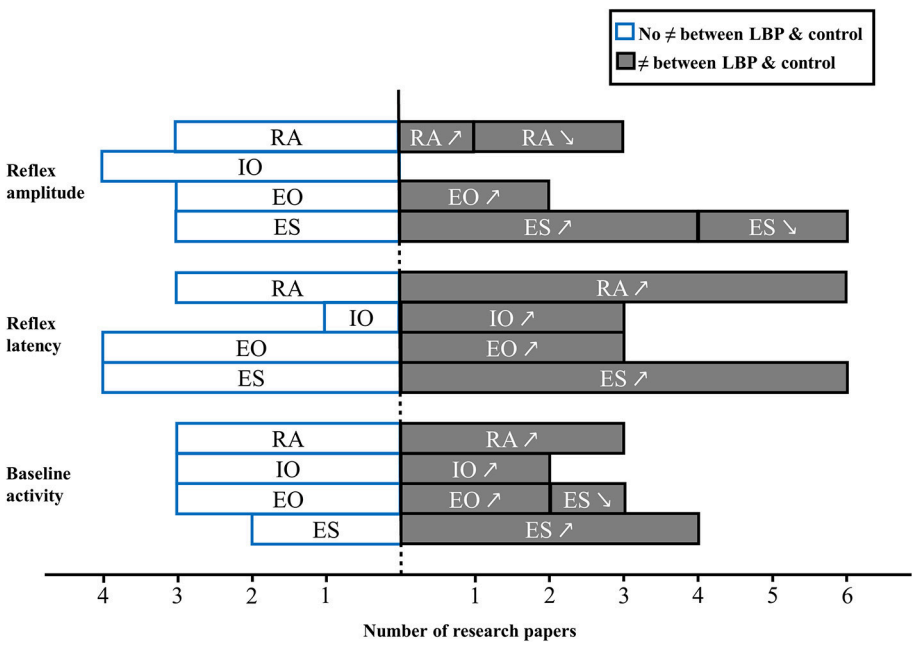

FIGURE 5 | Muscle activity reflex responses to unexpected postural perturbation of the trunk in patient with LBP expressed in number of research papers (↗, higher value in LBP group; ↘, lower value in LBP group; RA, rectus abdominis; IO, internal obliquus; EO, external obliquus; ES, erector spinae).

not report any difference between patients with chronic LBP (Lariviere et al., 2010; Liebetrau et al., 2013) or acute LBP (except for the external obliquus baseline activity which decreased in patients; Jones et al., 2012a) and healthy participants, while two studies reported an increase in baseline activity in patients with chronic (Jones et al., 2012a) or acute LBP (Stokes et al., 2006).

Reflex Latency

Among all studies investigating erector spinae reflex latency in patients with LBP, six studies found longer latencies in patients vs. healthy participants (Radebold et al., 2000, 2001; Reeves et al., 2005; Ramprasad et al., 2010; Shenoy et al., 2013; Gao et al., 2014), while four studies did not find significant differences between those two populations (Newcomer et al., 2002; Lariviere et al., 2010; Liebetrau et al., 2013; Akbari et al., 2015). As for external obliquus reflex latencies, results from three different studies showed longer latencies (Radebold et al., 2000, 2001; Reeves et al., 2005), while four studies did not find differences between patients with chronic LBP and healthy participants (Lariviere et al., 2010; Liebetrau et al., 2013; Gao et al., 2014; Akbari et al., 2015). Three studies reported increased internal obliquus reflex latencies in patients with LBP (Radebold et al., 2000, 2001; Liebetrau et al., 2013), while one did not (Akbari et al., 2015). Lastly, patients with LBP exhibited significantly longer reflex latencies over the rectus abdominis muscles in a majority of studies (Radebold et al., 2000, 2001; Reeves et al., 2005; Ramprasad et al., 2010; Liebetrau et al., 2013; Shenoy et al., 2013). However, three studies failed to identify differences between LBP patients and controls (Newcomer et al., 2002; Lariviere et al., 2010; Akbari et al., 2015). Overall, results of the meta-analysis showed that erector spinae reflex latency was increased in patients with LBP vs. healthy participants (SMD = 0.53; 95%CI: 0.19, 0.87; $I^2 = 62.3\%$; **Figure 6**).

Reflex Amplitude

Erector spinae reflex amplitude behavior in response to a sudden perturbation seemed in most cases to be increased in patients with chronic LBP (Lariviere et al., 2010; Jones et al., 2012a; Gao et al., 2014) as well as in patients with acute LBP (Jones et al., 2012b). However, two studies reported a decreased erector spinae muscle reflex amplitude in patients with chronic LBP (Ramprasad et al., 2010; Shenoy et al., 2013), while two others studies failed to identify differences between patients with chronic LBP and healthy controls (Jacobs et al., 2011; Liebetrau et al., 2013). Moreover, one study has found that the superficial multifidus reflex amplitude decreased in patients with chronic LBP compared to controls (MacDonald et al., 2010), while one study failed to found a difference between patients with chronic LBP and controls (Liebetrau et al., 2013). As for trunk flexors reflex amplitude, no difference were reported for internal obliquus muscle in people with acute or chronic LBP as compared to asymptomatic participants. External obliquus reflex amplitude was found to be increased in patients with chronic (Jones et al., 2012a) or acute LBP (Jones et al., 2012b), whereas three studies did not observed any difference (Jacobs et al., 2011; Liebetrau et al., 2013; Gao et al., 2014). Finally, no difference were reported for the rectus abdominis reflex amplitude response to a sudden perturbation between healthy participants and patients with chronic (Jacobs et al., 2011; Liebetrau et al., 2013) or acute LBP (Jones et al., 2012b).

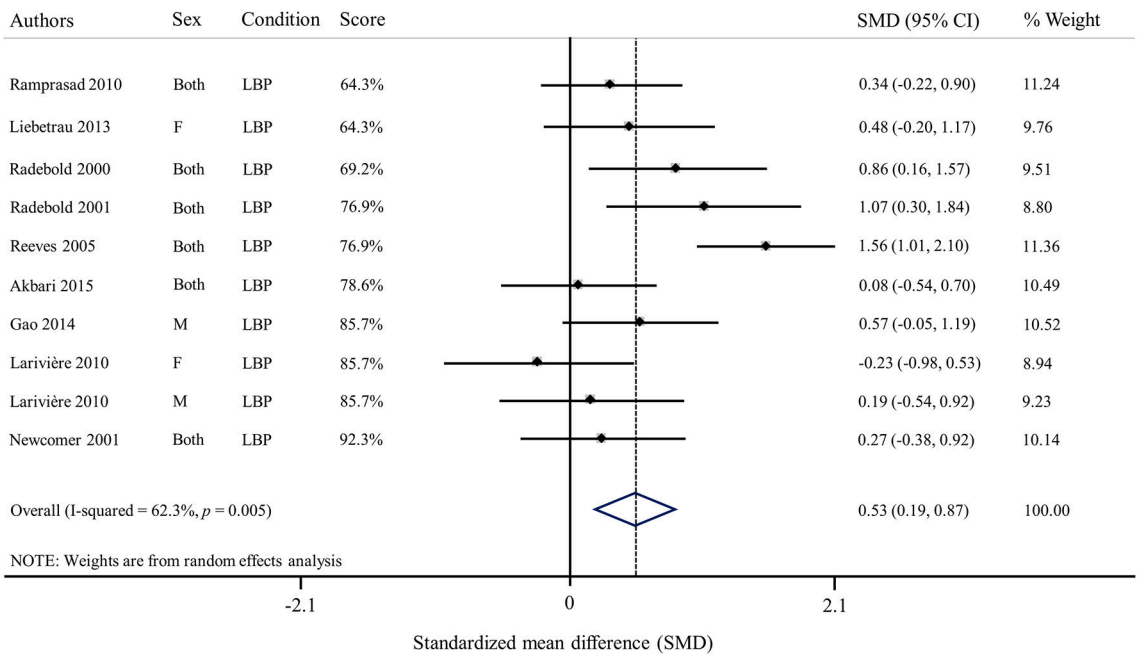

FIGURE 6 | Forest plot of erector spinae reflex latencies in patients with low back pain (SMD, Standardized mean difference).

DISCUSSION

To our knowledge, this is the first systematic review that explores the quality of evidence related to muscle activity reflex in response to unexpected trunk perturbation. Since a high heterogeneity was present among the selected studies, our ability to pool data and draw conclusions was limited.

Quality Assessment

The total score of the methodological quality assessment was 79%, with only one study scoring below 50% (Shenoy et al., 2013). Overall, it seems reasonable to suggest that the quality of the included studies was good. However, when quality checklist items are considered individually, some methodological weaknesses emerge. The characteristics of the participants included in the studies were clearly described in only half of the studies. Most studies only mentioned if their participants were healthy participants or patients with LBP without any further clinical details. In most cases, the description of the control group was limited to "healthy" and when a group of LBP was included, the duration and nature of LBP, or any other medical condition were often omitted in inclusion/exclusion criteria. Lack of specific inclusion and exclusion criteria may lead to inherent heterogeneity in patients responses to perturbation as it is known, that patients with acute or chronic LBP can exhibit various neuromuscular adaptations and that such adaptation may be influence by patient's clinical characteristics (Hodges and Tucker, 2011). Another significant methodological weakness identified was external validity. Indeed, only 6/29 studies identified the source population for the recruited participants. This suggest that the overall generalizability of results to the related population is limited. Furthermore, eight studies had small sample size, with fifteen or less participants included. Having such small sample sizes may lead to statistical power issues, which could potentially lead to type II error (Cohen, 1992). Finally, the lack of information concerning the p-values was identified in the methodological assessment. The absence of true p-value ($p \leq 0.05$) can lead to the misinterpretation of significant differences and overall interpretation of study results (i.e., $p = 0.049$ vs. $p = 0.011$). Moreover, even if not considered as a criteria of the Quality Index developed by Downs and Black, the 95% confidence interval should also be presented but was reported in only 3 of the included studies.

On the other hand, high methodological quality was found for the descriptions of sudden external perturbation experimental protocols. Moreover, descriptions of the fatigue and/or creep protocols were also appropriately detailed. This indicates that these experimental protocols would be replicable. Unfortunately, a high heterogeneity between experimental protocols makes the interpretation of the original study results difficult. Indeed, sudden external perturbations were applied in different positions (standing and semi-sitting) with different magnitudes, and sometimes using a familiarization perturbation protocol. As for EMG assessment, the overall quality was good. However, three items drawn from ISEK and SENIAM recommendations were absent in most of the studies: description of the inter electrode distance, the reference electrode and the normalization procedures. The inter electrode distance could influence data recording, due crosstalk effects (Hermens et al., 1999; De Luca et al., 2012), whereas the absence of normalization may lead to misinterpretation of results when comparing the amplitude of muscle activity (reflex amplitude or baseline activity prior to perturbation) between participants (Merletti, 1999).

Baseline Activity

Experiencing an unexpected perturbation limits the nervous system capacity to anticipate and preprogram a motor response. Yet, baseline muscle activity, was one of the most reported variable in studies that evaluated the effect of unexpected perturbation (19/29 of the included studies). Despite the absence of feedforward strategies, small changes in baseline activity have been described under muscle fatigue or in the presence of LBP, while baseline activity is not modified under the influence of spinal creep. Anxiety can also affect postural stability (Wada et al., 2001; Stambolieva and Angov, 2010) and therefore potentially modulate baseline activity while "waiting" for an external perturbation to happen. However, there is not enough evidence to strongly propose that baseline activity can be influenced by the varying perturbation delays. Indeed, this review could not reach any definite conclusion with regard to baseline activity since the included articles did not report specific perturbation delays. Most articles reported a variation of time delay (i.e., between 1 and 10 s) or they did not report any details.

Muscle Fatigue Effects on Spinal Stability

The relationship between muscle fatigue and spinal stability remains unclear. Despite the varying reflex latency values between studies, this review suggests that trunk muscle reflex response latencies do not change under the influence of back muscles fatigue. This suggest that, in order to stabilize the spine, the central nervous system generates earlier postural muscle adjustments similarly regardless of muscle fatigue presence. The results from the metanalysis should, however, be interpreted with caution. An I square superior to 80% suggests the presence of a substantial heterogeneity between those studies. As for baseline activity and reflex amplitude of erector spinae muscles, surprisingly, no consensus was found in this review. Since the presence muscle fatigue is usually characterized by an increase in the EMG amplitude signal in submaximal muscle contractions (De Luca, 1997), a higher trunk muscle EMG amplitude was expected, especially in muscles targeted by the fatigue protocol. The flexor muscle baseline activity and reflex amplitude did not seem to be affected by the presence of back muscle fatigue in most studies and only the rectus abdominis baseline activity increased prior to an unknown perturbation in the presence of muscle fatigue. However, these results should be interpreted with caution since only two studies reported such responses to muscle fatigue. This note of caution can also apply to trunk kinematic behaviors since the lack of any effect of erector spinae muscle fatigue on trunk kinematics was reported in very few studies. Overall, it could be hypothesized that muscle fatigue has a negligible impact on spinal stability. A previous study showed that even in the presence of upper limb muscle fatigue, movement accuracy with external perturbation remains constant (Takahashi

et al., 2006). Moreover, the lack of trunk movement changes in a fatiguing state could be explained by the trunk muscle system's redundancy which offers various adaptation possibilities to achieve a similar goal (Latash and Anson, 2006). Investigating neuromuscular strategies such as variability in muscle activity recruitment pattern should shed some light on the effects of trunk muscle fatigue during unexpected trunk perturbations.

Spinal Tissue Creep Effects on Spinal Stability

Overall, the presence of spinal tissue creep does not seem to affect spinal stability in a context of unexpected perturbation. Indeed, this review revealed that trunk muscle baseline activity prior to a perturbation does not change following either an active or a static deformation of passive spinal tissues. Following an unknown perturbation, participants showed similar trunk muscle reflex amplitude. Again, active vs. passive deformation do not yield distinct effects on reflex amplitude. Such result is surprising since it is expected that creep deformation will lead to an increase muscle activity amplitude (Olson et al., 2009; Abboud et al., 2016), which is believed to act as a spinal stabilization mechanism. Interesting new findings have shown that following a prolonged intermittent trunk flexion of 1 h, an increase of trunk stiffness is observed (Voglar et al., 2016). This observation confirms previous findings suggesting that in the first 30 min of cyclic trunk flexion, a decrease in intrinsic stiffness occurs, whereas, the following 30 min, spinal stiffness increases (Parkinson et al., 2004). Since spinal stiffness has been associated with spinal stability (Graham and Brown, 2012), it can be hypothesized that no adjustment of reflex amplitude is needed when intrinsic stiffness increases. However, studies included in this review cannot support this hypothesis, since spinal creep deformation lasting from 15 min to 1 h did not modify the reflex amplitude. As for reflex latency, no distinct effect of spinal tissue creep could be identified in the meta-analysis. In most cases, reflex latency did not change in the presence of spinal tissue creep. Once again, the results drawn from the metanalysis should be interpreted with caution due to the heterogeneity between the included studies ($I^2 = 69\%$). Overall, this review suggest that spinal tissue creep had no or only minor effects on trunk neuromuscular adaptations to unexpected perturbation. Moreover, no definite conclusion can be drawn for trunk kinematics since only three studies investigated the effect of spinal tissue creep and reported conflicting results. It seems reasonable to suggest that, in a context of spinal instability, the impact of transient spinal tissue deformation can be counteracted by recruiting other muscle groups and using alternate neuromuscular strategies. Indeed, it has already been proposed that the loss of viscoelastic tissues of ligaments, discs, and joint capsules properties can be counteracted by adjusting the co-contraction levels of agonist and antagonist muscles (Solomonow et al., 1999).

Musculoskeletal LBP Effects on Spinal Stability

The effect of LBP on spinal stability was the most common topic identified in the current review. Despite the number of studies available, no definite conclusion could be drawn. Results for most EMG reflex variables included in this review were found to be conflicting across studies. More studies found differences between a healthy population and populations of patients with chronic LBP than studies that did not, especially for the trunk muscles baseline activity. Similar observations were found in patients with acute or episodic LBP. On the other hand, studies investigating the effects of acute clinical LBP induced by experimental LBP, consistently reported no change in trunk muscle baseline activity prior to an unexpected perturbation (Gregory et al., 2008; Boudreau et al., 2011; Miller et al., 2013). Despite the overall conflicting observations, results from the meta-analysis showed a moderate effect indicating a longer reflex latency for erector spinae muscles in patients with chronic LBP compared to healthy participants. However, the meta-analysis results for reflex latency should be interpreted with care since the analysis was conducted using reflex latency values that were drawn directly from the article or provided by the authors. Although, no meta-analysis was conducted for reflex amplitude, erector spinae muscle reflex amplitude was found to be significantly higher in patients with acute or chronic LBP in most studies while two studies reported a decrease in the same population. It should be noted that, these two latter studies reporting a lower erector spinae reflex amplitude in patients with chronic LBP were among the studies with the lowest quality score (see **Table 4**). It is known that patients with LBP are highly heterogeneous and many studies have attempted to identify subgroups (O'sullivan, 2005; Fersum et al., 2010). Patients described in the included studies differed, from a study to another, with regard to their respective pain scores (2–4.7/10 on numerical pain scale), their disability scores (very low to moderate), as well as in the pain duration (3 months to several years). If these subgroups exist, one typical neuromuscular response could be associated with one typical subgroup. The heterogeneity of the results reported in this review highlights the importance of standardized and well described inclusion and exclusion criteria in experimental studies investigating patients' populations.

Limitations

Since no validated assessment checklist was available to evaluate the quality of laboratory studies using EMG assessments, a custom made quality checklist was adapted from an already validated existing checklist (Downs and Black, 1998). However, to improve the validity and reliability of our checklist, three independent assessors completed the quality checklist and showed a high level of agreement. A methodological limitation of this review is that only one author have extracted the data (Appendix C in Supplementary Material). Another limitation of this review is the limited number of studies investigating muscle fatigue, spinal tissue creep, and musculoskeletal pain effects. Diverse sensorimotor and biomechanical external perturbation, such as vibration (Arashanapalli and Wilson, 2008; Santos et al., 2008; Arora and Grenier, 2013; MacIntyre and Cort, 2014) and delayed onset muscle soreness (Hjortskov et al., 2005), were identified during the preliminary search. However, an insufficient

number of studies was available to consider these topics in the review.

This systematic review assessed the overall quality of the included articles. However, due to the large number of included studies, it was not feasible to contact all the authors of articles who omitted methodological details, such as inclusion/exclusion recruitment criterion, electrode placement, etc. Moreover, in order to guide future research, this review was designed to highlight the lack of standardization and information characterizing this type of study. This review did not assess the reliability and validity of the main outcomes. Besides, almost all studies did not provide data about EMG reflex variable reliability and/or validity, we decided not to penalize study who did not report theses information since EMG was already proven to be valid and reliable assessment tool in many studies. Instead, it was chosen to focus on the quality of EMG data acquisition and analyses which are considered key factors in the value and interpretation of results (De Luca, 1997). A final limitation of this review was the incapacity to conduct meta-analysis on variables other than reflex latency. Unfortunately, the use of different units (% of MVC, μV, normalized EMG with no unit, etc.) to express reflex amplitude or baseline activity made the meta-analysis virtually impossible.

Research Recommendations

It is clear that standardization for conducting and reporting EMG fundamental studies should be a priority in future research. The development of an adapted checklist for EMG fundamental and clinical studies may be a helpful tool to achieve such a goal. Moreover, future studies should establish the reliability of the EMG reflex variables. Despite the presence of a good reliability in the determination of reflex latency using SD methods (Hodges and Bui, 1996), reliability or validity of reflex amplitude and baseline activity have not been assessed in most studies. Given the various reflex outcomes studied and the overall heterogeneity of the studies included in this systematic review, determining how physical and physiological reflex responses adapt in various spinal instability conditions should remain an active domain of research. Future research should also consider exploring the impact of spinal instability on trunk kinematic behavior in the presence of expected and unexpected external perturbations.

AUTHOR CONTRIBUTIONS

Substantial contributions to the conception or design of the work; or analysis, or interpretation of data for the work: JA, AL, FB, CD, MD. Drafting the work and revising it critically for important intellectual content: JA, AL, FB, CD, MD. Final approval of the version to be published: JA, AL, FB, CD, MD. Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved: JA, AL, FB, CD, MD.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2016.00667/full#supplementary-material

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Influence of Lumbar Muscle Fatigue on Trunk Adaptations during Sudden External Perturbations

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Introduction: When the spine is subjected to perturbations, neuromuscular responses such as reflex muscle contractions contribute to the overall balance control and spinal stabilization mechanisms. These responses are influenced by muscle fatigue, which has been shown to trigger changes in muscle recruitment patterns. Neuromuscular adaptations, e.g., attenuation of reflex activation and/or postural oscillations following repeated unexpected external perturbations, have also been described. However, the characterization of these adaptations still remains unclear. Using high-density electromyography (EMG) may help understand how the nervous system chooses to deal with an unknown perturbation in different physiological and/or mechanical perturbation environments.

Aim: To characterize trunk neuromuscular adaptations following repeated sudden external perturbations after a back muscle fatigue task using high-density EMG.

Methods: Twenty-five healthy participants experienced a series of 15 sudden external perturbations before and after back muscle fatigue. Erector spinae muscle activity was recorded using high-density EMG. Trunk kinematics during perturbation trials were collected using a 3-D motion analysis system. A two-way repeated measure ANOVA was conducted to assess: (1) the adaptation effect across trials; (2) the fatigue effect; and (3) the interaction effect (fatigue × adaptation) for the baseline activity, the reflex latency, the reflex peak and trunk kinematic variables (flexion angle, velocity and time to peak velocity). Muscle activity spatial distribution before and following the fatigue task was also compared using *t*-tests for dependent samples.

Results: An attenuation of muscle reflex peak was observed across perturbation trials before the fatigue task, but not after. The spatial distribution of muscle activity was significantly higher before the fatigue task compared to post-fatigue trials. Baseline activity showed a trend to higher values after muscle fatigue, as well as reduction through perturbation trials. Main effects of fatigue and adaptation were found for time to peak velocity. No adaptation nor fatigue effect were identified for reflex latency, flexion angle or trunk velocity.

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Conclusion: The results show that muscle fatigue leads to reduced spatial distribution of back muscle activity and suggest a limited ability to use across-trial redundancy to adapt EMG reflex peak and optimize spinal stabilization using retroactive control.

Keywords: high-density electromyography, spinal stability, muscle fatigue, reflex, habituation

INTRODUCTION

Over the past years, several studies have shown that neuromuscular adaptations are observed under the influence of back muscle fatigue (Allison and Henry, 2001; Boyas and Guével, 2011; Monjo et al., 2015). Indeed, some authors have reported that a reorganization of motor strategies is used to prevent the onset of muscle fatigue (Fuller et al., 2011) and that such adaptations in muscle activity recruitment patterns are present, such as co-contraction phenomena (Allison and Henry, 2001), or within muscle changes in recruitment patterns, suggesting a spatial dependency in the control of motor units in the erector spinae (Tucker et al., 2009; Abboud et al., 2014). These neuromuscular adaptations have been also reported when participants are asked to perform a voluntary perturbation, such as goal-directed movements. Previous studies have shown that, in the presence of muscle fatigue, compensatory neuromuscular adaptations occur in order to maintain the task requirement (Côté et al., 2002; Missenard et al., 2009). Such neuromuscular strategies are part of the feedforward control, which allows the central nervous system to predict the muscle activation needed to achieve a desired motor task (Shadmehr and Mussa-Ivaldi, 1994). On the other hand, when subjected to unpredictable perturbations, neither feedback, nor anticipation strategies are sufficient to adjust movement on-line. Determining the influence of muscle fatigue during an unpredictable perturbation is therefore of great interest.

More specifically, this study focusses on understanding neuromuscular adaptations to unexpected trunk perturbation, which are believed to affect spinal stability. In everyday life, the human body is constantly under the influence of mechanical forces applied in different directions, sometimes unexpected and continuously triggering postural adjustments. Examples of such spinal perturbations can be drawn from various common activities such as sport contacts, tripping, slipping, weight lifting, etc. Panjabi (1992) described spinal stability as a complex mechanism involving three essential components: spinal muscles, passive spinal tissues and neuromuscular control (Panjabi, 1992). Alterations, such as physiological and/or mechanical ones, of one or more of these components have been shown to be a direct or indirect manifestation of spinal instability.

Despite the number of studies that have investigated fatigue and unexpected loading effects on spinal stability, results vary from one study to the other (Granata et al., 2001, 2004; Chow et al., 2004; Herrmann et al., 2006; Mawston et al., 2007; Grondin and Potvin, 2009; Dupeyron et al., 2010; Sánchez-Zuriaga et al., 2010). Such differences could be partly due to methodological choices in trunk perturbation experimental protocols, such as participant positions (standing vs. sitting), familiarization of the external perturbation, perturbation magnitudes, etc. Furthermore, variables selected to assess neuromuscular responses to a sudden trunk perturbation are far from consistent across studies. The most common variables used to assess the effect of unexpected trunk loading under muscle fatigue are baseline muscle activity, reflex latency and reflex amplitude. In a context of unexpected trunk perturbation, current evidence shows inconsistencies in baseline activity responses under the influence of muscle fatigue (Granata et al., 2001, 2004; Herrmann et al., 2006; Mawston et al., 2007; Grondin and Potvin, 2009; Dupeyron et al., 2010) with studies showing no adaptation after a back fatigue task (Herrmann et al., 2006; Mawston et al., 2007; Dupeyron et al., 2010), while other ones reveal an increase in baseline activity with muscle fatigue (Granata et al., 2001, 2004; Grondin and Potvin, 2009). On the other hand, most studies investigating neuromuscular responses following an unexpected trunk perturbation showed that reflex latency is not affected by the presence of low back muscle fatigue (Granata et al., 2004; Herrmann et al., 2006; Dupeyron et al., 2010; Sánchez-Zuriaga et al., 2010). As for the reflex amplitude of low back muscles, it was found not to be affected by muscle fatigue in several studies (Granata et al., 2004; Grondin and Potvin, 2009; Sánchez-Zuriaga et al., 2010), whereas few studies found a higher back reflex amplitude following a fatigue protocol (Herrmann et al., 2006; Dupeyron et al., 2010). Overall, the effect of muscle fatigue on neuromuscular adaptations during unexpected loading remains unclear.

Inconsistencies reported in the literature regarding neuromuscular responses under muscle fatigue during unexpected perturbation could also be explained by the fact that most of the studies have been limited by the amplitude and frequency behavior because of the use of classic bipolar electromyography (EMG), which covers only a small portion of the explored muscle. Recent technologies, such as high-density surface EMG (sEMG), because it can cover a large surface area, offer a unique perspective on muscle activity spatial distribution (Zwarts and Stegeman, 2003; Merletti et al., 2008; Holobar et al., 2009; Martinez-Valdes et al., 2016). Indeed, data extracted from high-density sEMG have enabled the mapping of muscle activity recruitment distribution in the low back region during a voluntary contraction. Results have revealed a shift in muscle activity spatial distribution to the lateral-caudal direction in the low back region during muscle fatigue (Tucker et al., 2009). This migration in muscle activity distribution could be associated with changes in muscle fiber recruitment to avoid overloading of the same fibers (Rantanen et al., 1994). Adopting non-uniform muscle activity recruitment may help participants develop motor strategies and facilitate adaptation to different physiological and/or mechanical perturbations of the spine. Low back muscle activity measured by high-density sEMG has also

been shown to discriminate patients with chronic low back pain from healthy individuals through different motor tasks (Abboud et al., 2014; Falla et al., 2014). To our knowledge, no study has investigated muscle activity reflex variables with high-density sEMG.

Reflex muscle activity has also been studied following a series of unexpected external perturbations. The first research exploring this question was conducted by Nashner (1976), who showed that neuromuscular adaptations, such as the attenuation of lower limb muscle reflex activation, occur following repeated ankle dorsiflexion to improve postural balance. More recently, similar results have been reported in presence of several unexpected external perturbations of the cervical region (Blouin et al., 2003; Siegmund et al., 2003). A reduction of neck muscle activity was observed across perturbation trials (Blouin et al., 2003; Siegmund et al., 2003). Back muscles seem to follow a similar response pattern during unexpected forward perturbation. Skotte et al. (2004) showed a reduction of the average erector spinae EMG amplitude from the first trial to the next one. A more recent study reported similar results in paraspinal muscle responses to a series of unexpected tilts from a surface platform (Oude Nijhuis et al., 2010). The authors observed that EMG amplitude responses adapted rapidly between the first two trials, whereas adaptation was more gradual over the next trials (Oude Nijhuis et al., 2010). Based on these results, it could be suggested that, whenever possible, the central nervous system attempts to minimize unnecessary or excessive responses to perturbation.

Moreover, adaptations throughout repetitions of the same perturbation have been previously shown to compensate for the effect of muscle fatigue (Takahashi et al., 2006; Kennedy et al., 2012). Such compensations were indeed observed following upper limb and ankle muscle fatigue when movement accuracy and postural stability were respectively maintained (Takahashi et al., 2006; Kennedy et al., 2012). However, in the study of Kennedy et al. (2012), the authors did not assess adaptation across repeated perturbation trials. Participants had to perform few perturbation trials to allow habituation to perturbations, to limit changes caused by habituation to the motor task. On the other hand, Takahashi et al. (2006) studied adaptation across perturbation trials. The unexpected perturbation was applied while participants reached to a target and results showed that even when participants were in a state of fatigue, they were still able to reach the target and adapt to perturbations.

The assessment of neuromuscular adaptations when the patients are submitted to the same perturbation during a rehabilitation protocols could be used to monitor progress and adaptations. As suggested by Hodges and Tucker (2011), adaptations to pain have immediate and short term benefit for the spinal system. They may, however, have detrimental long-term consequences and should therefore be monitored and perhaps treated in rehabilitation. The aim of the present study was to characterize trunk neuromuscular adaptations in response to a sudden external perturbation after a back fatigue task. Its second aim was to identify if trunk neuromuscular control can be modulated by a previous instability experience in the presence of back muscle fatigue using high-density sEMG. Based on current evidence, it was hypothesized that back muscle fatigue would alter trial-to-trial neuromuscular adaptions during a series of repeated sudden external perturbations. Moreover, it was hypothesized that trial-to-trial neuromuscular adaptations would lead to a migration of muscle activity within the erector spinae, and that this spatial muscle activity migration would be limited in the presence of muscle fatigue.

MATERIALS AND METHODS

Recruitment

Twenty-five healthy adult participants (22 men and 3 women) were recruited from the university community. Participants with one of the following criteria were excluded: history of acute/chronic thoracic or low back pain in the past 6 months, ankylosing spondylitis, trunk neuromuscular disease, inflammatory arthritis, scoliosis ($\geq$15°), and previous spinal surgery. Participant mean (*M*) age, height, weight and BMI were respectively 26.8 (standard deviation (*SD*) = 5.5) years, *M* = 1.76 (*SD* = 0.7) m, *M* = 76.6 (*SD* = 12.1) kg and *M* = 24.5 (*SD* = 3.1) kg/m^2. The project received approval from the university's ethics committee for research with humans (Comité d'éthique de la recherche avec des êtres humains). All participants gave their written informed consent prior to their participation in this study.

Experimental Protocol

First, EMG electrodes and light-emitting diodes from the 3-D motion analysis system were installed over the participants. The experimentation protocol was divided in three phases: pre-fatigue perturbations, fatigue protocol and post-fatigue perturbations. Before the first phase, two or three isometric trunk flexion maximal voluntary contractions (MVC) were performed, as well as two or three isometric maximal contractions in trunk extension. The third trial of MVC was only performed if the participants' second MVC was superior to the first one. MVC was assessed in a semi-seated position on a modified ergonomic back chair custom-built for the study (**Figure 1**). For the trunk flexion MVC, participants were asked to pull anteriorly against a cable. Their trunk was attached at T8 level to a load cell (Model LSB350; Futek Advanced Sensor Technology Inc., Irvine, CA, USA) with a cable using a pulley system. As for trunk extension MVC, participants were asked to pull posteriorly against the cable. Since no warm up exercise was provided, participants were invited to perform some trunk extension and flexion contractions before the MVC protocol. The goal of these contractions was to help participants familiarize with the MVC protocol.

The first phase of the protocol, pre-fatigue perturbations, consisted in a series of 15 sudden external perturbations. Participants were asked to adopt the same position as the one used during the MVC protocol (**Figure 1**). Their trunk was attached to a perturbation trigger with a cable using a pulley

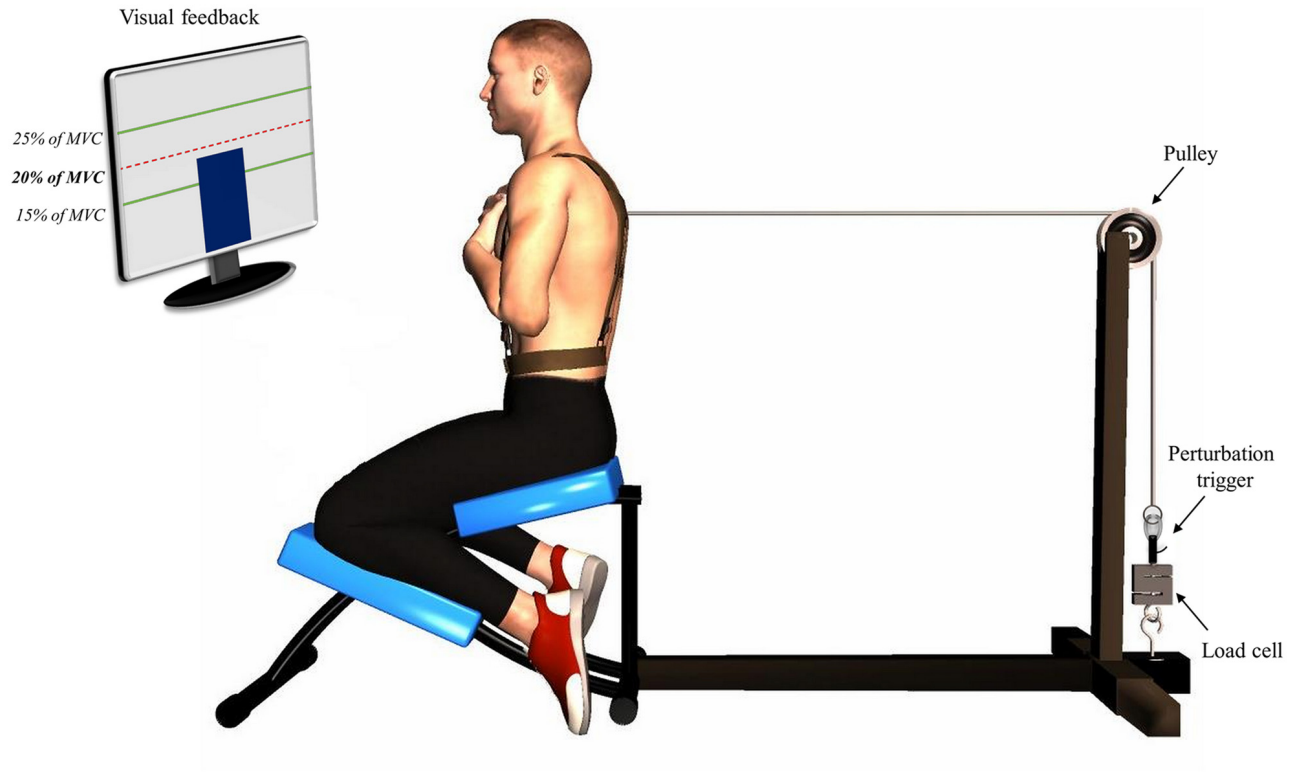

FIGURE 1 | Illustration of the perturbation protocol. Participants were positioned in a semi-seated position with their trunk attached to a manual trigger by a cable using a pulley system. A visual feedback was provided using a screen indicating the target of 20% of their trunk flexion maximal voluntary contraction.

system. This set-up was designed to generate a posterior to anterior perturbation of the trunk. The trigger was connected to a load cell (Model LSB350; Futek Advanced Sensor Technology Inc., Irvine, CA, USA) to objectively measure the pulling trunk flexion force exerted by participants. Participants were asked to maintain a pulling force corresponding to 20% of their trunk flexion MVC and to return to the neutral equilibrium position as quickly as possible after the perturbation. The perturbation magnitude corresponded on average to 55N, ranging from 37N to 76N across participants, which is similar to the perturbation magnitude used in similar perturbation protocols (Radebold et al., 2000; Reeves et al., 2005). The higher value of trunk flexion MVC was used to determine the target force for the perturbation protocol. To help participants reach and stabilize their pulling target force, a visual feedback was provided using a screen indicating real time traction (**Figure 1**). Once the force was stabilized, one of the assessors triggered the perturbation after 1, 3 or 5 s according to a random sequence. The perturbation sequences were different for each participant and each condition (pre- and post-fatigue) to avoid any anticipation of the perturbation onset.

Following the first phase, the fatigue task consisted of a modified version of the Sorensen endurance test (Champagne et al., 2009). Participants were asked to lay in a prone position on a 45° Roman chair, with the iliac crests aligned with the chair cushion edge. In order to quickly induce muscular fatigue, participants had to lift a 12.5-kg weight plate during the task, and hold it as close as possible to their chest. The participants' trunk was maintained unsupported in a horizontal position relative to the ground for as long as possible. The investigators gave similar verbal encouragement to all subjects. Perceived effort scale (6–20; Borg, 1982), measuring the intensity of the fatigue task, was rated by each participant at the end of the fatigue test. Before and after the fatigue protocol, an MVC protocol was performed in the same position as the fatigue task; a belt was fixed to the ground and installed over the participants' shoulders and they were asked to perform a maximal trunk extension contraction against the belt.

The last phase of the experimentation, post-fatigue perturbations, was performed immediately after the fatigue protocol. To avoid the attenuation of muscle fatigue effects, the transition between the fatigue protocol and the second series of perturbation was made as quickly as possible. The time needed between the end of the fatigue protocol and the acquisition of the data ranged from 2 min to 4 min. In this last phase, participants were submitted to 15 more perturbations, identical to the ones received before the fatigue protocol. This part of the experiment lasted no more than 8 min. The total duration of the last phase of the experimentation ranged from 10 min to 12 min.

Data Acquisition

Two different EMG acquisition systems were used to record trunk muscle activity. sEMG of the right and left erector spinae muscles was recorded using two adhesive matrices of 64 electrodes (model ELSCH064; LISiN-OT Bioelettronica; Torino, Italy). The array grid consisted of 64 electrodes placed in an 8 × 8 matrix (10 mm inter-electrode distance). The center of each grid was located at L3 level, and one bracelet ground electrode was placed on the right wrist. The bipolar EMG signals were amplified (64-channel sEMG amplifier, SEA 64, LISiN-OT Bioelettronica; Torino, Italy; –3 dB bandwidths 10–500 Hz) by a factor of 5000 during the perturbations' protocol, while a 2000 factor was applied during the fatigue protocol. The signal was sampled at 2048 Hz and converted to digital form by a 12-bit A/D converter. Rectus abdominis and external obliquus abdominis muscle activity were recorded using a differential Ag sEMG sensor with a common mode rejection ratio of 92 dB at 60 Hz, a noise level of 1.2 μV, a gain of 10 V/V ± 1%, a bandwidth of 20–450 ± 10% (Model DE2.1, Delsys Inc., Boston, MA, USA), amplified by a factor 10,000 and sampled at 2048 Hz with a 12-bit A/D converter (PCI 6024E, National Instruments, Austin, TX, USA). Each bipolar signal was digitally band-pass filtered in the frequency bandwidth-30-450 Hz (2nd order Butterworth filter). Notch filters were also applied to eliminate the 60 Hz and 100 Hz power line interference and its harmonics. To avoid inter-rater variability, anatomical structures palpation and placement of electrodes were assessed by the same investigator for all participants. The electrode position for rectus abdominis and external obliquus was located over the midsection of the muscle and parallel to the fibers orientation, as described by Criswell and Cram (2011). Before the application of an electrode, skin impedance was reduced by shaving body hair, gently exfoliating the skin with fine-grade sandpaper (Red DotTrace Prep, 3 M; St. Paul, MN, USA) and wiping the skin with alcohol swabs. The data from both EMG acquisition systems were collected using the OT Bioelettronica custom software and processed by Matlab (MathWorks; Natick, MA, USA). Trunk extensor and trunk flexor myoelectric signals from EMG were normalized with respect to the trunk extension and flexion MVC values.

Finally, trunk kinematics during perturbation trials was collected using a 3-D motion analysis system (Optotrak Certus, Northern Digital, Waterloo, ON, Canada). Light-emitting diodes were positioned on the left side of the participants over two anatomical landmarks: (1) L1, (2) T11. A third light-emitting diode was placed on the trigger perturbation. Data were sampled at 100 Hz and low-pass filtered by a dual-pass, fourth-order Butterworth filter with a cut-off frequency of 5 Hz. EMG data and kinematic data were synchronized through a signal triggered by OT Bioelettronica software and Matlab (MathWorks). Both EMG and kinematics were recorded for 10 s.

Data Analysis

From high-density sEMG signals, in order to confirm the presence of erector spinae muscle fatigue, the mean normalized slope of the median frequency (MDF; mean of the 64 electrodes of each matrix) was calculated from adjacent non-overlapping signal epochs of 0.5 s. Moreover, the percentage of EMG amplitude root mean square (RMS) diminution between the MVC pre-fatigue and MVC post-fatigue was calculated. Finally, four variables were extracted: the baseline activity, the reflex latency, the reflex peak and the area of muscle activity spatial distribution. Left and right erector spinae muscles were analyzed separately. From abdominal EMG signals, reflex activity was also computed. For all variables, reflex responses latencies superior to 300-ms from the perturbation onset were not analyzed to avoid inclusion of any voluntary responses.

Baseline Activity

Erector spinae baseline activity was quantified as the mean EMG amplitude RMS using a 500-ms window prior to the onset of the perturbation. The mean of all electrodes for each high-density sEMG (left and right) was calculated.

Reflex Latency

Reflex latency of erector spinae muscles was defined as the time delay from the perturbation onset to the EMG reflex onset. To calculate the reflex onset, EMG signals were Butterworth filtered (sixth-order, 50 Hz cut-off frequency) and assessed using a sliding window of 25-ms (Larivière et al., 2010). Muscle activity onset was then determined when the EMG signals exceeded three SD (Hodges and Bui, 1996) above the mean baseline EMG amplitude, which was calculated from a 1-s window before the perturbation onset (**Figure 2**). Reflex latency was also identified by a visual inspection of the EMG recordings by the same investigator. The reflex onset was defined as the beginning of the first peak EMG post perturbation that exceeded approximately two times the mean baseline activity. Due to the high number of electrodes, visual detection technique was only applied on four electrodes by trials. Mean of these four reflex latencies were used during subsequent statistical analyses.

Reflex Peak

The reflex peak corresponded to the highest RMS value following perturbation onset. Reflex peak had to be present in a 300-ms window following the perturbation onset to be considered a reflex response (**Figure 2**).

Area of Reflex Activity Spatial Distribution

To characterize reflex activity, spatial distribution of the dispersion variable representing the muscle activity range of displacement (centroid) was extracted from the bipolar EMG signals. As described in our previous study (Abboud et al., 2014), the centroid was defined as the mean RMS of all 64 electrodes of each high-density EMG. Specifically, the centroid value from each EMG signal was obtained by calculating the mean of RMS value from a window of 100-ms, divided equally (50-ms) on either side of the reflex peak. This operation was repeated through the 15 sudden perturbation trials pre- and post-fatigue protocol to produce dispersion values (see **Figure 3** for more details). The dispersion of erector spinae muscles has been shown to be highly reliable (Abboud et al., 2015).

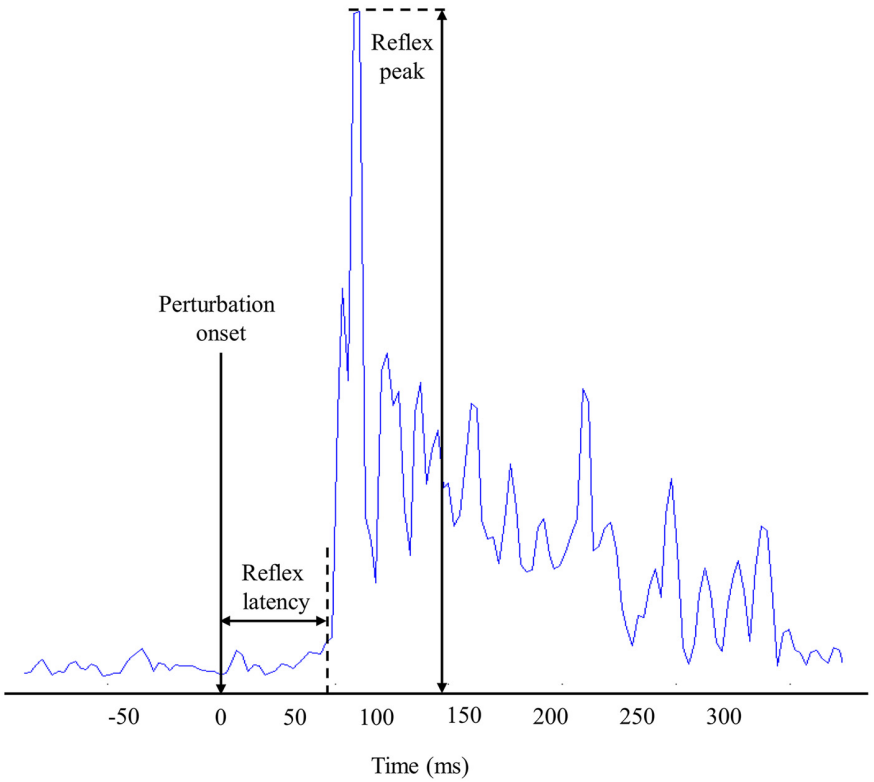

FIGURE 2 | Representation of muscle reflex variables extracted from one high-density electromyography (EMG) electrode during one perturbation trial.

Abdominal Reflex Activity

Since reflex activity in the rectus abdominis and external obliquus rarely occurred after the perturbation, mean RMS values of the abdominal muscles were computed based on the same window of 100-ms used for erector spinae signal analyses. Since no difference was identified between left and right sides, mean values of left and right rectus abdominis as well as mean values of left and right external obliquus were used for the analyses.

Trunk Kinematic

Trunk kinematics were analyzed using the two adjacent LED to create a vector. Lumbar spine motion was obtained by calculating the trunk flexion angle between the T11-L1 vector and a horizontal vector relative to the ground. The angle values corresponded to the range of motion between the starting position before the perturbation, and the maximal trunk flexion following perturbation onset. From the trunk flexion angle, peak velocity and time to peak velocity were calculated. The third kinematic LED was used to determine the exact moment when the perturbation started.

Statistical Analysis

Normality of distribution for every dependent variable was assessed using the Kolmogorov—Smirnov test, in addition to visual inspection of the data. Student *t*-tests for dependent samples were used to compare EMG amplitude RMS between MVC pre- and post-fatigue. Student *t*-tests for dependent samples were also used to compare muscle activity spatial distribution before and following the fatigue task. The first trial pre-fatigue was also compared to the first trial post-fatigue for each dependent variables using *t*-tests for dependent samples. A mixed model two-way repeated measure ANOVA was conducted to assess: (1) the adaptation effect across trials; (2) the fatigue effect; and (3) the interaction effect (fatigue $\times$ adaptation) for each dependent variable (baseline activity, reflex latency, reflex peak, abdominal reflex activity and trunk kinematic). For the variables: baseline, reflex latency, reflex peak and kinematic variables, the means of the first and last five perturbation trials before and after fatigue were considered for the two-way repeated measures ANOVA. When necessary, the Tukey *post hoc* test was performed for pair-wise comparisons. Repeated measures ANOVA followed by quadratic polynomial contrast trend analyses were also conducted for reflex peak values to assess adaptation across perturbation trials before and after muscle fatigue. The reliability of the reflex latency values were estimated by the intraclass correlation (ICC, type 3,1). $ICC_{3,1}$ evaluated inter-rater reliability, using the Matlab software (MathWorks; Natick, MA, USA) representing one rater and visual detection the other one. The standard error of measurement (SEM) was also assessed using the formula SEM = SD * $\sqrt{1 - \text{ICC}}$. For all statistical analyses, $p < 0.05$ was considered to be statistically significant.

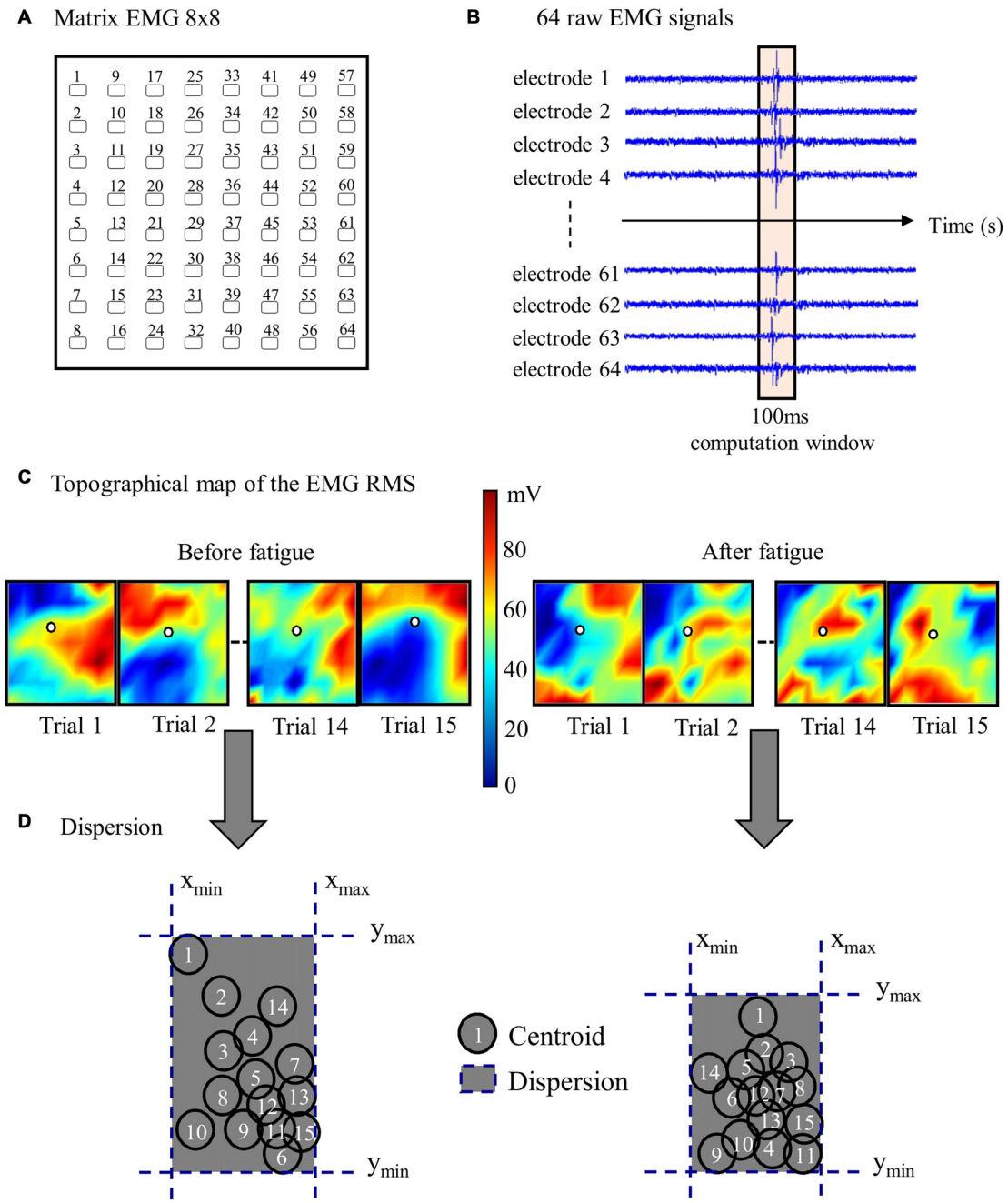

FIGURE 3 | Stages of high-density EMG data analyses. (A) Representation of one 64-electrode matrix used in the recording of erector spinae muscle activity. **(B)** Myoelectric signals from 64 electrodes of one matrix in a random healthy participant during one perturbation trial. **(C)** Centroid migration from topographical representation of root mean square (RMS) reflex values computed within 100 ms windows at each trial. Note the difference between muscle activity recruitment pattern (color variation) between pre- and post-fatigue. **(D)** Dispersion representation from the 15 centroid position before and after the fatigue protocol.

RESULTS

From the 25 original participants, one participant was excluded from all analyses due to the impossibility of identifying the beginning of the perturbation. Moreover, 2% of all perturbation trials from high-density sEMG were not considered for the analyses due to the absence of a reflex response. As for abdominal muscle reflex activity analyses, three participants were excluded due to the poor quality of EMG signals.

Presence of Low Back Muscle Fatigue

The mean endurance time of the fatigue protocol was 125 s (*SD* = 39.4). During the fatigue protocol, a negative slope of MDF values was observed. MDF slope values were −0.184 (*SD* = 0.09) on the right side and −0.165 (*SD* = 0.09) on the left side of the erector spinae. As expected, a significant reduction of EMG amplitude RMS was found between MVC pre- and post-fatigue on the right side of the erector spinae ($p \leq 0.001$) and on the left side ($p \leq 0.001$). Moreover, reductions of EMG amplitude RMS of 28% and 24% on the right and left side, respectively, were found. The perceived effort mean score was 17.6 (*SD* = 1.7), which corresponds to the "very hard" level of perceived effort on the Borg scale. Such level is described as the highest level of activity you can sustain (Borg, 1982).

First Perturbation Trial

In most of cases, the first perturbation trial response pre- and post-fatigue was not affected by the presence of muscle fatigue. Dependent *t*-tests revealed no significant difference between the first perturbation trial before fatigue and the first perturbation trial after fatigue on both sides of the erector spinae muscles for the baseline activity (right side, $p = 0.55$; left side, $p = 0.14$), the reflex latency (right side, $p = 0.84$; left side, $p = 0.49$), the reflex peak (right side, $p = 0.91$; left side, $p = 0.29$), as well as for the rectus abdominis ($p = 0.41$) and external obliquus ($p = 0.05$) reflex amplitudes. As for the kinematic variables, dependent *t*-tests revealed no significant difference between the first perturbation trial before fatigue and the first perturbation trial after fatigue for the trunk flexion angle ($p = 0.78$) and the peak velocity ($p = 0.46$), while a significant decrease between the first perturbation trial before fatigue and the first perturbation trial after fatigue was found for time to peak velocity ($p = 0.007$).

Trunk Kinematic

Most of the trunk kinematic variables did not change with the presence of muscle fatigue and did not adapt over perturbation trials. Only the time to peak velocity were found to be altered. The mixed model repeated measure ANOVA revealed no significant adaptation effect across trials ($F_{(1,23)} = 1.06$, $p = 0.31$) nor a main effect of fatigue ($F_{(1,23)} = 0.22$, $p = 0.64$) for the trunk flexion angle. As for peak velocity, the analyses showed no main effect of fatigue ($F_{(1,23)} = 0.72$, $p = 0.41$) and no adaptation effect ($F_{(1,23)} = 3.56$, $p = 0.07$). Results from the mixed model repeated measure ANOVA also showed a main effect of fatigue for time to peak velocity, with a longer time to peak velocity before the fatigue task ($F_{(1,23)} = 27.25$, $p \leq 0.001$). Additionally, a significant reduction of time to peak velocity was found, representing a main effect of adaptation across trials ($F_{(1,23)} = 7.01$, $p = 0.01$; see **Table 1** for mean and SD values).

Baseline Activity

Small changes were observed in baseline activity after the muscle fatigue protocol as well as over the perturbation trials. The analyses yielded a main effect of fatigue for baseline activity with a higher baseline value after the fatigue task on the left side ($F_{(1,23)} = 5.18$, $p = 0.03$), but not on the right side ($F_{(1,23)} = 1.90$, $p = 0.18$). Similarly, a significant main effect of adaptation, represented by a reduction of baseline activity through the perturbation trials, was observed on the left side ($F_{(1,23)} = 6.63$, $p = 0.02$), but not on the right side ($F_{(1,23)} = 0.33$, $p = 0.57$; see **Table 1** for mean and SD values).

Reflex Latency

Erector spinae reflex latency remained unchanged with or without muscle fatigue and over the perturbation trials. The mixed model repeated measure ANOVA showed no significant

TABLE 1 | Mean values SD of the first and last five perturbation trials before and after the fatigue protocol (maximal voluntary contraction, MVC; L, left side of the erector spinae; R, right side of the erector spinae).

			First five trials mean	Last five trials mean	*p**	
					Fatigue	Adaptation
Flexion angle (°)		Pre-fatigue	6.2 (4.0)	5.9 (4.1)	$p = 0.64$	$p = 0.31$
		Post-fatigue	6.0 (3.9)	5.8 (3.4)		
Peak velocity (°/s)		Pre-fatigue	21.3 (10.8)	19.5 (9.4)	$p = 0.41$	$p = 0.07$
		Post-fatigue	21.8 (10.8)	20.5 (7.1)		
Time to peak velocity (ms)		Pre-fatigue	238 (86)	217 (86)	$p \leq 0.001$	$p = 0.01$
		Post-fatigue	205 (67)	187 (79)		
Baseline (% MVC)	L	Pre-fatigue	8.2 (4.1)	7.6 (3.9)	$p = 0.03$	$p = 0.02$
		Post-fatigue	9.6 (5.1)	9.1 (4.6)		
	R	Pre-fatigue	9.9 (5.2)	9.6 (5.6)	$p = 0.18$	$p = 0.57$
		Post-fatigue	10.7 (6.1)	10.6 (5.7)		
Reflex latency (ms)	L	Pre-fatigue	94.3 (31.9)	89.3 (32.5)	$p = 0.19$	$p = 0.08$
		Post-fatigue	102.1 (39.2)	96.1 (42.4)		
	R	Pre-fatigue	93.8 (29.5)	98.2 (44.8)	$p = 0.75$	$p = 0.25$
		Post-fatigue	95.9 (39.1)	97.9 (36.7)		
Reflex peak (% MVC)	L	Pre-fatigue	60.1 (26.7)	49.5 (23.9)	$p = 0.38$	$p \leq 0.001$
		Post-fatigue	60.4 (26.9)	54.4 (24.4)		
	R	Pre-fatigue	66.7 (25.6)	52.5 (17.6)	$p = 0.02$	$p \leq 0.001$
		Post-fatigue	70.2 (27.9)	65.4 (25.1)		

p based on the repeated measures ANOVA.

main effect of fatigue on both sides of the erector spinae (for the right side ($F_{(1,23)}$ = 0.11, p = 0.75); for the left side ($F_{(1,23)}$ = 1.80, p = 0.19). No significant adaptation effect was observed on either sides (for the right side ($F_{(1,23)}$ = 1.41, p = 0.25); for the left side ($F_{(1,23)}$ = 3.34, p = 0.08); see **Table 1** for mean and SD values). The ICC obtained for reflex latency values was moderate ($ICC_{3,1}$ = 0.63, 95% CI = 0.31–082) and the SEM was small (SEM = 0.016).

Reflex Peak

Following the muscle fatigue task, erector spinae reflex peak value was increased, while adaptations over perturbation trials were altered. Results from the mixed model repeated measure ANOVA showed a main effect of fatigue for reflex peak with a higher peak value after the fatigue task on the right side ($F_{(1,23)}$ = 6.47, p = 0.02), but not on the left side ($F_{(1,23)}$ = 0.80, p = 0.38). Moreover, a significant main effect of adaptation, represented by a reduction of reflex peak amplitude through the perturbation trials, was observed on the right side ($F_{(1,23)}$ = 19.55, $p \leq 0.001$), and on the left side ($F_{(1,23)}$ = 19.70, $p \leq 0.001$). The analyses also showed a significant fatigue × adaptation interaction effect on the right side ($F_{(1,23)}$ = 7.68, p = 0.011); a similar tendency, although not significant, was observed on the left side ($F_{(1,23)}$ = 3.16, p = 0.089; see **Table 1** for mean and SD values). As illustrated in **Figure 4**, *post hoc* analyses revealed higher reflex peak values in the first perturbation trials vs. the last ones in the condition pre-fatigue, but not under the influence of muscle fatigue ($p \leq 0.001$). Moreover, a significant higher peak reflex value was found in the last perturbation trials after vs. before fatigue protocol ($p \leq 0.001$).

Since the first trial reaction is known to have a higher impact on postural balance (Allum et al., 2011), all these analyses were performed a second time without taking into account the first trial before and after the fatigue protocol. This procedure was conducted to explore whether or not the reflex peak attenuation observed over perturbation trials was only due to the first trial. Once again, results from the repeated measure ANOVA showed a main effect of fatigue for reflex peak with a higher peak value after the fatigue task on the right side ($F_{(1,23)}$ = 8.35, p = 0.008; **Figure 5**), but not on the left side ($F_{(1,23)}$ = 2.02, p = 0.17). A significant main effect of adaptation was also observed on the right side ($F_{(1,23)}$ = 6.99, p = 0.015), and on the left side ($F_{(1,23)}$ = 9.66, p = 0.005). The analyses also showed a significant fatigue × adaptation interaction effect on the right side ($F_{(1,23)}$ = 12.09, p = 0.002), but not on the left side ($F_{(1,23)}$ = 0.96, p = 0.33). As illustrated in **Figure 4**, *post hoc* analyses showed higher reflex peak values in the first perturbation trials vs. the last ones in the condition pre-fatigue, but not under the influence of muscle fatigue ($p \leq 0.001$). *Post hoc* analyses also revealed that a significant higher peak reflex value was found in the last perturbation trials after the fatigue protocol vs. the last trials performed before muscle fatigue ($p \leq 0.001$).

Polynomial quadratic trend analyses yielded a significant adaptation (decreasing response) before the fatigue protocol on both sides (for the right side p = 0.01, contrast estimate of 0.99; for the left side p = 0.007, contrast estimate of 1.02), but not under the influence of muscle fatigue (for the right side p = 0.45, contrast

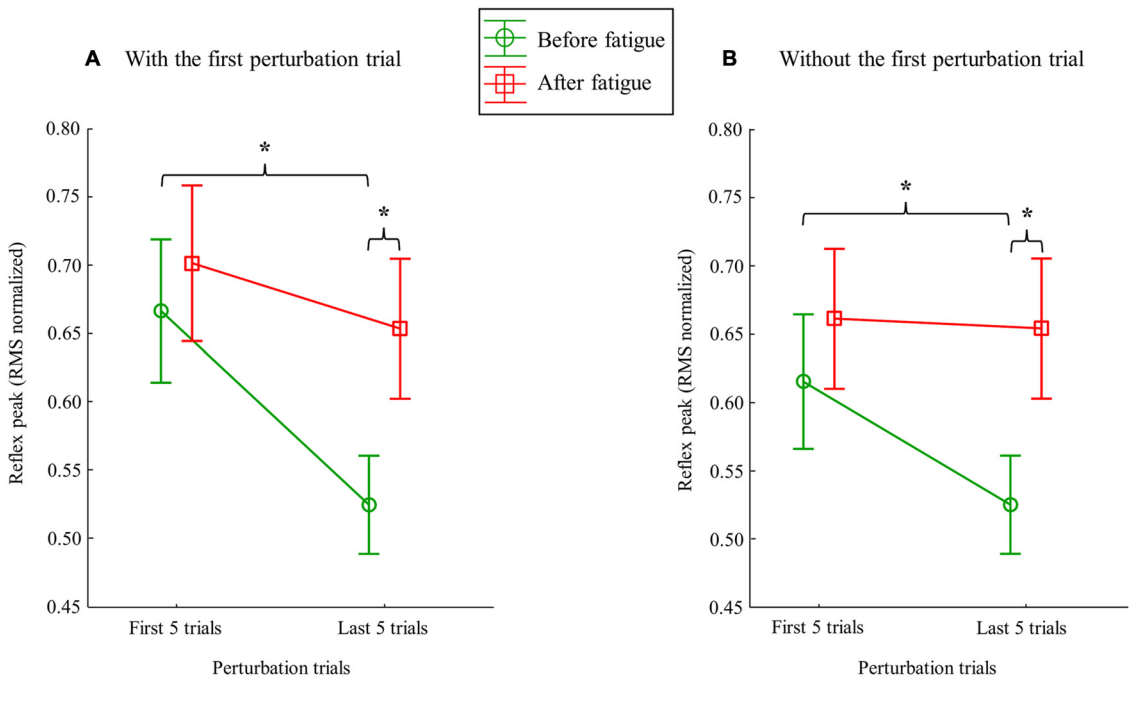

FIGURE 4 | Mean RMS peak results on the right side with (A) and without **(B)** the first perturbation trial on the right side. Error bars indicate standard errors. Significant *post hoc* results are illustrated by $*p \leq 0.001$.

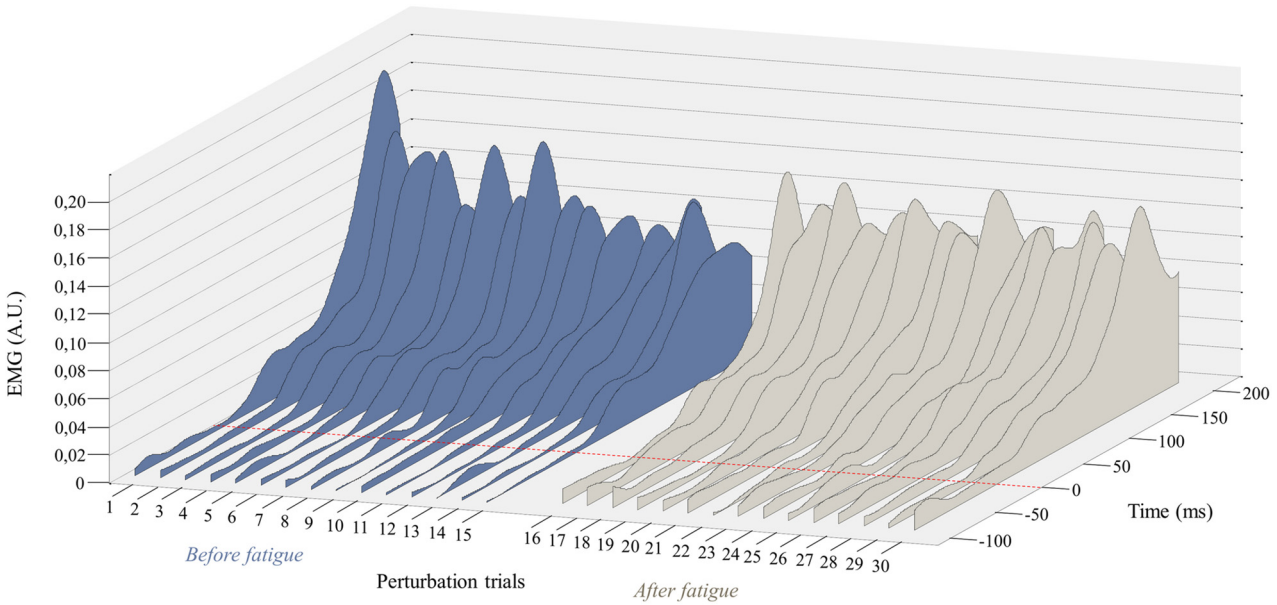

FIGURE 5 | Representation of the mean EMG activity traces for the right erector spinae before (perturbation trials 1–15) and after (perturbation trials 16–30) the fatigue task. The red dotted line represents the perturbation onset. (A.U. Arbitrary Unit).

estimate of 0.35; for the left side $p = 0.26$, contrast estimate of 0.46).

Reflex Spatial Distribution

A higher reflex spatial distribution was observed before the fatigue protocol. Dependent *t*-tests revealed a significant difference between the protocol before fatigue ($M = 1.13$, $SD = 0.25$) and after ($M = 0.95$, $SD = 0.29$) for the dispersion variable on the left side of the erector spinae ($p = 0.02$). A higher dispersion value, yet not significant ($p = 0.08$), was found on the right side before the fatigue ($M = 1.16$, $SD = 0.34$) when compared to trials performed following fatigue (mean = 1.03, $SD = 0.30$).

Dependent *t*-tests were repeated a second time without taking into account the first trial before and after the fatigue protocol. Results from the left side also revealed a significant higher value before the muscle fatigue ($M = 1.10$, $SD = 0.22$) compared to the trials following muscle fatigue ($M = 0.93$, $SD = 0.29$; $p = 0.02$). Once again, a higher dispersion value, yet not significant ($p = 0.07$), was found on the right side before the fatigue ($M = 1.12$, $SD = 0.35$) compared to the trials following muscle fatigue ($M = 0.99$, $SD = 0.29$).

Figure 6 provides an illustration of the complex and variable muscle activity distribution pattern during the perturbation trials before and after the fatigue task. Results showed a smaller centroid migration through the perturbation trials after the fatiguing task.

Abdominal Reflex Activity

Results from the repeated measures ANOVA showed a main effect of fatigue for abdominal reflex activity with a decrease of reflex activity after the fatigue task for the rectus abdominis ($F_{(1,20)} = 8.82$, $p = 0.008$) and the external obliquus ($F_{(1,20)} = 9.50$, $p = 0.006$). Moreover, a significant main effect of adaptation, showing a reduction of abdominal reflex activity, was found only for the rectus abdominis ($F_{(1,20)} = 8.01$, $p = 0.01$), but not for the external obliquus ($F_{(1,20)} = 0.79$, $p = 0.39$).

DISCUSSION

Understanding the neuromuscular responses to unexpected loading of the trunk is highly relevant in view of everyday life and to the investigation of spinal stability and movement control. The present study assessed how erector spinae muscle adapts after a fatigue task fatigue following a series of repeated sudden external perturbations. Using high-density sEMG, this study is the first one showing variability in lower back muscle activity recruitment pattern strategies with a condition perturbing spinal stability. Moreover, this neuromuscular adaptation was altered following back muscle fatigue.

Methodological Considerations

Some fatigue recovery may have occurred over the 15 perturbation trials following the fatigue protocol. Several measures were taken to limit attenuation of muscle fatigue effects. The transition between the fatigue protocol and the second series of perturbation was made as quickly as possible. The time needed between the end of the fatigue protocol and the acquisition of the data ranged from 2 min to 4 min, while it took less than 8 min to conduct the 15 perturbation trials. A study demonstrated that recovery from back muscle fatigue occurs after approximately

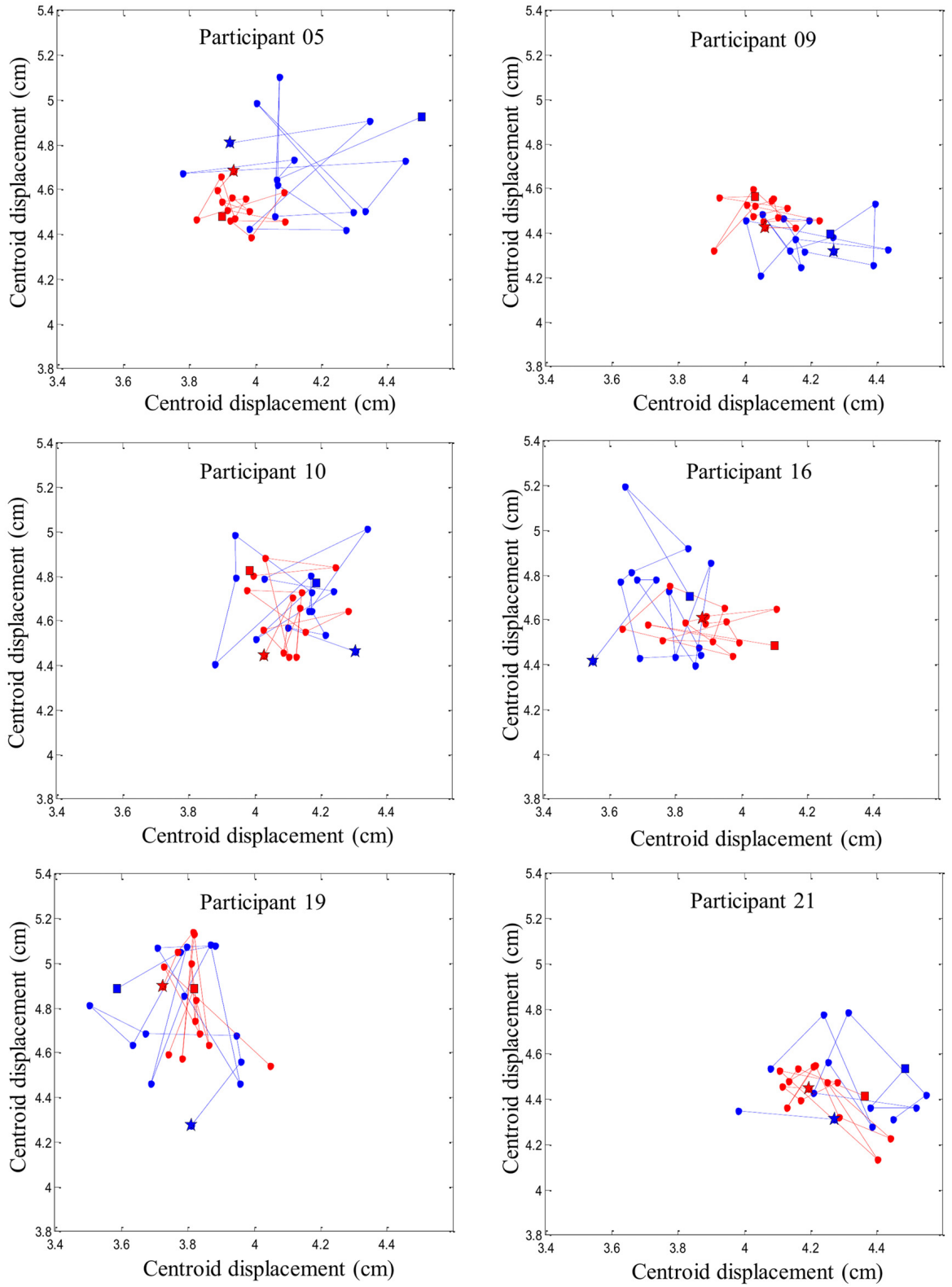

FIGURE 6 | Representation of six random participants' centroid displacement between perturbation trials on the right erector spinae muscles. Blue line represents centroid displacement before the fatigue task. Red line represents centroid displacement after the fatigue task. Stars represent the first trials and squares represent the last trials of each condition (pre- and post-fatigue).

10–15 min of rest (Larivière et al., 2003). However, in this study, participants had to perform a 30 s trunk extension at 75% of their MVC. In the present study, there was no time-limit for the fatigue task and participants were encouraged to maintain position until total exhaustion was reached.

The different acquisition frequencies used in EMG (2048 Hz) and kinematics (100 Hz) system can be considered as a methodological limitation of the study. The difference between acquisition frequencies could lead, under a worst case scenario, to a 10-ms margin of error, when identifying the onset of perturbations. However, the perturbation onset was only used to compute the reflex latencies and consequently did not affect other EMG variables.

Muscle Fatigue Effect

During the experiment, muscle fatigue manifestation in the erector spinae muscles was confirmed by a marked decreased in the MDF slope (De Luca, 1984; Mannion and Dolan, 1994). Moreover, participants perceived the fatigue task as a very hard exertion (Borg, 1982). Finally, a decrease in erector spinae EMG amplitude during post-fatigue MVC is also considered as a valid indicator of muscle fatigue (Enoka and Duchateau, 2008). These observations taken together suggest that the participant were in a fatigue state following the fatigue task. Regarding the impact of muscle fatigue on kinematic variables, results showed no difference between pre- and post-fatigue for trunk flexion angle following the perturbation. This observation is in accordance with previous studies that have also demonstrated that trunk flexion angle is not affected by acute back muscle fatigue following an unexpected perturbation (Granata et al., 2004; Mawston et al., 2007). Moreover, participant peak velocities remained unchanged with the presence of muscle fatigue. On the other hand, the present study is the first one showing that in the presence of muscle fatigue, participants decreased their time to peak velocity in response to the perturbation. These results suggest that fatigue did induce some changes in the neuromuscular control of postural balance, but the sensorimotor system remained partly efficient when the low back region was fatigued. This strategy could be explained by the trunk muscle system's redundancy which offers various adaptation possibilities to achieve a similar goal (Latash and Anson, 2006). Even if the trunk flexion angle were similar with or without fatigue, there were probably other neuromuscular strategies that prevented the effect of fatigue, such as variability in muscle activity recruitment pattern (see "New Insights into Motor Adaptation to Spinal Instability" Section for further explanation).

Using high-density sEMG, this study is the first one exploring EMG reflex variables with muscle fatigue. In the current study, baseline activity seemed to show a slight trend towards higher muscle activation after the fatigue protocol (only significant on one side of the erector spinae). Current evidence have not find a common understanding on baseline activity prior a perturbation under the influence of muscle fatigue (Granata et al., 2001, 2004; Herrmann et al., 2006; Mawston et al., 2007; Grondin and Potvin, 2009; Dupeyron et al., 2010). Baseline activity is directly linked to EMG amplitude signals, which corresponds to the number of active motor units. Muscle fatigue is characterized by an increase of active motor units (De Luca, 1997), which is usually reflected by an increase in EMG amplitude signals in submaximal muscle contractions. A recent review has shown that muscle fatigue induced by a submaximal isometric contraction is associated with variable responses in motor units firing rates according to the intensity of the fatiguing task (Taylor et al., 2016). For example, motor unit behavior during submaximal isometric contraction at moderate intensity (50% MVC), which correspond to the Sorensen test (Demoulin et al., 2006), is first associated with a decrease in firing rate followed by an increased motor units recruitment (Heckman and Enoka, 2012). Since others studies have used different fatigue protocol, with effort intensity varying from approximately 20–60% of the MVC (Granata et al., 2001; Herrmann et al., 2006; Dupeyron et al., 2010), a variation in motor unit behavior could partly explain discrepancies across studies. In the current study, two methods were used to determine the exact time between the onset of the perturbation and the reflex response. Despite a moderate reliability between those detection methods (ICC 0.63), reflex latency values (≈95 ms) are similar to those observed in the studies (ranging from ≈60 ms to 125 ms) measuring the impact of muscle fatigue on reflex latency (Chow et al., 2004; Granata et al., 2004; Herrmann et al., 2006; Dupeyron et al., 2010; Sánchez-Zuriaga et al., 2010). Furthermore, no change was observed under the influence of muscle fatigue in the present study. This observation is consistent with most of the studies (Granata et al., 2004; Herrmann et al., 2006; Dupeyron et al., 2010; Sánchez-Zuriaga et al., 2010). In the literature, reflex amplitude of low back muscles was found not to be affected by muscle fatigue in several studies (Granata et al., 2004; Grondin and Potvin, 2009; Sánchez-Zuriaga et al., 2010), whereas two studies found a higher back reflex amplitude following a fatigue protocol (Herrmann et al., 2006; Dupeyron et al., 2010). In the present study, an increase in reflex peak values was observed after the fatiguing task. An interesting assumption to explain the discrepancy in reflex peak results could be the presence of an association between baseline activity responses, reflex peak and muscle fatigue. Indeed, studies who have reported an increase in baseline activity are the same that did not observe a change in reflex peak amplitude after muscle fatigue (Granata et al., 2004; Grondin and Potvin, 2009), and vice versa (Herrmann et al., 2006; Dupeyron et al., 2010). It could be hypothesized that increased muscle pre-activation is sufficient to counteract the fatigue effect in response to an external perturbation. On the other hand, with negligible change in pre-activation level, as observed in our study, neuromuscular adaptations are reflected in the variation of reflex peak amplitude.

In parallel to the observation of an increased reflex activity amplitude in the back muscle following fatigue, a decreased abdominal reflex activity was identified. This observation suggests that an increase in erector spinae activity would be sufficient to increase spinal stability in order to compensate for acute back fatigue effect (Cholewicki et al., 2000; Andersen et al., 2004). However, these results should be interpreted with caution

since abdominal muscle EMG reflex amplitude remained higher than 50% of their activity during the MVC.

Trial-to-Trial Adaptation

In the current study, participants were submitted to a series of the exact same unexpected perturbation of the trunk. Kinematic variables including trunk flexion angles and velocity peaks remained constant through the perturbation trials. However, a decrease in time to peak velocity was observed across trials of the same unexpected perturbation. This suggest that participants adapted to the unexpected perturbation by taking less time to stop their trunk movement. A group of authors have also shown, across 10 trunk perturbation trials, a progressive reduction in the time interval between forward trunk movement initiation and complete cessation of trunk movement (Skotte et al., 2004). These observations suggest that, when first facing an unexpected perturbation, the sensorimotor systems allows irrelevant components of a motor task to fluctuate. According to the minimal intervention principle, the irrelevant aspects from the resulting behavior should be left uncorrected in order to maximize motor performance (Todorov and Jordan, 2002). Based on this principle and the findings of this study, one could argue that trunk movements triggered by the perturbations (6° on average) were not sufficient, and consequently no adaptation of the trunk flexion angle was needed to optimize spinal stabilization. In such context, trunk flexion angle and peak velocity would be considered irrelevant aspect of spinal stability while time to peak velocity would have more significant consequences on stability and potential tissue damage.

Across perturbation trials, a small attenuation of baseline activity was observed, while no adaptation was found for the reflex latency. The absence of reflex latency trial-to-trial adaptation was also observed in a previous study (Skotte et al., 2004). As for reflex peak amplitude, a clear reduction of amplitude values through the repetition of the unexpected trunk perturbation was found in the present study. It is known that the first trial reaction to an unexpected perturbation has a higher impact on postural balance in standing or seated positions (Allum et al., 2011). Results from the present study have shown that even without considering the first trial response, an attenuation of the reflex response still occurred. However, it is important to note that as we get closer to the last perturbation trial, the attenuation lessens. Similar observations were found following unexpected tilts of a surface platform, with authors showing a rapid adaptation of EMG amplitude between the first two trials, whereas adaptation was more gradual over the next trials (Oude Nijhuis et al., 2010). Again, based on this motor behavior, it could be suggested that, in the presence of an unknown movement or perturbation, the optimal strategy would be to first adopt a broader but less specific motor response (Todorov and Jordan, 2002). Following repetitions of the same unexpected perturbation, the trunk muscle system's redundancy could offer corrections by using the appropriate number of degrees of freedom (Latash and Anson, 2006). Such adaptations would also explain the progressive time to peak velocity reduction across perturbation trials.

Interestingly, this progressive decrease continued throughout perturbation trials following the fatigue task. This suggests that even when muscle fatigue is present, participants continued their adaptation to perturbations by taking less time to stabilize their trunk. Since trunk flexion angle and velocity peak remained unchanged, it suggests that participants were able to stabilize trunk movement using alternative neuromuscular strategies. Indeed, following muscle fatigue, the trial-to-trial adaptation of the EMG reflex peak appeared to be limited. To our knowledge, the present study is the first one showing that adaptation of the reflex peak across perturbation trials is altered following muscle fatigue. The amplitude of the reflex peak remained almost constantly at the same level from the first to the last external perturbation. It could be hypothesized that muscle fatigue limited the possibility of using across-trial redundancy to adapt and optimize spinal stabilization using retroactive control. Moreover, since postural balance, expressed as a trunk angle, also remained constant throughout the perturbation trials with or without muscle fatigue, it could be suggested that alterations of the EMG reflex adaptation are an attempt to preserve a constant postural balance despite the presence of muscle fatigue.

As discussed in the methodological considerations section, some recovery may have been present throughout the last perturbation trials. In a previous study, the effect of recovery from muscle fatigue on adaptation to external perturbations was explored (Takahashi et al., 2006). Results showed that recovery affects recall of the internal model. The authors suggested that participants overestimated the muscle activity required to counteract the perturbation because their muscle force-generation capacity recovered during rest. Although fatigue and recovery effects cannot be teased out, results from the present study show that following a fatigue protocol, a modification of EMG reflex peak and trunk kinematics (time to peak velocity) occurred whereas trial-to-trial adaptation in EMG reflex peak was found to be limited following a protocol of fatigue.

Finally, the adaptation throughout the first perturbation trial following muscle fatigue was almost inexistent. Results from the present study showed that only time to peak velocity was affected when participants experienced, for the first time, an unexpected perturbation following a fatigue task. Similarly to the adaptation phenomenon observed across perturbation trials, participants took less time to stabilize their trunk following the fatigue protocol. These findings suggest that in most cases, the neuromuscular component of spinal stability is not significantly challenged in the presence of muscle fatigue, regardless of the number of exposure to a specific trunk perturbation.

New Insights into Motor Adaptation to Spinal Instability

Using high-density sEMG, dispersion of muscle activity, representing the area of reflex activity spatial distribution, was

used to better understand trial-to-trial adaptation with and without muscle fatigue. A higher variability in muscle activity spatial distribution was observed before muscle fatigue was induced, while under the influence of fatigue, a reduction of the centroid migration was found. Changes in muscle activity distribution to different regions of the lumbar erector spinae could be associated with changes in variation in the control of motor units within this muscle. As mentioned earlier, adaptation of muscle reflex activity occurred through the repetition of similar sudden external perturbations. This observation suggests that the trial-to-trial adaptation was associated with higher levels of muscle activity spatial distribution. Conversely, such adaptation was not present when erector spinae muscles were in a state of fatigue. This suggests that changing spatial distribution of EMG activity, consistent with increased motor variability (Latash, 1998), may help face a series of unexpected perturbation. On the other hand, the reduced muscle activity spatial distribution observed in presence of muscle fatigue could be explained by the initiation of protective and restrictive neuromuscular strategies. This study suggests that under the influence of fatigue, the nervous system chooses to adopt a more stable muscle activity distribution when spinal stability is challenged. This observation are complementary with the work of Missenard et al., which showed that muscle fatigue increases the variance of motor commands during voluntary movements (Missenard et al., 2008, 2009). Motor variability can be measured using multiple parameters, such as muscle activity, kinetic or kinematic components of the movement pattern, or external force developed (Srinivasan and Mathiassen, 2012). In the present study, a more stable pattern of muscle activity distribution following fatigue, can be explained by the decreased number of motor unit available to generate muscle responses during perturbations. This reduced number of available motor unit may lead to more stable spatial distribution as illustrated by the reduced centroid migration in the presence of muscle fatigue (**Figure 6**). Moreover, muscle fatigue by reducing the number of available motor units may increase the variability in movement patterns (Missenard et al., 2008, 2009).

It is also important to note that the migration of muscle activity was highly variable between participants before and after the fatigue task. While spatial muscle activity distribution has been shown to shift laterally and caudally during a fatigue task in the low back region (Abboud et al., 2014), no distinctive muscle activity migration pattern was identified following a repeated unexpected perturbation. A recent study has provided similar results when a group of healthy participants were injected with a saline solution to induce acute low back pain (Hodges et al., 2013). After the injection, none of the participants activated their trunk muscles in the same manner in response to an external trunk perturbation (Hodges et al., 2013). These results reflect the complexity of the redundant trunk system, which offers various motor possibilities to achieve a similar goal. This raises the question whether these adaptations are maintained across various perturbation tasks or if the nervous system triggers individual similar adaptations for each person. Further research will be needed to verify if the alteration of trial-to-trial response is also present in a different external environment trunk perturbation such as chronic low back pain or spinal tissue creep.

In conclusion, the results of the present study suggest that participants adapt differently under the influence of muscle fatigue when they experience an unknown perturbation. While the EMG reflex amplitude remains constant over perturbation trials after the fatigue task, participants continue to habituate their trunk movements. Moreover, this study suggests that the nervous system chooses to adopt a more restrictive muscle activity recruitment pattern, when the unknown perturbation is repeated after a muscle fatigue task. Since this study is the first one describing such motor adaptations, it seems reasonable to propose that following muscle fatigue, the motor system can still generate proper stabilizing responses to spinal perturbations using alternative strategies. These strategies, however, may have detrimental long-term consequences that should also be considered in the context of spine rehabilitation.

AUTHOR CONTRIBUTIONS

JA, FN, AL, CD and MD: substantial contributions to the conception or design of the work, or acquisition, analysis, or interpretation of data for the work; drafting the work and revising it critically for important intellectual content; final approval of the version to be published; agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Holding a Handle for Balance during Continuous Postural Perturbations—Immediate and Transitionary Effects on Whole Body Posture

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When balance is exposed to perturbations, hand contacts are often used to assist postural control. We investigated the immediate and the transitionary effects of supportive hand contacts during continuous anteroposterior perturbations of stance by automated waist-pulls. Ten young adults were perturbed for 5 min and required to maintain balance by holding to a stationary, shoulder-high handle and following its removal. Center of pressure (COP) displacement, hip, knee and ankle angles, leg and trunk muscle activity and handle contact forces were acquired. The analysis of results show that COP excursions are significantly smaller when the subjects utilize supportive hand contact and that the displacement of COP is strongly correlated to the perturbation force and significantly larger in the anterior than posterior direction. Regression analysis of hand forces revealed that subjects utilized the hand support significantly more during the posterior than anterior perturbations. Moreover, kinematical analysis showed that utilization of supportive hand contacts alter posture of the whole body and that postural readjustments after the release of the handle, occur at different time scales in the hip, knee and ankle joints. Overall, our findings show that supportive hand contacts are efficiently used for balance control during continuous postural perturbations and that utilization of a handle has significant immediate and transitionary effects on whole body posture.

Keywords: falls, handle, grasping, postural balance, balance recovery

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INTRODUCTION

With aging society, falls are becoming an increasingly large problem. A large proportion of falls occur due to the improper weight shifts (Robinovitch et al., 2013) and impaired postural control is a landmark of aging (Maki and McIlroy, 2006; Mansfield and Maki, 2009). When postural control is impaired, handrails, canes and handles are often used to assist maintaining balance by providing additional supportive contacts with the environment. This indicates that holding onto a physical aid is beneficial for postural control.

With respect to the use of hand contacts for postural control, one of the widely investigated phenomena is "light touch" (Jeka, 1997; Krishnamoorthy et al., 2002). These light, fingertip contacts with stationary objects can extend the base of support (Bateni and Maki, 2005) and provide an additional sensory input, which helps individuals to better position them in space (Jeka, 1997). Such sensory information improves postural control in quiet standing by reducing the amplitude of center of pressure (COP) movement (Jeka, 1997; Johannsen et al., 2007; Kouzaki and Masani, 2008; Wing et al., 2011).

On the other hand, in case of perturbed balance reaching arm movements with the aim to grasp for a nearby object is a widely utilized change-in-support strategy (Maki and McIlroy, 2006). Such hand contacts provide mechanical support in addition to the sensory augmentation of the light touch and thus offer a better stabilizing potential in the presence of perturbations (Maki and McIlroy, 1997). Specifically, holding onto a handle increases the base of support of a standing individual and enables a person to generate necessary hand forces to better counteract the perturbations (Babič et al., 2014; Sarraf et al., 2014). A recent study by Babič et al. (2014) showed that the location of the supporting hand contact is important to maximize its stabilizing potential and that the peak forces exerted at the handle during the support surface perturbations are related to the location of the handle.

Aforementioned studies were based on the discrete perturbations of balance which predominantly evoke feedback postural responses. A major component of such responses is comprised of motor actions that are related to various sensorimotor reflexes and to a lesser extent to the feed-forward components of the postural control (Mergner, 2010). Moreover, the discrete perturbations evoke reach-to-grasp arm movements even when the perturbations are so light that they do not physically disturb postural balance (McIlroy and Maki, 1995; Corbeil et al., 2013). In contrast to the discrete perturbations of balance, perturbations that continuously disturb postural balance evoke both feedback and feed-forward components of motor action and in this sense offer a complementary insight into the postural control (Dietz et al., 1993; Schmid et al., 2011).

The remaining question is what is the role of hand contact during continuous perturbations? Therefore, the aim of this article is to study situations where balance of an individual is challenged by continuous postural perturbations and to investigate the role of supportive hand contact in counteracting postural perturbations. Specifically, our goal was to investigate the immediate and the transitionary effects of a supportive hand contact on postural control of an individual whose balance is challenged by continuous anteroposterior perturbations of stance.

Our hypothesis is that a supportive hand contact has a significant influence on postural balance by reducing the COP excursion during the perturbation and that the utilization of the hand contact is more prominent for postural perturbations in the backward direction which are more threatening than the perturbations in the forward direction. Moreover, we hypothesize that utilization of the additional hand support not only alters posture of the human body while the hand is in contact with the environment but also after the release of the handle. To effectively address these hypotheses, we developed an experimental framework where we continuously perturbed postural balance and investigated the relationships between the perturbation force and the COP displacement, kinematical parameters of the human body, and the forces exerted by the supportive hand.

MATERIALS AND METHODS

Participants

Thirteen healthy right-handed young adults participated in this study after giving their written consent. Data of three subjects were excluded from the analyses due to technical problems during acquisition, therefore we used the data of ten subjects (average age = 22.3 years, SD = 2.2 years, average height 179.2 cm, SD = 5.9 cm and average weight = 76.9 kg, SD = 8.2 kg). The experimental procedures conformed to the latest revision of the Declaration of Helsinki and were approved by the Slovenian National Medical Ethics Committee (No. 112/06/13).

Measurement Protocol

Subjects were asked to step on a force plate, stand straight with the feet placed at hip width and look straight ahead. They were required to keep upright posture and maintain balance without making any unnecessary corrective steps while their balance was continuously perturbed in anteroposterior direction by a motorized waist-pull system (Peternel and Babič, 2013) as depicted in **Figure 1**. During the experiment, the subjects were not allowed to change their base of support. We marked their individual standing position on the force plate prior to the start of the experiment which was used as a reference for foot position during the experiment. This ensured that the different stance width would not affect subjects' balance since it has been shown by Bingham and Ting (2013) that active torque at ankle and hip joints scale with stance width. To emulate mild, daily life perturbations such as those during riding on buses, subways and trains (Graaf and van Weperen, 1997) the motorized waist-pull system perturbed the subjects using a band-pass filtered white noise signal (0.25–1.00 Hz) with the maximal perturbation force of 11% of the subjects' body weight (**Figure 2**).

The experiment consisted of two consecutive 5 min trials of different standing conditions: balancing while holding to a handle [*with-handle (WH)*] and without holding to a handle [*no-handle (NH)*]. First, the subjects were exposed to 5 min of perturbations in the *WH* trial. In the *WH* trial, subjects held onto a stationary handle (diameter = 3.2 cm, length = 12 cm) positioned at shoulder height with their right hand. After 5 min the perturbation stopped, subjects released the handle and folded their arms across their chest. Then, on average less than 60 s later, the second trial of 5 min of perturbation started (*NH* trial). In the *NH* trial, subjects were standing with their arms folded across their chest. In both trials, subjects were instructed to look straight ahead at all times at a fixed point positioned at the subject's eyelevel and 3 m in front of the experimental setup.

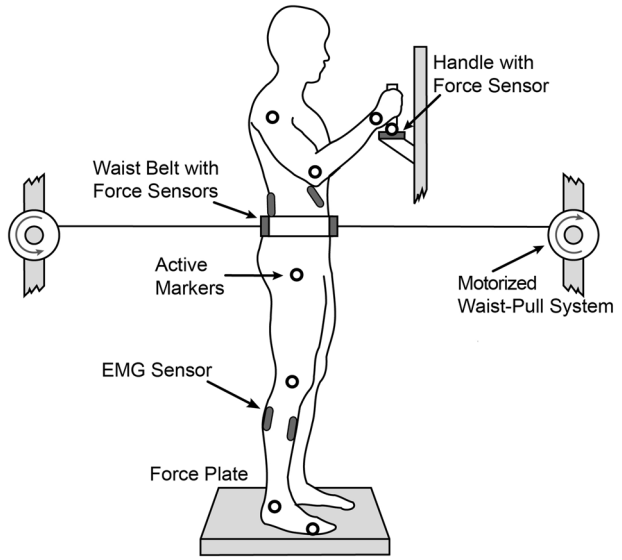

FIGURE 1 | Experimental setup. The subject is standing on a force plate, wearing a waist belt connected to the motorized waist-pull system which generated translational force perturbations in the anterior-posterior direction using a band-filtered white noise signal constructed to emulate mild, daily life perturbations.

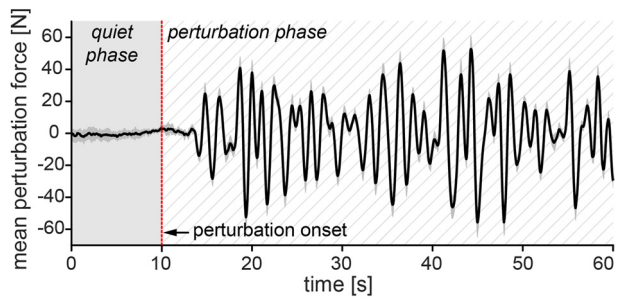

FIGURE 2 | Perturbation signal sample. Solid black curve represents first 60 s of mean perturbation signal from all 10 subjects with ±1 standard error of the mean (gray shade around the curve). In the first 10 s of each trial the perturbation value was at 0 N—quiet phase. After 10 s (perturbation onset), the perturbation gradually increased with alternated direction and amplitude—perturbation phase. Positive values of mean perturbation force represent forces in anterior direction and negative values represent forces in posterior direction. The perturbation signal was identical in both trials.

To induce response adaptations (Van Ooteghem et al., 2008; Schmid et al., 2011), the subjects were allowed to familiarize with the experimental procedures prior to the main experimental trials.

Kinetic data were collected using a force plate (9281CA, Kistler Instrumente AG, Winterthur, Switzerland) under the subjects' feet and a 3-axis force sensor (45E15A, JR3, Woodland, CA, USA) on the handle, both at 1000 samples/s.

Kinematic data were collected at a sampling rate of 100 samples/s using a contactless motion capture system (3D Investigator, Northern Digital Inc., Waterloo, ON, Canada) consisting of a 3 × 3 camera array. Nine active markers were placed at the apparent axis of rotation of the fifth metatarsophalangeal, ankle, knee, hip, shoulder, elbow and wrist joints on the subject's right side as well as at the base of the platform and the handle.

Anteroposterior displacement of the subject's COP was derived from the force plate data. In the first 10 s of each trial, the subjects stood quietly (holding a handle with right hand in the first trial, or both arms folded across their chest in the second trial) and no perturbation was applied at the waist (see **Figure 2** for reference regarding perturbation signal). The mean COP position from this time period (we refer to this as *quiet phase*) served as a baseline for calculation of COP excursions in the anterior and posterior direction in the following perturbations (*perturbation phase*).

Handle forces were calculated by considering the torques of the lever (distance from force sensor to the middle of the subject's hand on the handle). Kinematic data were low pass filtered (zero lag, 2nd order Butterworth filter with a cut-off frequency 20 Hz). Ankle angle was calculated as the angle between the foot (line connecting the fifth metatarsal and ankle) and the shank (line connecting the ankle and the knee), knee angle as the angle between the shank and thigh (line connecting the knee and the hip), and hip as the angle between the thigh and torso (line connecting the hip and the shoulder). To evaluate the adaptation effects of releasing the handle in the *NH* trial, an exponential fit of group average joint angles was calculated (Franklin et al., 2003). Adaptation was considered as final once the given joint angle reached the plateau defined by three time constants of the fitted exponential decay function, i.e., once the fitted exponential decay function fell to 5% of its starting value (Honeine et al., 2015; Assländer and Peterka, 2016).

Electromyographical (EMG) electrodes were placed on the right leg (TA, Tibialis Anterior; GA, Gastrocnemius Lateralis; and trunk (MF, Multifidus; OE, Obliques Externus) muscles and their activity was measured using Biometrics DataLOG MW8X at a sampling rate of 1000 samples/s. Preparation of the skin and positioning of the electrodes was performed according to the SENIAM protocol (Hermens et al., 2000). Before the start of the experiment, subjects performed three maximal voluntary contractions (MVC) against resistance of each of the measured muscles. MVC's were used in EMG post-processing for normalization, to establish a common ground when comparing data between subjects. All EMG signals were band-pass filtered (zero lag, 2nd order Butterworth filter with cut-off frequencies of 20 and 450 Hz), full-wave rectified and low pass filtered (zero lag, 2nd order Butterworth algorithm, 10 Hz cut-off frequency). Finally, EMG signals were normalized with respect to the MVCs and integrated over time (iEMG) to express the magnitude of muscle activity.

We divided COP excursions and contact forces exerted on the handle in two data sets based on their direction—anterior and posterior. For each data set, average values from all 10 subjects were calculated and used in the statistical analysis.

Average hip, knee and ankle angles over the 5 min for each subject were calculated and used for statistical analysis.

Differences between COP displacement in the anterior and posterior directions and subject average joint angles were analyzed using paired samples *t*-tests. Differences between the *WH* and *NH* trials in subject average COP displacements were analyzed for the anterior and posterior directions separately, using a paired samples *t*-test. The relationship between group average COP excursion and the magnitude of the perturbation and between group average perturbation magnitude and the exerted handle contact force was analyzed using separate linear correlations for anterior and posterior directions. All statistical analyses were performed using SPSS 21 Inc., Chicago, IL, USA at $\alpha = 0.05$. Effect size (d) was calculated using standard Cohen's equation (Cohen, 1988).

RESULTS

Supportive Hand Contact has Significant Influence on Postural Balance by Reducing COP Excursion during Perturbation

The diagram in **Figure 3** shows the comparison of mean COP excursion between the conditions when the subjects counteracted postural perturbations without using the additional hand contact (NH) and when they did use the handle (WH). Paired samples *t*-test showed significant effect in reducing the mean COP excursion when the subjects were holding to the handle compared to when they did not hold to the handle. The differences of COP excursion were significantly larger both in the anterior direction (difference of 20.3 mm, $t_{(9)} = 7.78$, $p = 0.001$, $d = -4.15$) and posterior direction (difference of 23.9 mm, $t_{(9)} = -11.09$, $p = 0.001$, $d = -3.8$).

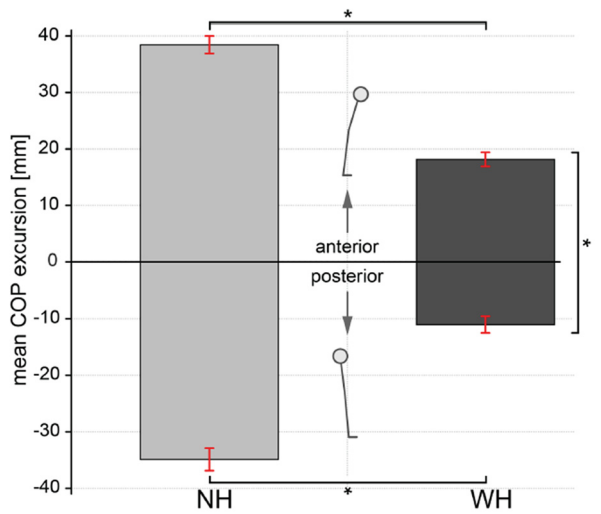

FIGURE 3 | Comparison of center of pressure (COP) excursion between trials when subjects either used additional hand contact or not. Bars represent mean COP excursion during no-handle (NH) and with-handle (WH) trials for the anterior (positive) and posterior (negative) directions. Error bars indicate ±1 standard error of the mean. Statistically significant differences are indicated (*$p \leq 0.02$).

Utilization of Hand Contact is more Prominent for Postural Perturbations in Backward Direction than for Perturbations in Forward Direction

In both, *NH* and *WH* trials, the COP excursion was larger in the anterior direction (mean ± SE: *NH* 38.5 ± 1.6 mm, *WH* 18.2 ± 1.2 mm) compared to the posterior (mean ± SE: *NH* −34.9 ± 2 mm, *WH* −11.0 ± 1.5 mm), but this difference was significant only for the *WH* trial ($t_{(9)} = 2.81$, $p = 0.02$, $d = 1.52$).

We further assessed the effects of utilizing the additional hand contact, and the direction and intensity of perturbation on the maximal COP displacement. The diagrams in **Figure 4** show correlations between the perturbation force and the group average COP excursion during *NH* and *WH* trials. Additionally, the correlation between the perturbation force and the handle force is shown for the *WH* trials. The group average COP excursion was strongly correlated with perturbation force in both posterior ($r_p = 0.77$ and $r_p = 0.67$) and anterior ($r_a = 0.82$ and $r_a = 0.89$) directions in the *NH* and *WH* trials, respectively (all $p < 0.001$). Similarly, the forces that

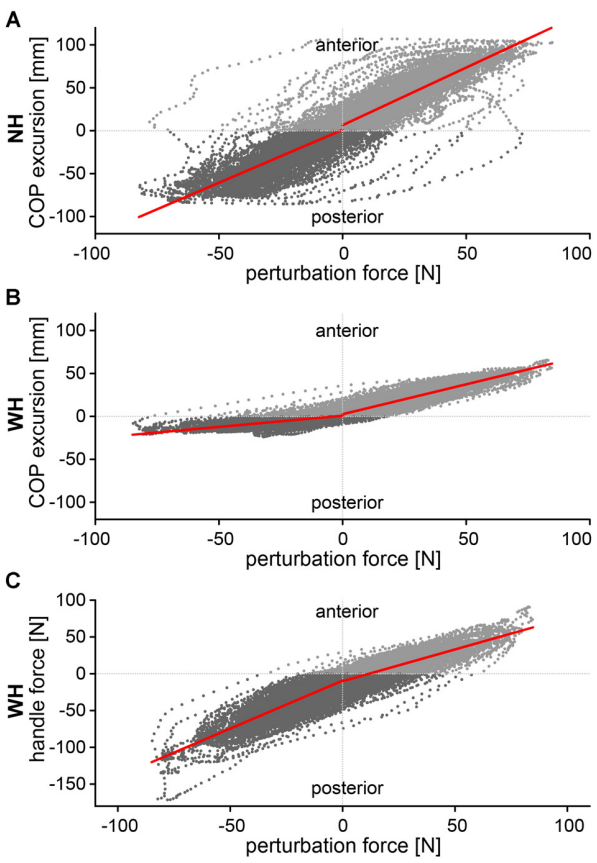

FIGURE 4 | Correlations between perturbation force and (A) COP excursion in NH trial, (B) COP excursion in WH trial and (C) handle force in the WH trial. Correlations were calculated separately for the anterior (positive) and posterior (negative) direction.

subjects applied on the handle was also strongly correlated with the perturbation force (**Figure 4C**) in both anterior ($r_p = 0.85$, $p < 0.001$) and posterior directions ($r_a = 0.81$, $p < 0.001$). Moreover, the slope of the regression line is significantly larger for perturbations in the posterior direction ($k_p = 1.3$), compared to the perturbations in the anterior direction ($k_a = 0.86$).

Supportive Hand Contact Affects Whole Body Posture

To investigate how the additional hand contact affects the body posture during the perturbations, we compared the mean values of ankle, knee and hip joint angles between the conditions when the subjects counteracted perturbations without the additional hand contact (NH) and when they did use the handle (WH). The comparison is shown in the diagram in **Figure 5**.

Multiple paired samples *t*-tests showed significant effect of the hand contact on all three observed joint angles. Specifically, mean joint angles were significantly lower during the *NH* trials compared to the *WH* trials. Differences were the largest in the knee (mean ± SE: 165.1 ± 1.9° for NH, 173.2 ± 1.5° for WH, $t_{(9)} = -6.70$, $p < 0.001$, $d = 1.4$), followed by the hip (mean ± SE: 171.4 ± 2.8° for NH, 181.5 ± 1.6° WH, $t_{(9)} = -6.68$, $p < 0.001$, $d = 1.1$) and the ankle (mean ± SE: 108 ± 1.2° for NH, 112 ± 1.1° WH, $t_{(9)} = -5.67$, $p < 0.001$, $d = 1.1$).

Utilization of Hand Contact has Non-Uniform Transitionary Effect on Whole Body Posture after Release of Handle

To investigate the effect of supportive hand contact on the body posture, an exponential curve was fitted to the group average ankle, knee and hip joint angles calculated during the *NH* trial that immediately followed the *WH* trial (**Figure 6**).

Exponential fits revealed that postural readjustments after the release of the handle did not occur simultaneously throughout the body. Instead, the readjustments occurred at different time scales in the hip, knee and ankle joints. Specifically, joint angles stabilized first in the ankle (mean ± SE: 133 ± 103.5 s after perturbation onset), followed by the hip (mean ± SE: 188 ± 90.8 s after the perturbation onset) and finally in the knee (mean ± SE: 195 ± 92.5 s after the perturbation onset). However, a paired-samples *t*-test did not show statistically significant difference between any of the compared pairs due to the high variability of data.

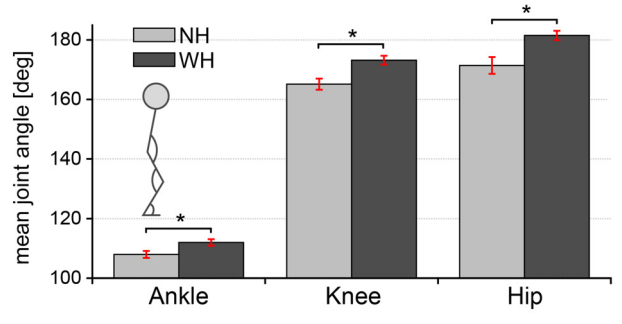

FIGURE 5 | Comparison of body posture between trials when subjects either used additional hand contact or not. Bars represent mean ankle, knee and hip joint angles during NH and WH trials. Error bars indicate ±1 standard error of the mean. Statistically significant differences are indicated (*$p \leq 0.02$).

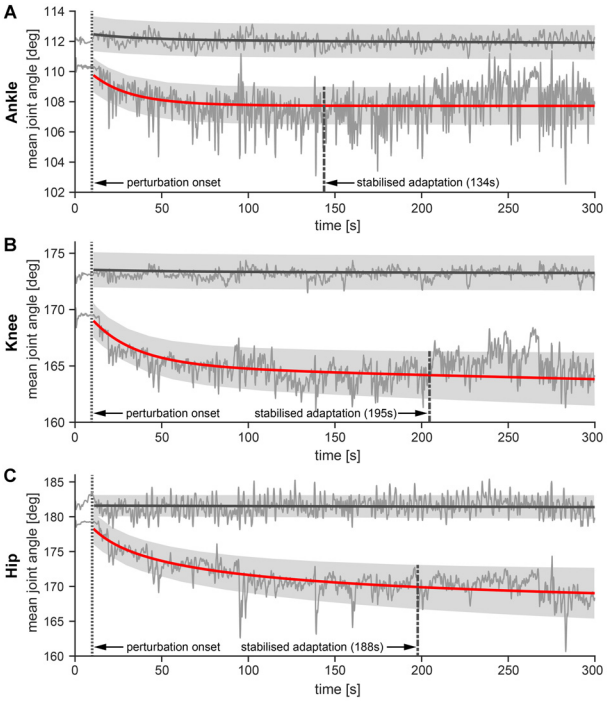

FIGURE 6 | Ankle (A) knee (B) and hip (C) angles over the time course of the perturbation. Thin solid lines represent mean joint angles from all 10 subjects during NH and WH trials. Thick solid lines represent exponential curve fit denoting adaptation of joint angles in the NH (red color) and WH trials (gray color), while shaded areas represent ±1 standard error of the mean of the exponential decay curve. Mean R^2 value for the exponential decay curves for ankle joint in the NH trial was mean ± SE: 0.27 ± 0.06, for the knee joint mean ± SE: 0.31 ± 0.08 and for the hip joint mean ± SE: 0.61 ± 0.08. The dotted vertical lines represent perturbation onset while the dashed vertical lines indicate the mean time of stabilized changes in the joint angles after perturbation onset.

Analysis of Muscle Activity

Muscle activity was significantly lower during the WH trial than during the NH condition both for the leg muscles (GA $t_{(9)} = 3.57$, $p = 0.04$, $d = -0.89$; TA $t_{(9)} = 6.41$, $p = 0.002$, $d = -23$ 1.85) and one of the trunk muscles (MF $t_{(9)} = 6.5$, $p = 0.001$, $d = -1.01$), as can be seen in **Figure 7**. Leg muscle activity was 18.4 ± 4.9% lower in the GA (mean ± SE: NH: 28.9 ± 6.5% MVC, WH: 10.6 ± 2.3% MVC) and for 23.7 ± 3.5% in the TA (mean ± SE: NH: 27.2 ± 4% MVC, WH: 3.47 ± 1.88% MVC), while the trunk muscle activity was 14.3 ± 2.1% lower in the MF (mean ± SE: NH: 36.2 ± 4.5% MVC, WH: 21.8 ± 3.7% MVC), but no significant change was observed in the OE (mean ± SE: NH: 10.4 ± 7.4% MVC, WH: 8.97 ± 4.63% MVC).

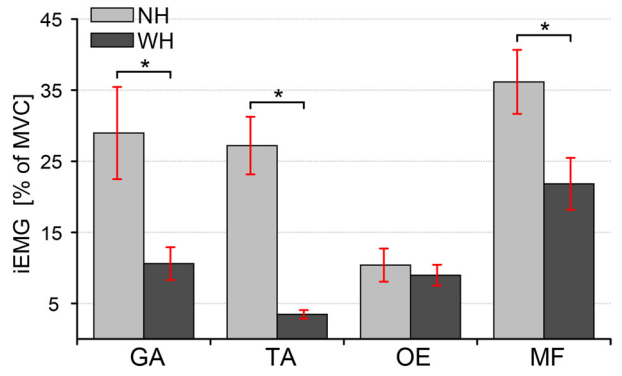

FIGURE 7 | Comparison of integrated Electromyographical (EMG) between trials when subjects either used additional hand contact or not. Bars represent iEMG of four muscles (GA, Gastrocnemius Lateralis; TA, Tibialis Anterior; OE, Obliques Externus; MF, Multifidus) during NH and WH trials. Error bars indicate ±1 standard error of the mean. Statistically significant differences are indicated (*$p \leq 0.02$).

DISCUSSION

We investigated how subjects used an additional hand support (handle) to maintain upright posture when exposed to mild and continuous perturbations elicited by waist-pull apparatus in the anteroposterior directions. The use of handle reduced the destabilizing effect of the applied perturbation by reducing the excursions of COP. These results are in line with previous studies that investigated light-touch contacts. Those studies found a reduction of COP excursions during bipedal stance with (Johannsen et al., 2007; Hausbeck et al., 2009) and without externally applied perturbations (Jeka, 1997; Krishnamoorthy et al., 2002; Kouzaki and Masani, 2008). However, in our case the handle compensated for a significant load and served more than just a light-touch contact. The mean force in the handle was over 24 N (mean ± SE: 24.5 ± 7.9 N) where in other light-touch studies, contact forces usually did not exceed 3 N (Krishnamoorthy et al., 2002; Johannsen et al., 2007; Kouzaki and Masani, 2008). Comparison between measured mean handle force and mean perturbation force, which was ∼20 N (mean ± SE: 19.5 ± 1.7 N), indicates that a significant portion of perturbation on postural stability was counterbalanced by the hand.

COP excursions were strongly correlated with the perturbation force in both directions, indicating the perturbations were effective, albeit mild. When holding a handle, the excursions of the COP were larger in the anterior than in posterior direction and less correlated with the perturbation force. Due to the specifics of our design, i.e., the use of a continuous perturbation, it was impossible to investigate pure feedback postural responses to the specific direction of the perturbation. However, asymmetry in COP excursion might to be due to a differential use of the handle, indicated by a steeper slope of the regression line between the perturbation force and the forces exerted on the handle for the posterior direction. This indicates that subjects have utilized the handle more when they counteracted the posterior COP excursions. This may be related to a more threatening situation due to the inability of the subjects to see (look) behind them, as the directions to the subjects were to look straight ahead at all times, and due to smaller stability margin in the posterior direction (Pai and Patton, 1997; Hof et al., 2005). This finding is in line with our previous study using a similar handle location and discrete perturbations caused by support platform translations, in which COP excursions were larger in the anterior direction (Babič et al., 2014).

Using a handle for balance support was beneficial, since it resulted in less displacement of COP and a smaller deviation from the neutral posture, as evident by the average joint angles. Measured joint angles in *WH* condition stayed closer to the neutral anatomic position than joint angles in the *NH* condition. Additionally, leg and trunk muscle activity was also significantly lower during the *WH* trial compared to the *NH* trial. This is consistent with the decreased leg muscle activity reported previously, when subjects had to hold (Cordo and Nashner, 1982) or touch (Sozzi et al., 2012) a surrounding object. Unlike other muscles, we found no decrease of muscle activity in the OE, which controls the rotation of the torso (Ng et al., 2001). The unilateral hand support might have caused a rotation of the trunk, which the subjects had to counteract by the OE activity. Prior to experiments we instructed subjects to use the handle in any way they prefer. Overall reduced muscle activity in legs and trunk and increased activity in arm muscles in case of using handle indicate that a portion of significant perturbation load was shifted from legs/trunk to arms. The same can be confirmed by high measured handle forces and lesser COP excursions in case of *WH* trial. The use of hand contact to compensate a significant portion of perturbation, even though it could be counteracted solely by legs/trunk, might be preferred since legs in a stance already have to compensate the load of the body mass (Bateni and Maki, 2005; Mergner, 2010).

Finally, when subjects had to release the handle for balance control they prepared for the more difficult *NH* condition even before the perturbation onset, as evident from differences in the starting joint angles. When the perturbation began this preparation was even more pronounced and joint angles changed further. These postural readjustments appear to occur at different time scales in the hip, knee and ankle joints, however that was not statistically confirmed. The subjects bended their ankle, knee and hip joints which resulted in a more flexed leg and lower hip position. Hip position can serve as an indication of the COM position and lowering of the COM could facilitate balance control (Rosker et al., 2011). Hence, these changes indicate feed-forward preparation to ease control of balance when expecting more challenging conditions, i.e., in the absence of handle. Along the same line, anticipation of the upcoming perturbations was also reported to cause changes in kinematics during quiet stance (Santos et al., 2010), walking (Pijnappels et al., 2001), recovery stepping (Pater et al., 2015) and tripping (Potocanac et al., 2014).

AUTHOR CONTRIBUTIONS

JC, LP and JB designed the study. JC and LP performed the experiments. JC, LP, ZP and JB analyzed the data and wrote the manuscript.

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Calibration of the Leg Muscle Responses Elicited by Predictable Perturbations of Stance and the Effect of Vision

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Motor adaptation due to task practice implies a gradual shift from deliberate control of behavior to automatic processing, which is less resource- and effort-demanding. This is true both for deliberate aiming movements and for more stereotyped movements such as locomotion and equilibrium maintenance. Balance control under persisting critical conditions would require large conscious and motor effort in the absence of gradual modification of the behavior. We defined time-course of kinematic and muscle features of the process of adaptation to repeated, predictable perturbations of balance eliciting both reflex and anticipatory responses. Fifty-nine sinusoidal (10 cm, 0.6 Hz) platform displacement cycles were administered to 10 subjects eyes-closed (EC) and eyes-open (EO). Head and Center of Mass (CoM) position, ankle angle and Tibialis Anterior (TA) and Soleus (Sol) EMG were assessed. EMG bursts were classified as reflex or anticipatory based on the relationship between burst amplitude and ankle angular velocity. Muscle activity decreased over time, to a much larger extent for TA than Sol. The attenuation was larger for the reflex than the anticipatory responses. Regardless of muscle activity attenuation, latency of muscle bursts and peak-to-peak CoM displacement did not change across perturbation cycles. Vision more than doubled speed and the amount of EMG adaptation particularly for TA activity, rapidly enhanced body segment coordination, and crucially reduced head displacement. The findings give new insight on the mode of amplitude- and time-modulation of motor output during adaptation in a balancing task, advocate a protocol for assessing flexibility of balance strategies, and provide a reference for addressing balance problems in patients with movement disorders.

Keywords: moving platform, balancing behavior, adaptation, kinematics, EMG, reflex and anticipatory response, vision

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Abbreviations: A-P, antero-posterior; CC, cross-correlation; CoM, center of mass; EC, eyes closed; EO, eyes open; FPR, fall preventing response; LLR, long latency response; MLR, medium latency response; PAR, proactive response; SLR, short latency response; Sol, Soleus; TA, Tibialis Anterior.

INTRODUCTION

Practice improves movement kinematics and diminishes the accompanying metabolic and cognitive cost. Motor adaptation implies a gradual shift from a more conscious control of behavior to automatic processing, which is less resource- and effort-demanding, and produces a gradual modification of the behavior that makes it more fit under the conditions of its environment (Shadmehr et al., 2010). Adaptation is common to both voluntary movements, where repetition and task practice improve performance (Lotze et al., 2003), and movements in which automatism prevails (Saling and Phillips, 2007) as in locomotor (Prokop et al., 1995) and postural tasks (Nashner, 1976). Balance perturbations can be of very different nature, from displacement of the base of support (Nashner, 1976; Horak and Nashner, 1986) to vibratory proprioceptive (De Nunzio and Schieppati, 2007; De Nunzio et al., 2008) and galvanic vestibular stimulation (Fransson et al., 2007; Tjernström et al., 2010a). Berger et al. (1992) and Dietz et al. (1993) described leg muscle activity and biomechanical patterns in subjects standing on an unstable support basis, such as a treadmill moving backward and forward. Their pioneer study suggested that the aim of the control process is to stabilize the position of the body's center of gravity relative to the feet, while the forces acting on the body during the treadmill movements are minimized.

Balance perturbations delivered by repeated sinusoidal translations of the support base have been employed frequently in both control subjects and patients, in order to investigate balancing behavior under dynamic conditions, as opposed to quiet stance. Within the frame of a reproducible general pattern, an ample range of variability has been observed for successive cycles of the same perturbation, suggesting flexibility of dynamic postures (Schieppati et al., 2002; Cappa et al., 2008; Kennedy et al., 2012). Clear-cut differences in balancing behavior have also been observed in the presence or absence of vision (Buchanan and Horak, 1999; Corna et al., 1999; Fujiwara et al., 2006; Schmid et al., 2011). For instance, when vision is gradually degraded experimentally, good visual acuity strongly reinforces a "head-fixed-in-space" behavior, while poor vision and no vision rather produce a "head-moving-with-platform" displacement (Schmid et al., 2007, 2008). Notably, aging is associated with reduced head stabilization in the absence of vision, particularly for high-frequency platform translations (Nardone et al., 2000). The balancing behavior is fairly resistant to abnormal proprioceptive noise obtained by postural muscle vibration (De Nunzio et al., 2005) and is hardly affected in patients with neuropathy and with Parkinson's disease (Nardone and Schieppati, 2006; Nardone et al., 2006, 2007), pointing to significant intervention of feed-forward mechanisms.

In the above cited reports, the first few cycles of the sequence of oscillations were deliberately excluded from the analysis in order to get rid of the initial large EMG activation bursts and body movements elicited by the supposed startling effect of the onset of the perturbation (Nonnekes et al., 2015), and to describe and measure the adapted behavior at steady state. The question of the initial EMG adaptation had been addressed with a sequence of discrete impulsive perturbations by Keshner et al. (1987), who suggested that adaptation is due to a generalized habituation in the postural control system. Fujiwara et al. (2007) described adaptation of the balancing strategy to continuous floor oscillation. By recording event-related potentials, reflecting cortical activation by sensory information related to the postural disturbance, they suggested that attention to information processing decreases with adaptation (Fujiwara et al., 2012, 2016). Mierau et al. (2015) also reported adaptation of the negative cortical potential and reduced muscle co-contraction during a prolonged balancing task under critical standing-balance condition. Notably, at the beginning of the perturbation series, the extra facilitatory effect from higher centers on the spinal motoneuronal pools gradually vanishes as automatisms prevail (Solopova et al., 2014).

Siegmund et al. (2008) advised that the large muscle response to a novel transient perturbation consists of combined postural and startle responses. On the other hand, Oude Nijhuis et al. (2009) and Allum et al. (2011) reported on the response to the first perturbing trial of a sequence, and compared that response to a startle reaction elicited by an acoustic stimulus. They highlighted the substantial differences between the "true" startle reaction and the response to the first trial of a balance perturbation, and concluded that future studies should no longer discard the latter response, but routinely include it in the analysis (Tang et al., 2012).

Short- and long-latency leg muscle reflexes are elicited by the displacement of the body segments, and produce balance correcting effects (Horak et al., 1989; Nardone et al., 1990). Proactive strategies (Massion, 1992; Bouisset and Do, 2008) are also produced to counteract the balance perturbations elicited by the platform displacement reversal (Rogers et al., 2003; Jacobs and Horak, 2007). These anticipatory postural adjustments may not necessarily be optimally tuned to the complex combination of active and passive body movements from the beginning of the perturbation sequence (Aruin et al., 1998, 2015). In the assumption that both reflex responses and proactive strategies are contributing to the balancing behavior on the continuously translating platform (Laessoe and Voigt, 2008) and that both undergo adaptation with the repetition of the perturbation cycles (Dietz et al., 1993; Taube et al., 2007; Kennedy et al., 2012), we set out to record activity of the leg flexor and extensor postural muscles and body kinematics. Our attempt was to better identify the muscle responses and the potentially different adaptation pattern thereof, and to assess any relationship between the adaptation of muscle activity and the balancing behavior by using support surface translation stimuli. We expected to get an answer to the following questions. What is the time course of adaptation? Is adaptation common to both muscles acting on the ankle joint? Is this process accompanied by modulation of co-contraction rate of both antagonist muscles? Is it similar for muscle activities having a presumed different origin (reflex vs. proactive)? Does adaptation imply amplitude modulation of EMG bursts, or does their latency also change over time? Is there a correspondence between adaptation of leg muscle activity and changes in the position of the center of mass (CoM)? To what extent does

vision affect adaptation? What are the functional advantages of adaptation?

MATERIALS AND METHODS

Subjects and Task

Ten healthy subjects (5 males and 5 females, mean age 30.8 years ± 6.3 SD, height 173.7 cm ± 5.3 SD, weight 66.2 kg ± 10.9 SD) stood with bare feet spaced about 10 cm apart on a mobile platform, translating in a sinusoidal way in the antero-posterior (A-P) direction at 0.6 Hz and 10 cm amplitude. They were not aware of the onset of the movement of the platform, which started pseudo-randomly within 5–10 s from the acquisition onset (known to the subjects). Subjects wore soundproof earphones in order to mask the noise made by the platform. Each acquisition was composed of three parts: subjects stood on the still platform (5–10 s); the platform made 59 consecutive oscillation cycles (total duration 100 s); the platform stopped and subjects stood on the still platform for 5 s more. Subjects performed one single such trial with the eyes closed (EC), and one trial with the eyes open (EO) in a separate session after 5–7 days. Felt-tip pen marks on the skin helped to place the electrodes in the same position during the two test conditions. No randomization was performed. In parallel experiments, a second group of naive subjects was studied ($n = 10$; 4 males and 6 females, mean age 25.5 years ± 2.9 SD, height 171.8 cm ± 9.2 SD, weight 68.6 kg ± 16.3 SD), to which EO condition only was administered. This allowed checking any persistence of adapted behavior due to the EC trial preceding the EO trial in the former group of subjects. All subjects were naive to the experimental procedures or to any balance-oriented experiments and all succeeded in performing the trials. Experiments were performed in accordance with the Declaration of Helsinki. The institutional ethics committee (Central Ethics Committee, Fondazione Salvatore Maugeri, approval number # 905 CEC) specifically approved the study and the consent procedures, which were carried out with the adequate understanding and written informed consent.

Data Acquisition

Kinematic data were recorded by means of an optoelectronic device (Smart-D, BTS, Italy). For computation of CoM and orientation in space of the body segments, 19 reflective markers were placed bilaterally on these body positions (Winter, 2009): vertex and lateral head, acromion, C7, L5, anterior superior iliac spinae, greater trochanter, lateral epicondyle of the femur, lateral malleolus, heel and forefoot (dorsally, about over the 1st metatarso-phalangeal joint). Subjects' arms were folded not to interfere with marker capture. The marker positions in space were recorded by 12 cameras at 140 Hz and stored in a PC for off-line analysis. For subsequent analysis, the kinematic data were resampled at a frequency of 1000 Hz after linear interpolation by the BTS proprietary software, in order to display both kinematic and EMG data on the same scale.

EMG was recorded by pairs of surface electrodes placed, for both legs, over the muscle bellies of Tibialis Anterior (TA) on the anterior aspect of the upper third of the leg, and of Soleus (Sol) posteriorly, 5 cm below the insertion of the gastrocnemii in the Achilles' tendon. The distance between the recording leads was 1.5 cm. EMGs were wirelessly recorded (Freeemg, BTS, Italy) at 1000 Hz. Signals were filtered with a high-pass filter (cut-off 50 Hz), full-wave rectified and then filtered with a low-pass filter with a cut-off frequency of 200 Hz. EMG signals were acquired through the same Smart-D system, and were synchronized with the kinematic data.

The EMGs of TA and Sol of both legs were also recorded in each subject during *ad hoc* trials in which subjects produced bursts of maximal activity, for each muscle separately, before each EC and EO trial. For each muscle and leg, three maximal isometric contraction efforts, each lasting 2–4 s, were performed. For TA, during standing, the foot was blocked to the ground preventing foot dorsiflexion. For Sol, while subjects were sitting on a chair, the knee was blocked against a resistance to keep ankle and knee angles at about 90°. The level of EMGs activity recorded during the balancing trials were expressed as percent of the maximal voluntary activity of the respective muscles.

Data Analysis

EMG Activity and Burst Identification

We offline separated the cycles of the platform perturbation by a software developed using Labview (National Instruments, Austin, TX, USA), where each cycle began with the platform forward translation. For a clearer representation of what happened during each cycle, in the **Figures 4–9** a time-window starting 0.2 s before the initial forward movement of the platform and lasting 2.5 s is depicted, whereas the analyses were made on a time-window having a duration equal to the oscillation cycle (1.7 s) starting from the backward-most platform position.

The mean value of TA and Sol activity within each of the successive cycles was calculated in each subject. In addition, the traces of the rectified TA and Sol activity of all consecutive cycles were averaged. Different bursts of activity were regularly present on the TA and Sol mean traces. The time-windows, in which TA or Sol bursts were consistently present, are highlighted by shaded areas in **Figure 4**. For TA, we classified: (a) a reflex response, the first part of which occurred at about 80 ms after the beginning of the forward translation of the platform and lasted about 100 ms; this response was named medium-latency response (MLR), following Schieppati and Nardone (1995) and Nardone and Schieppati (1998); (b) a second part of the reflex response occurred at about 200 ms after the forward platform translation and lasted about 100 ms; this was the long-latency response (LLR; Nardone et al., 1990); (c) a burst just around the anterior platform turn-around point, starting about 700 ms after the forward translation and lasting about 200 ms, was arbitrarily named fall-preventing response (FPR) and (d) a burst roughly in correspondence with the period of backward platform movement, starting at around 1.2 s after the forward translation

and lasting around 300 ms; this was arbitrarily named proactive response (PAR), since it brakes the CoM backward displacement just prior to the forward platform movement of the subsequent cycle. For Sol, the bursts were almost superimposable to those of TA when the Sol trace was shifted by $\frac{1}{2}$ cycle, so that stretch and anticipatory responses would match the corresponding platform displacement (forward for TA and backward for Sol). Hence, following the same criteria used for TA and referring to the onset of forward translation, we identified: (a) a burst before the peak of the forward excursion, starting about 300 ms after forward translation and lasting about 300 ms (PAR), this response mainly occurs during Sol shortening, and would correspond to the TA PAR; (b) a double-peak reflex response, occurring at about 800 ms after the forward translation (at the beginning of the backward platform displacement) and lasting about 100 ms; in the Sol, a short-latency stretch response is evoked immediately prior to the MLR (hence, this burst was named SLR + MLR); (c) a burst in correspondence with the backward platform movement, starting at around 1.1 s after the forward translation and lasting around 100 ms (LLR); and (d) a burst after the peak of backward excursion, starting about 1.5 s after the forward translation and lasting about 100 ms (FPR). Then, for each cycle of each subject, the actual onset and termination of each response was visually identified by means of a custom-made Labview software on the display of each EMG trace. The response identification was aided by the superimposition of the traces of the homonymous muscles of both legs. Two experimenters (SS and MS) agreed on the identification of the burst onset and termination. In the subsequent analysis, the onset latency of each TA response was referred to the onset of platform forward movement, and for Sol to the onset of platform backward movement.

The area (time-integral) of the rectified TA and Sol muscle EMG measured within the time-interval defined by onset and end of each response was expressed as a percentage of the area of the EMG corresponding to the maximal voluntary contraction, calculated on an equal time-interval as the individual response bursts. The area of the TA and Sol bursts were plotted against the ankle angular velocity measured 50 ms before the onset of the respective TA or Sol burst in order to check the hypothesis that the response is related to muscle stretch and represents a short-latency response to muscle lengthening. The 50 ms interval was arbitrarily selected for all responses, based on the presumed "average" latency of the TA and Sol reflex activation by muscle stretch, and assuming that the muscles had no slack due to their background activation.

Kinematics

The CoM was computed according to the Winter (2009) protocol by a software developed in Matlab (MathWorks Inc., Natick, MA, USA). In order to infer changes in muscle length and velocity occurring during the perturbation cycles, the ankle angle of both legs was computed from the position in space of the markers placed on the lateral femoral condyle, lateral malleolus and forefoot. The changes in foot dorsum deformation were estimated from the height of the marker placed on malleolus. The marker traces were filtered with a low-pass filter (cut-off 3 Hz). The velocity of ankle angular variation was the derivative of the ankle angle. Positive velocities corresponded to TA stretch (or Sol lengthening).

For each subject, the standard deviation of all the values of the A-P displacement trace of CoM and head vertex was calculated for the entire duration of the platform perturbation, and considered a global index of displacement amplitude (small and large standard deviations pointing to stable and unstable segment position in space, respectively; Corna et al., 1999). For each subject and oscillation cycle, a cross-correlation (CC) analysis was performed between the traces of platform and CoM A-P displacement (both referred to the laboratory space). The CC coefficient (R) at time lag = 0 s was calculated by means of the CC routine of the software Origin (OriginLab Corporation, Northampton, MA, USA). A positive coefficient indicates in-phase displacement of CoM and platform, a negative coefficient indicates anti-phase displacement. The time lag was the time interval at which the absolute value of R was maximum. The 95% confidence interval of the highest CC value was used to assess if the time lag between platform and CoM displacement was statistically significant (Li and Caldwell, 1999). A positive time lag indicates that CoM movement lagged the platform movement.

The CoM back-and-forth displacement with respect to the malleolus was also plotted against the ankle angle and the coefficient of determination (r^2) of the regression line was calculated for each subject and successive cycle.

Adaptation Rate Assessed by Exponential Fit

In order to grossly quantify the adaptation process, we fitted the relevant data with an exponential function ($y = A + Be^{-t/\tau}$). To this aim, the exponential-fit routine of the software Origin was used, τ (tau) being the time-constant, A the value at steady state (asymptote), A + B the intercept with the ordinate (Sozzi et al., 2011). A, B and τ parameters were computed by using the Levenberg-Marquardt algorithm. Using this procedure, we fitted over time the mean CoM A-P position, the time lags between platform and CoM displacement. The changes in the relationship between CoM displacement and ankle angle identified by the r^2 coefficient of the regression lines were also fitted in the same way. The mean EMG activity of TA and Sol of each cycle was plotted as a function of the successive cycles: these values generally exhibited a rapid initial variation and a trend to plateau with time. Of note, the exponential fit was made on the entire sequence of cycles, including the first one. The time, at which steady state was reached, was estimated by 3 * τ, which corresponds to a reduction to less than 5% of the initial value.

In addition, we fitted a double exponential function ($y = Ae^{-t/\tau 1} + Be^{-t/\tau 2} + C$) to the area data of the identified bursts of the successive cycles in order to take into account the possibility that a dual process (Huberdeau et al., 2015) featuring a complex evolution over time underpins the adaptation of both reflex and proactive bursts. τ_1 and τ_2 were the time-constants (expressed in cycle number), C

the value at steady state, A + B + C the intercept with the ordinate. The values of the asymptote and of the intercept at the second oscillation cycle of the fitted exponentials (therefore excluding the "first-trial effect") served to assess the amplitude adaptation of the EMG responses. When the software did not converge to the imposed exponential, we simply interpolated the data with a linear fit, and estimated the amplitude of adaptation by the difference between the values of the fitted line at the second and last cycle.

Assessment of the TA-Sol Co-Contraction Pattern

In order to quantify the possible co-contraction of TA and Sol muscles and its variation over time, for each cycle the instantaneous rectified EMG activity of the two muscles of the right leg was plotted one against the other. For each subject and cycle, we defined a co-contraction index as follows: each value of the level of TA activity was multiplied by the corresponding value of Sol activity, and all products were averaged. Each co-contraction index of each cycle was then identified by a variable k (the mean value of all products within the cycle). Hence, for each subject, the k values across all successive cycles were fitted with the exponential function $y = A + Be^{-t/\tau}$, in order to assess any change over time of the co-contraction pattern.

Statistical Analysis

Statistical computations are listed below in the order of appearance in the "Results" section. All variables had normal distribution, as tested by the Kolmogorov-Smirnov test. Systematic effects (EO vs. EC, TA vs. Sol) often produced substantially different data variability, as tested by Levene's test. However, since the coefficients of variations were remarkably constant across conditions, the log transformation was applied (Lison, 1960) prior to applying parametric statistics.

The mean activity across cycles of TA and Sol was compared by a 3-way repeated measures ANOVA with muscles (TA and Sol), visual condition (EC and EO) and leg (right and left) as factors. Across subjects, the time-constants of the mean activity values of TA and Sol were compared by a 2-way repeated measures ANOVA, with muscles and visual condition as factors. The mean EMG activities at steady state (the asymptotic value of the exponential fit) were compared by a 2-way repeated measures ANOVA, with muscle and visual condition as factors.

The time-constants of EMG adaptation (TA and Sol) between the group that received the EO perturbations only and the group that received the EO after the EC perturbations were compared, separately for the two muscles, with a Student's t-test.

Three-way repeated-measures ANOVAs, with muscle, vision, response type (MLR or SLR + MLR, LLR, FPR and PAR) as factors, were used to compare: onset latency, duration and area of TA and Sol response bursts, and ankle angular velocities. Four one-way ANOVA were used to assess differences in the mean latencies of various TA EC responses across cycles.

The changes in the area of TA and Sol responses across the successive cycles were interpolated with a double exponential function. When the algorithm converged to the exponential model, the time-constants thus obtained (τ_1 and τ_2) were compared by a 4-way repeated-measures ANOVA with τ_1 and τ_2, muscle, visual condition, response type (MLR or SLR + MLR, LLR, FPR and PAR) as factors.

To estimate the adaptation in burst amplitude, the differences between the intercept values at the second oscillation cycle and the asymptotic values were compared with a 4-way repeated-measures ANOVA with EMG level at second cycle and steady-state, muscle, visual condition and response type as factors.

The standard deviations of CoM and of head periodic displacement (arbitrarily taken as a global index of segment instability) were compared with a 2-way repeated measures ANOVA with variables (CoM and head) and visual condition (EC and EO) as factors.

The time-constants obtained by fitting the exponential functions to the CC coefficients and to the time-lag between CoM and platform across cycles were compared between EO and EC by paired Student's t-test. The time-constant of the changes over the successive cycles of the r^2 coefficient of the lines best fitting CoM against ankle angle and that of the parameter k (indicating co-contraction) were compared with a 2-way repeated measures ANOVA with variables (time-constants of r^2 and k) and visual conditions as factors. For all ANOVAs, the *post hoc* analyses were made with the Fisher's LSD test. The software package used was Statistica (StatSoft, Tulsa, OK, USA).

RESULTS

Changes in EMG and Kinematics Over Time

Figure 1 illustrates the adaptation phenomenon: the top trace **(A,B)** is the platform periodic displacement, identical for the EC and EO condition. Figures **(C–F)** show the grand mean (of the 10 subjects, who performed the EO after the EC trial) of the rectified traces of the TA and Sol muscle activity over the entire perturbation period. Displacements of CoM and head vertex are reported for EC and EO in **(G–J)**, respectively. A progressive reduction in the TA activity was obvious with EC **(C)**. Sol activity diminished rapidly to then remain sustained until the end of the acquisition period **(E)**. TA activity was much smaller under EO than EC condition, both at the beginning and at steady-state **(D)**, which was reached within very few cycles. Conversely, the level of Sol activity with EO **(F)** was broadly similar to that recorded with EC. CoM displacement was consistent from the beginning to the end of the translation cycles, and was similar under EC and EO condition. Still, the head back-and-forth displacement was much larger and more variable for EC than EO. Overall, these patterns of EMG and kinematic changes were common to all subjects.

TA and Sol Activity Across Successive Cycles: Levels and Time-Constants

The mean activity of TA and Sol was averaged cycle by cycle across subjects, for EC and EO. It was similar between right and left leg, both EC (gray bars in **A** and **E**) and EO (white bars in **A** and **E**) ($F_{(1,9)} = 2.16$, $p = 0.17$; **Figure 2**). Hence,

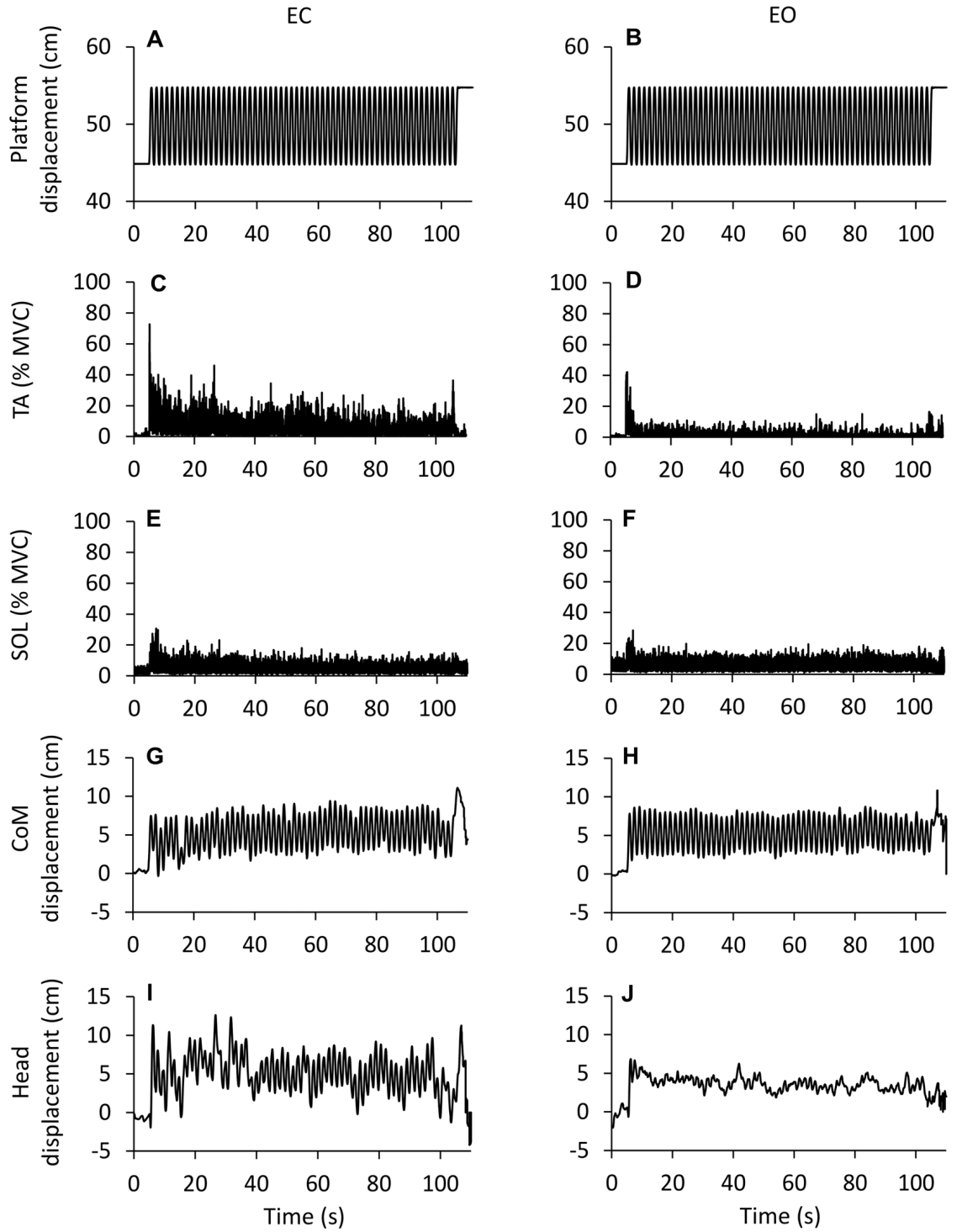

FIGURE 1 | Changes in EMG and kinematics over time. Grand mean ($n = 10$ subjects) of the traces recorded during eyes closed (EC) and eyes open (EO) conditions. **(A,B)** show the platform sinusoidal translation (10 cm, 0.6 Hz) in the antero-posterior (A-P) direction (forward upwards). The first cycle begins after 5 s from the acquisition onset, the last cycle ends at 105 s. **(C–F)** show the grand mean of the rectified EMG traces of the Tibialis Anterior (TA) and Soleus (Sol) expressed as percent of the maximal voluntary contraction. There is a progressive reduction in muscle activity EC and EO. TA activity is much smaller EO than EC (not so for Sol). **(G,H)** Displacement of center of mass (CoM). **(I,J)** Displacement of head (marker on the vertex). The CoM back-and-forth displacement is similar EC and EO, whereas the head back-and-forth displacement is larger EC than EO. The larger deflections of the EMG and kinematic traces at the very end of the acquisition are connected with the sudden halt of the platform.

further analysis was performed on the mean EMG values of the two legs. **Figure 2** also shows the grand mean of the EMG activity of each of the successive perturbation cycles, for TA **(B,C)** and Sol **(F,G)** during the EC and EO conditions. With EC, a gradual decrease in TA activity is obvious **(B)**. The exponential curve fitted to the data points has a time-constant of about 5 cycles ($\tau = 5.1$ cycles); therefore, after about 15 cycles ($\sim 3 * \tau$), i.e., about 25 s considering that each cycle lasts 1.7 s, TA activity reached a value close to the asymptotic value (steady-state). A gradual decrease was also present for Sol activity with EC (**F**, $\tau = 4.3$ cycles). The mean values of the time-constants of the exponentials fitted to the profiles of TA and Sol activity of each subject were 6.5 ± 4.8 cycles (TA) and 5.9 ± 5.6 cycles (Sol) (not shown in Figure). With EO, both TA **(C)** and Sol **(G)** activities diminished rapidly and reached steady state very quickly ($\tau = 1.1 \pm 0.7$ cycles, TA; 3.4 ± 3.7 cycles, Sol). ANOVA on the time-constants of TA and Sol, after log transformation, showed a difference between visual conditions ($F_{(1,9)} = 23.75$, $p < 0.001$), no difference between muscles ($F_{(1,9)} = 3.23$, $p = 0.1$) and an interaction between muscles and vision ($F_{(1,9)} = 11.46$, $p < 0.01$). The time-constants of TA EO were just smaller than those of Sol EO (*post hoc*, $p < 0.01$), while there was no difference between TA and Sol in the EC condition (*post hoc*, $p = 0.36$). Moreover, there was no difference in the time-constant of Sol between EC and EO (*post hoc*, $p = 0.1$).

At the end of the perturbation cycles (**Figure 2D**), there was a difference in the mean level of EMG activity between TA and Sol ($F_{(1,9)} = 11.4$, $p < 0.01$). This was due to their different behavior as a function of the visual condition. There was a difference between EC and EO ($F_{(1,9)} = 16.37$, $p < 0.01$) and an interaction between muscles (TA and Sol) and visual condition ($F_{(1,9)} = 8.9$, $p < 0.05$). TA activity at steady state was smaller with EO than EC (*post hoc*, $p < 0.01$), while the level of Sol activity was not affected by vision ($p = 0.99$).

Also in the 10 subjects who performed the EO condition only, TA and Sol reached steady state very quickly ($\tau = 1.50 \pm 1.0$, TA, and 3.3 ± 6.3, Sol). Overall, there was no difference in the mean time-constants between the two groups (Student's *t*-test, $p > 0.3$, for TA and Sol muscles, separately analyzed). Therefore, for simplicity and for exploiting repeated-measures tests, we analyzed the findings pertaining to EC and EO behavior only in the group that performed EC before EO.

Co-Activation Turns to Reciprocal Activation During Adaptation

Not only did muscle activity decrease over time, but there was also a change in the pattern of recruitment of the antagonist TA and Sol muscles. For all cycles, the TA activity profile was plotted against that of Sol in order to detect any prevalent activation pattern (reciprocal activation or co-activation). Each individual symbol of **(A)** to **(C)** of **Figure 3** corresponds to one TA and Sol EMG sample (1000 Hz) recorded during three non-consecutive cycles in a representative subject (the cycles were arbitrarily chosen as examples of the pattern of activity recorded during the first (1st to 20th cycle) and third (41th to 59th cycle) segment of the entire sequence, see **Figure 4**). The value (k) of TA and Sol co-contraction index (see "Materials and Methods" Section) diminished over the cycles. The lower panels (**D**, EC and **E**, EO) show the grand means of k of all subjects over cycles, featuring a progressive reduction of the k value, therefore a shift from co-activation to reciprocal activation. For each subject, the k value was then plotted as a function of the successive cycles and fitted with an exponential function. The average time-constant of the adaptation of k (panel **F**) was

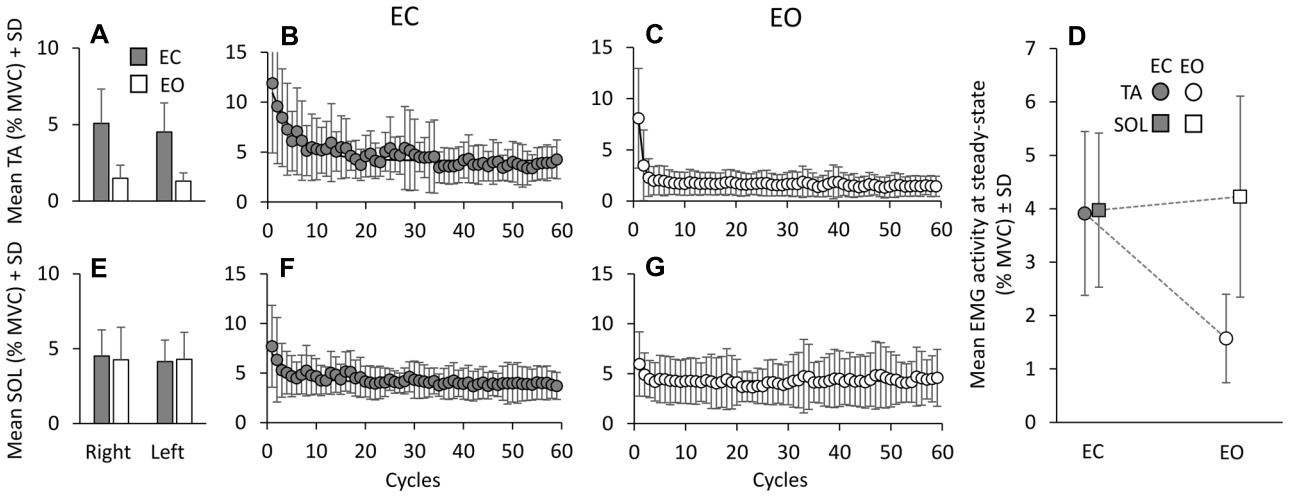

FIGURE 2 | Mean TA and Sol activity. Mean muscle activities, across cycles and subjects in EC (gray bars) and EO (white bars) conditions, are almost the same between legs, for TA **(A)** and Sol **(E)**. The mean activity of TA **(B,C)** and Sol **(F,G)** are calculated for each platform cycle, EC and EO. With EC, both TA and Sol activities gradually decrease to steady state. The exponential functions fitted to the EC data are $y = 4.15 + 6.77e^{-t/5.1}$ for TA and $y = 4.09 + 2.87e^{-t/4.3}$ for Sol. With EO, both TA and Sol activities reach steady state very soon. The functions best fitting the mean muscle activities with EO are: $y = 1.63 + 6.42e^{-t/0.8}$ for TA and $y = 4.26 + 1.71e^{-t/0.97}$ for Sol. **(D)** shows that the mean Sol activity level at steady state is similar EC and EO, while TA is greatly reduced EO.

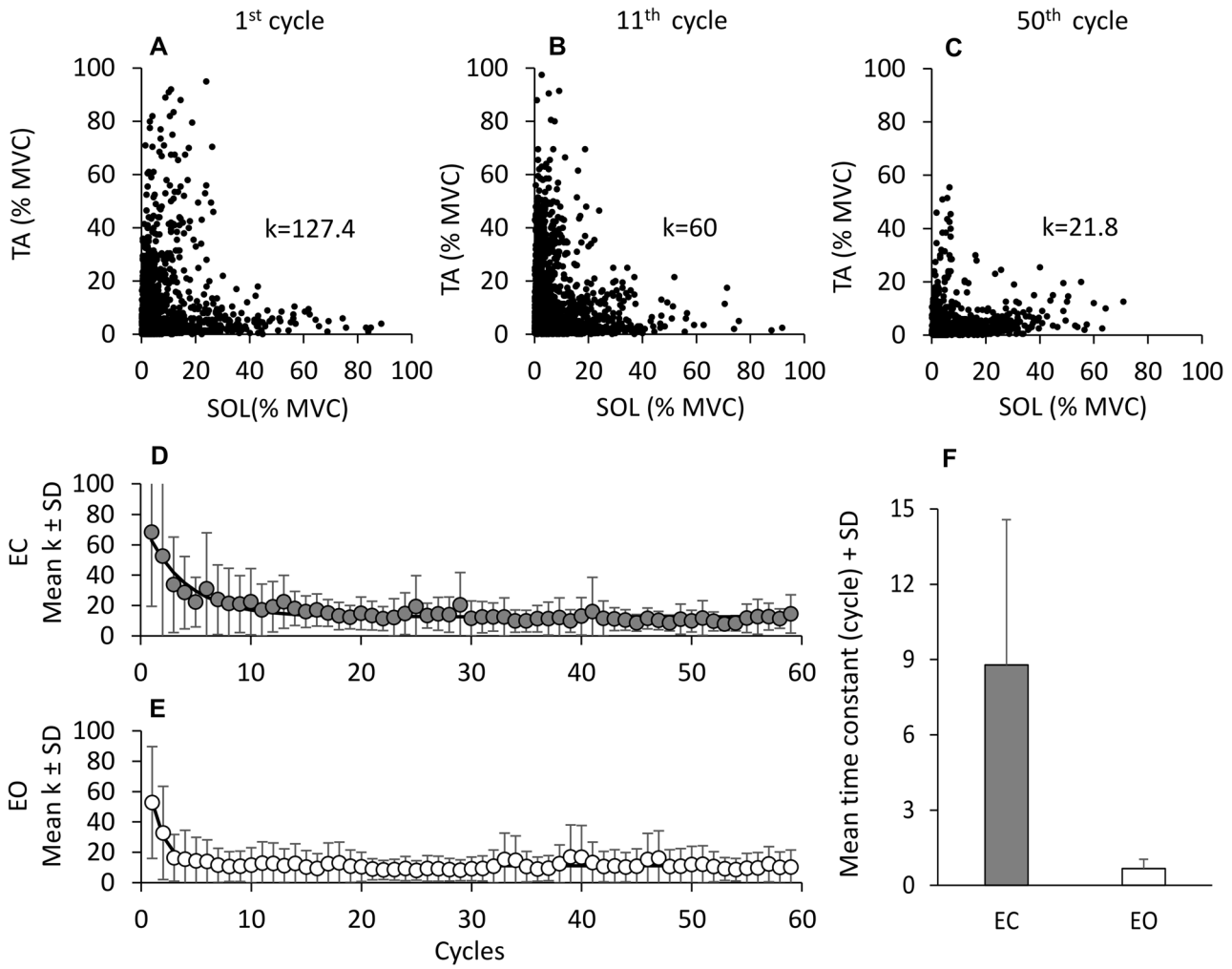

FIGURE 3 | Reciprocal activation of TA and Sol. In **(A–C)**, TA activity is plotted against that of Sol for three non-consecutive cycles in one subject to show the progressive decrease in the co-activation pattern. The value of *k* (the TA and Sol co-contraction index) diminishes with cycle repetition. **(D,E)** show the grand means of k, obtained by averaging the *k* of each subject for each subsequent cycle, EC **(D)** and EO **(E)**. The exponential functions fitted to the data points are $y = 12.4 + 50.4e^{-t/4.2}$, EC; and $y = 8.5 + 34.8e^{-t/1.2}$, EO. **(F)** show the mean time-constants obtained by fitting an exponential function to the data points of each subject and of each condition. The time-constant of the "co-activation" adaptations is much longer EC (gray bar) than EO (white bar).

much larger with EC (8.8 cycles ± 5.8 cycles) than EO (0.6 cycles ± 0.4 cycles; *post hoc*, $p < 0.001$), indicating that the initial co-activation patterns disappeared much more rapidly for EO than EC. Overall, it appears that co-contraction of the antagonist leg muscles promptly subsides with adaptation, more or less rapidly as a function of visual condition, to give way to reciprocal activation.

Reflex and Anticipatory Responses

TA and Sol bursts showed consistent features across perturbation cycles. The bursts were easily identified in the successive cycles, both EC and EO. This is obvious in **Figure 4**, showing the grand mean of the rectified EMGs obtained by averaging the traces across subjects and cycles. The gray traces refer to the TA **(C,D)** and Sol burst **(E,F)** recorded during the first cycle. The three superimposed colored traces are the result of averaging the EMG traces of the same muscles recorded during the cycles from 2nd to 20th, 21th to 40th and 41th to 59th (black to green in that order). Activity was much larger in the first cycle (particularly for TA) under both EC and EO condition. The bursts took place within the same time-windows from the beginning to the end of the perturbation cycles. In spite of their diminishing amplitude, TA and Sol profiles were almost reciprocal, underlining the conclusion of the previous paragraph. The four bottom panels of **Figure 4** show the grand means of the changes in the ankle angle **(G,H)** and in its angular velocity **(I,J)**. The ankle angle had an average range of about 2°, which would have produced minor, but not negligible changes in length of the muscles around the joint. The angular velocity was overall positive (ankle angle increases and TA lengthens/Sol shortens) during the

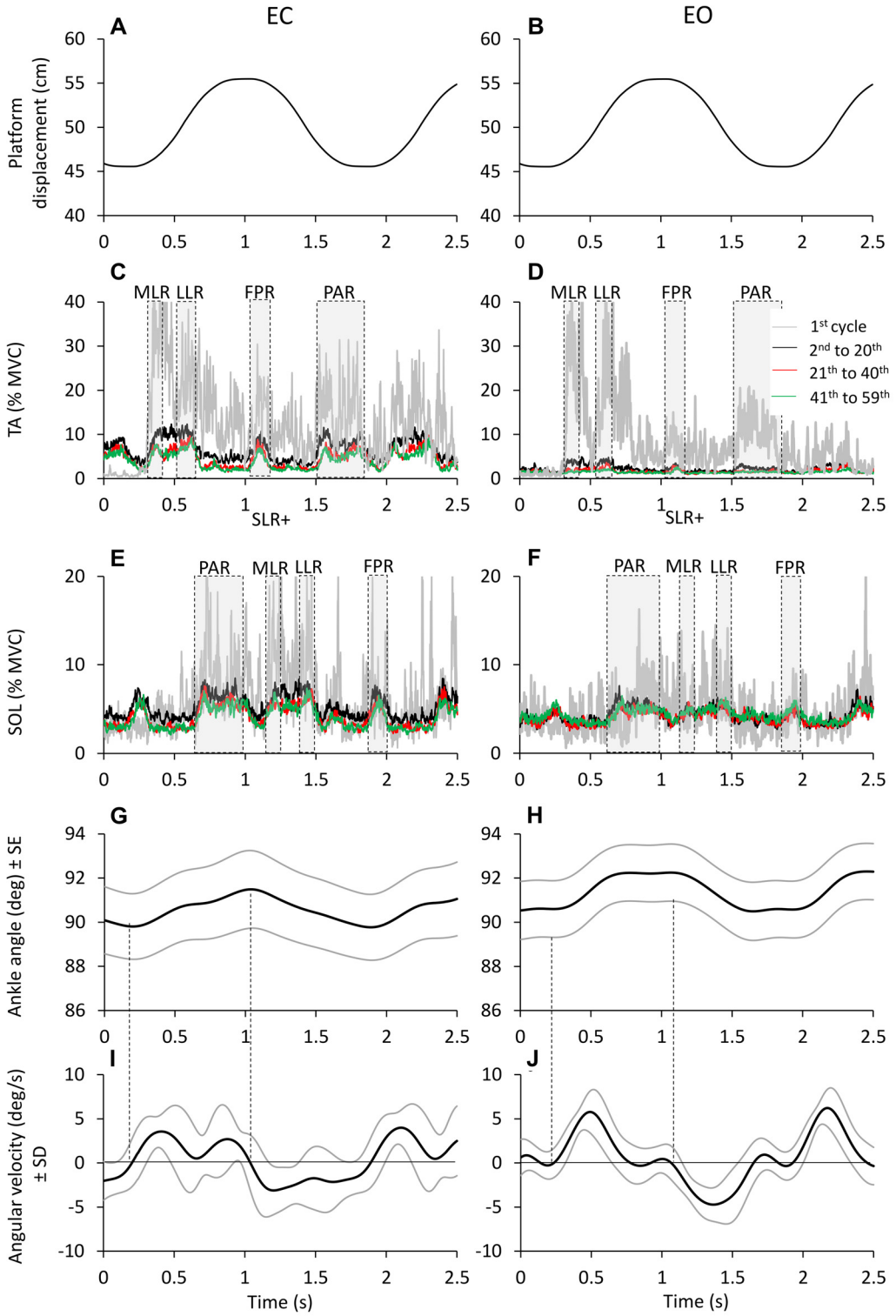

FIGURE 4 | Time windows of TA and Sol bursts. Platform displacement **(A,B)**. Mean across subjects of TA **(C,D)** and Sol **(E,F)** EMG of the first cycle (gray traces) 2nd to 20th cycle (black traces), 21th to 40th (red traces) and 41th to 59th (green traces), EC (left panels) and EO (right panels). TA and Sol EMG are almost reciprocal and segmented in different bursts. These bursts rise and decrease sharply as a sign of high synchronization and consistency across subjects. The different time windows of activation of TA and Sol are highlighted by gray dashed boxes. **(G,H)** show the grand averages of the ankle angle changes (subjects and cycles collapsed) and **(I,J)** show the corresponding changes in angular velocity. The black lines refer to the grand mean of ankle angle and angular velocity changes; the gray lines show the standard error for the ankle angular changes and the standard deviation for the angular velocity changes.

platform forward translation and negative (ankle angle decreases and TA shortens/Sol lengthens) during the platform backward translation.

Figure 5 shows that these bursts had a remarkably constant latency throughout the successive cycles, in spite of the mentioned changes in size. Latencies were measured from the onset of the forward translation of each cycle for the TA (**A**, one subject) and from the onset of the backward translation for Sol (**C**). We compared the onset latencies of the four identified TA bursts (EC) across cycles and subjects. ANOVA showed no significant effect of the cycle number on the mean latencies (MLR: $F_{(1,58)} = 0.75$, $p = 0.9$; LLR $F_{(1,58)} = 1.3$, $p = 0.08$; FPR: $F_{(1,58)} = 1.07$, $p = 0.4$; PAR: $F_{(1,58)} = 1.28$, $p = 0.09$). Moreover, the *post hoc* analysis showed no difference in the mean latencies among the first 5 cycles ($p > 0.05$, for all responses). Not only the latencies were consistent within each subject, but they were almost superimposed in all the subjects, as shown by the small standard deviation of the bars reporting the mean latency values for each burst (**B** and **D**). Furthermore, the mean latencies were not different between EC and EO ($F_{(1,9)} = 0.04$, $p = 0.85$).

To account for the variability in the latency of the reflex or PARs, for each subject the standard deviation of the onset latency of the various TA burst (EC) were calculated and compared across responses by the Levene's test ($F_{(3,36)} = 8.89$, $p < 0.001$). The variability of PAR response proved to be significantly larger than that of the other bursts (*post hoc*, $p < 0.01$ for the four comparisons), while there was no difference across the other responses (*post hoc*, $p > 0.3$).

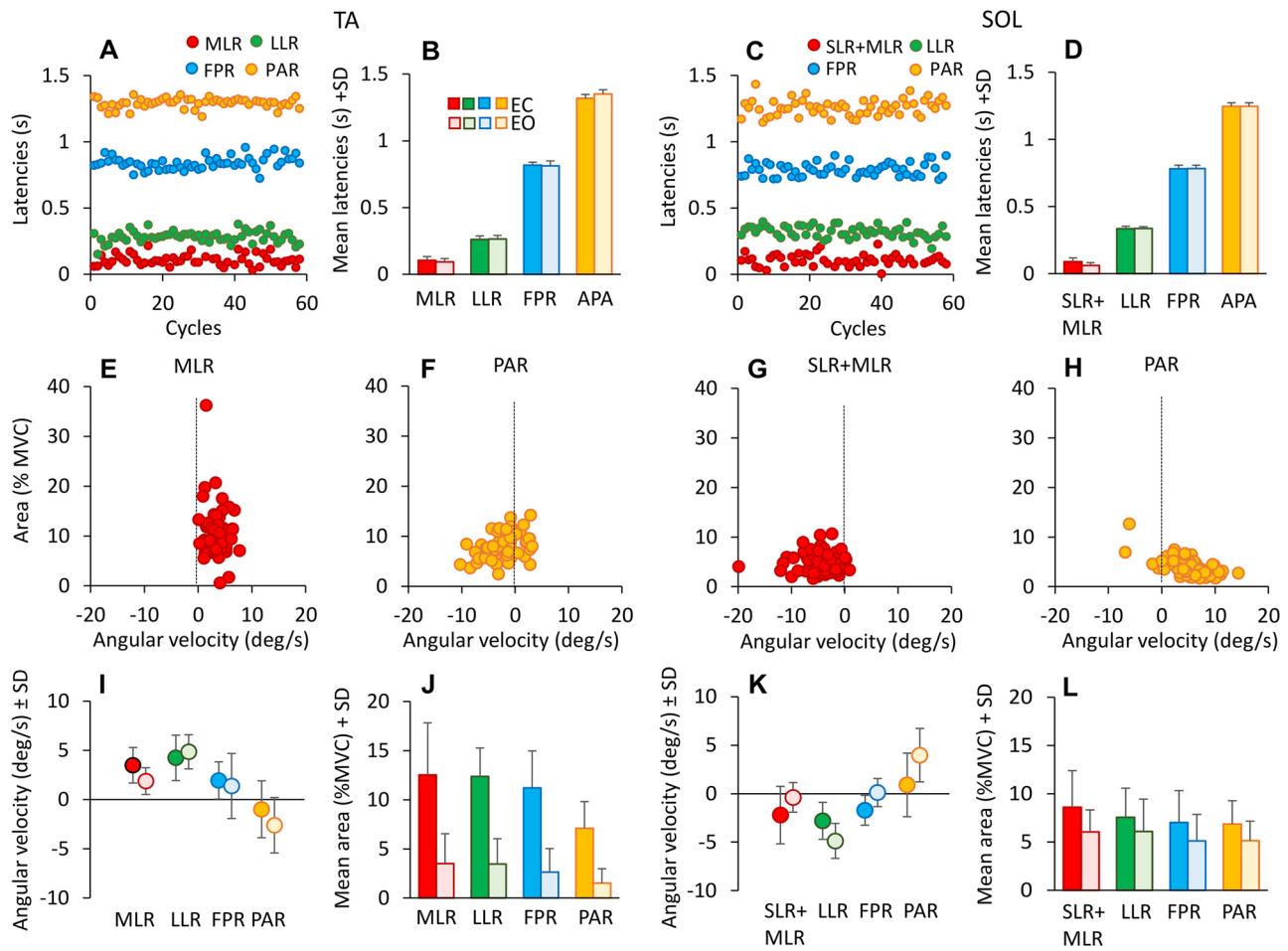

FIGURE 5 | Latencies of TA and Sol bursts. These are expressed with respect to the onset of platform forward movement (TA, left panels), and to the onset of backward movement for Sol (right panels). **(A,C)** show the onset latencies for TA and Sol bursts, in one subject cycle by cycle and for all response types (red medium-latency response (MLR) or SLR + MLR, green long-latency response (LLR), blue fall-preventing response (FPR) and yellow proactive response (PAR)). The grand means of the onset latencies of TA **(B)** and Sol **(D)** responses are reported. There are no differences in burst latencies between EC and EO, for both TA and Sol. **(E–H)** show TA (MLR, **E**; PAR, **F**) and Sol (SLR + MLR, **G**; PAR, **H**) burst areas against the corresponding ankle angular velocities for all cycles in one subject EC. TA and Sol reflex responses occur during muscle lengthening (positive ankle velocity for TA, negative for Sol), whereas PAR responses do not, for either TA or Sol. **(I,K)** show the grand means of ankle angular velocities preceding TA **(I)** and Sol **(K)** bursts EC and EO. Velocities are similar between EC and EO, but not across responses. **(J,L)** show the grand means of TA **(J)** and Sol **(L)** response area EC and EO. Bursts are smaller EO than EC for all responses. TA activity diminishes more than Sol activity passing from EC to EO.

The mean duration of the bursts across subjects (not shown in the Figure) ranged from about 60 ms (MLR) to about 250 ms (PAR) for TA and from about 65 ms (SLR + MLR) to about 360 ms (PAR) for Sol. For each response, the mean duration of the bursts was not different between EC and EO conditions ($F_{(1,9)} = 0.075$, $p = 0.79$), but was different between muscles ($F_{(1,9)} = 87.9$, $p < 0.01$). There was also an interaction between muscle and vision ($F_{(1,9)} = 38.3$, $p < 0.01$), since durations were generally longer with EO for Sol and with EC for TA, but significantly so only for PAR and FPR response (*post hoc*, $p < 0.05$, for all comparisons).

Figures 5E–H also show the result of the attempt to correlate the size of the bursts to the angular velocity of the ankle angle, in order to identify reflex and non-reflex responses. Some burst proved to be directly connected to stretch of the homonymous muscle, while others were not. The TA bursts at the beginning of each platform forward translation (MLR) were associated with the increase in ankle angle (positive angular velocities in **E**), while other bursts occurred in the absence of consistent positive angular velocity or even with negative velocity (for instance, TA PAR was often present when the ankle angle decreased, corresponding to TA shortening, see **F**). A similar pattern occurred for Sol (**G,H**; note that negative velocities stand here for the reduction in ankle angle, therefore Sol lengthening). The third row (**I** and **K**) summarizes this finding, where the successive points belong to reflex or anticipatory responses within a cycle. Each response occurred at different mean ankle angular velocity, for both TA ($F_{(3,24)} = 12.88$, $p < 0.001$) and Sol ($F_{(3,27)} = 16.03$, $p < 0.001$). In particular, for TA, across subjects and cycles, the mean angular velocities were positive for MLR, LLR and FPR and negative for PAR (there was a difference between the ankle angular velocity for PAR and for the other three responses, *post hoc* $p < 0.001$ for the three comparisons). **Figures 5J,L** show that burst area was smaller with EO than EC for all TA and Sol responses ($F_{(1,9)} = 32.35$, $p < 0.001$). There was an interaction between muscle and vision ($F_{(1,9)} = 17.81$, $p < 0.01$), since with EO, TA area was much smaller than Sol area, for all responses (*post hoc*, $p < 0.005$). There was a difference between response types ($F_{(3,27)} = 10.11$, $p < 0.001$), and an interaction between the response and vision ($F_{(3,27)} = 3.17$, $p < 0.05$).

Figure 6 shows the change over time in the mean values of the area of the reflex burst (MLR, A and SLR + MLR, B), of the FPR **(C,D)** and of the PAR **(E,F)** for both TA and Sol, EC. For each subject, the decay of the areas of the bursts was described by exponential functions with two time-constants. The mean time-constants for the various responses of all subjects are reported in panels **(G,H)** for TA and SOL, EC and EO. Both TA and Sol showed an initial rapid decrease (τ_1); then, the EMG activity of both muscles continued to decrease more slowly (τ_2). The fitting algorithm did not converge to the exponential model for $n = 4$ bursts of TA PARs (EO condition only) and for $n = 17$ bursts of Sol (comprising both EC and EO proactive and reflex responses), since the amplitude of those bursts proved to be almost constant from the beginning to the end of the perturbation sequence. On averaging the valid time-constant values, τ_1 proved to be shorter than τ_2 ($F_{(1,115)} = 106.5$, $p < 0.001$). All time-constant collapsed, there was a difference between TA and Sol (TA longer than Sol, $F_{(1,115)} = 6.98$, $p < 0.05$) and between visual condition (τ_1 and τ_2 were longer with EC than EO, $F_{(1,115)} = 59.96$, $p < 0.001$). There was an interaction between τ_1 and τ_2, muscles and vision, since vision decreased τ_1 and τ_2 to a larger extent in TA than Sol ($F_{(1,115)} = 4.89$, $p < 0.05$). Vision significantly decreased τ_2 for all TA bursts (*post hoc*, $p < 0.05$ for the four comparisons). All types of response (reflex or proactive) decreased over time with similar time-constants in both muscles ($F_{(3,115)} = 1.7$, $p = 0.17$). This was true both for τ_1 and for τ_2 (interaction between time-constants and type of response, $F_{(3,115)} = 0.9$, $p = 0.44$). With EC, the TA reflex responses exhibited the shortest initial rapid decrease (τ_1, MLR = 0.7 ± 0.5 cycles, TA LLR = 1.1 ± 0.1 cycles) suggesting that the "first trial effect" had vanished already at the 2nd cycle. τ_1 was instead just longer for the proactive than the reflex responses (1.7 ± 0.2 cycles for FPR and 2.3 ± 0.1 cycles for PAR) but not significantly so (*post hoc* $p > 0.10$ for all comparisons).

In order to assess the amount of reduction in the burst area during adaptation, for each burst we calculated the difference between the values of the burst at the second oscillation cycle and the asymptotic value, based on the exponential fit. **Figures 6I,J** report the amount of reduction calculated for the different responses, for TA **(I)** and Sol **(J)**. A great difference between the value of a response at the second oscillation cycle and the asymptotic value points to a large response adaptation. Conversely, short histogram bars (e.g., **(J)**, EO data) point to minimal amplitude adaptation. Under EO condition, in six subjects, TA responses disappeared in the final perturbation cycles and in two subjects the TA FPR response was never present. The entity of the reduction in amplitude was larger with EC than EO ($F_{(1,9)} = 8.54$, $p < 0.05$) for all the responses and greater for TA than for SOL ($F_{(1,9)} = 13.88$, $p < 0.01$). There was also a difference between type of response ($F_{(3,27)} = 12.7$, $p < 0.001$) and an interaction between type of response and muscles ($F_{(3,27)} = 13.48$, $p < 0.001$). For TA, both under EC and EO condition, the entity of adaptation of the reflex responses (MLR and LLR) was larger than that of the PARs (FPR and PAR; *post hoc*, $p < 0.05$, for all comparisons).

Head and CoM A-P Behavior During the Entire Perturbation Period

The value of the standard deviation of the entire trace of the head and CoM displacements was calculated (not shown) to get a global index of the segment oscillation amplitude. This mean across-subjects oscillation index was for the CoM: 3.1 ± 0.8 cm (EC), and 2.3 ± 0.8 cm (EO), and for the head: 5.1 ± 2.0 cm (EC), and 2.3 ± 0.7 cm (EO). ANOVA showed an effect of vision on the oscillation indexes ($F_{(1,9)} = 34.25$, $p < 0.001$), a difference between head and CoM index ($F_{(1,9)} = 7.74$, $p < 0.05$), and an interaction with vision ($F_{(1,9)} = 94.92$, $p < 0.001$).

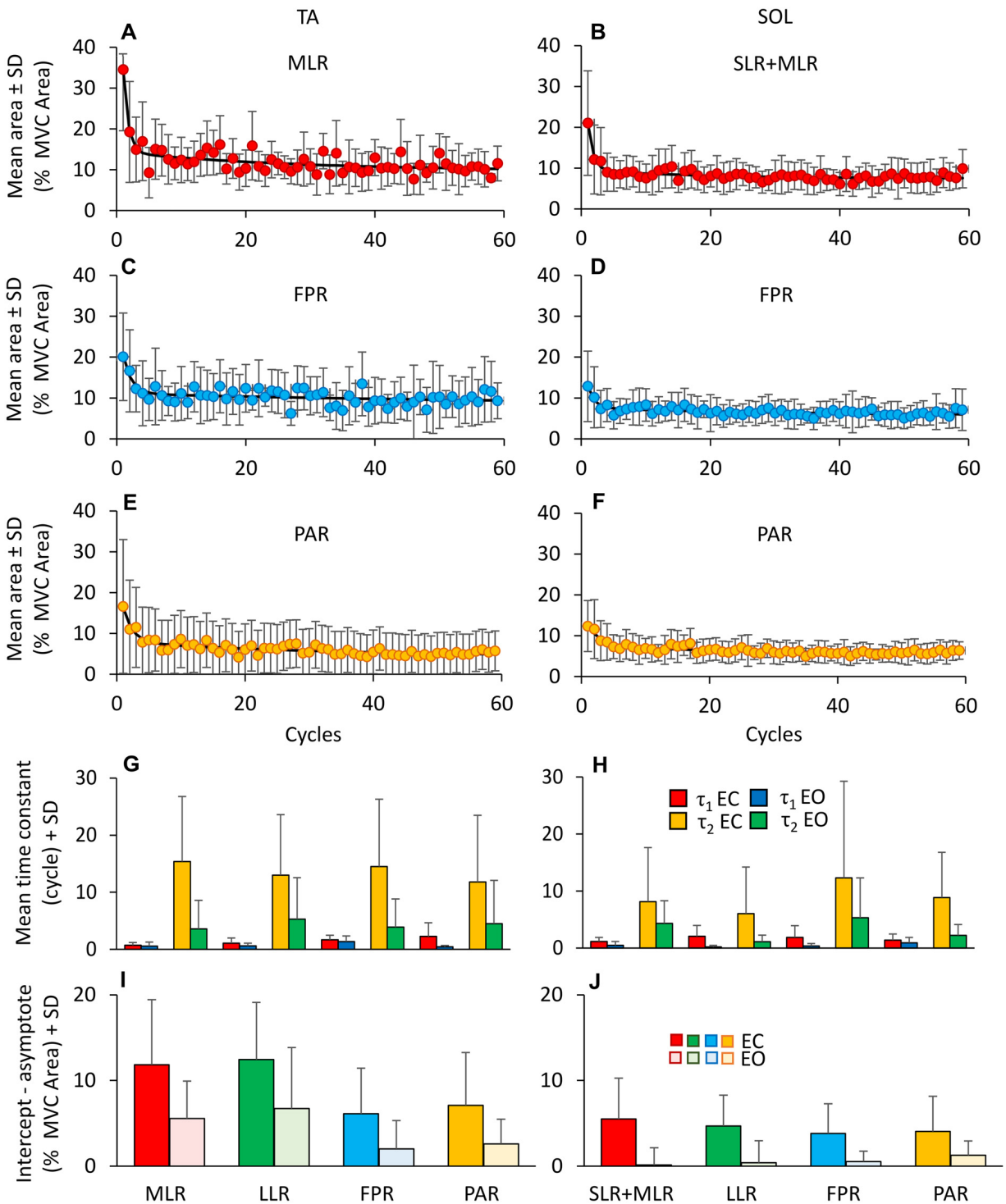

FIGURE 6 | Adaptation of reflex and anticipatory response. (A–F) Shows the adaptation of the different TA (MLR, **A**; FPR, **C**; PAR, **E**) and Sol responses (SLR + MLR, **B**; FPR, **D**; PAR, **F**). For TA, the exponential functions fitting the mean burst area are $y = 9.7 + 20.3e^{-t/0.8} + 4.5e^{-t/26.8}$ for MLR, $y = 8.3 + 9.4e^{-t/1.3} + 2.8e^{-t/62.6}$ for FPR and $y = 4.3 + 8.5e^{-t/1.5} + 3.6e^{-t/32.1}$ for PAR. For Sol, the exponential functions are $y = 7.46 + 11.5e^{-t/0.8} + 2e^{-t/17.1}$ for SLR + MLR, $y = 5.7 + 5.4e^{-t/1.0} + 1.9e^{-t/29.8}$ for FPR and $y = 5.5 + 5.2e^{-t/1.8} + 2e^{-t/22.4}$ for PAR. **(G,H)** show the mean time constants obtained by fitting with a double exponential function the TA **(G)** and Sol **(H)** responses EC (τ_1, red bars; τ_2, yellow bars) and EO (τ_1, blue bars; τ_2, green bars). The time constants differ between EC and EO and between TA and Sol. The extent of adaptation in the amplitude of the response bursts **(I,J)** is higher for TA than Sol, higher with EO than EC and different between reflex and anticipatory responses.

On average, the oscillation indexes of head and CoM were not different with EO (*post hoc*, $p = 0.05$), while closing the eyes induced a larger oscillation for head than CoM (*post hoc*, $p < 0.001$).

The CoM A-P positions with respect to malleolus are critical to balance, since any translation of the CoM behind the malleolus increases the risk of falling backwards. There was no difference in the CoM position between EC and EO condition ($F_{(1,9)} = 0.12$, $p = 0.7$), both at the beginning (the intercept value of the exponential fit, *post hoc*, $p = 0.34$) and end of the perturbation cycles (the asymptotic value of the fit, *post hoc*, $p = 0.75$; **Figures 7A,B**). The CoM mean positions **(A,B)** exhibited a moderate shift forwards of about 1 cm with respect to its position in the first cycle, with a time-constant of 3.4 ± 2.9 cycles (EC) and 2.0 ± 1.9 cycles (EO). There was no difference in the time-constant between EC and EO (*t*-test, $p = 0.2$), but a difference in the CoM position between the first cycle and the final cycles ($F_{(1,9)} = 20.45$, $p < 0.05$), both for EC and EO (*post hoc*, $p < 0.05$). After the initial forward shift, the CoM position remained remarkably constant throughout the following cycles with both EC and EO, indicating an overall similar inclination of the body with respect to the ankle joint. The bottom panels show that, on collapsing all trials and subjects, CoM **(C)** and head **(D)** backward-most positions infrequently (EC) and never (EO) bypassed the position of the malleolus. The graphs also show the limited scatter of CoM compared with the larger head data scatter (EC) across subjects and trials. Overall, the control of the CoM position relative to the base of support (critical for preventing backward fall) proved to be effective from the beginning to the end of the perturbation cycles regardless of the major attenuation of the EMG bursts.

The anterior displacement of the CoM was accompanied by an increase in the height of the malleolus marker, as a sign of deformation of the foot arch. The direct relationship between CoM advancement and malleolus height in a representative subjects during EC condition is shown in **Figure 7E**. Across subjects, the average slope of the line best fitting that relationship **(F)** was 0.019 ± 0.012 (EC) and 0.018 ± 0.016 (EO) (*t*-test, $p = 0.95$), indicating that the malleolus height increased by about 0.2 mm for 1 cm of CoM advancement, both under EC and EO condition.

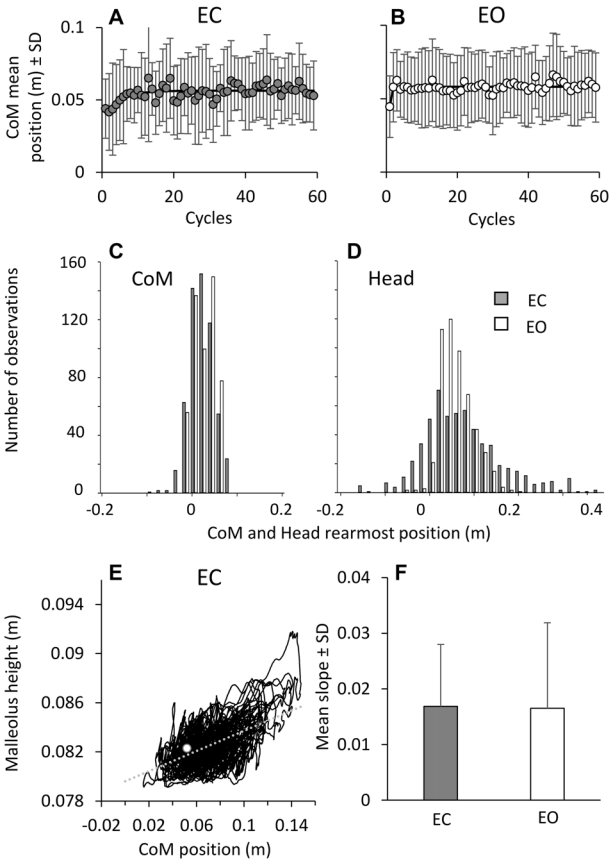

FIGURE 7 | Changes in CoM positions over time. During the perturbation cycles, the CoM mean positions with respect to malleolus **(A,B)** exhibited a minor shift forwards, both EC (left) and EO (right). The exponential functions fitted to the mean positions of CoM are $y = 0.056 - 0.015e^{-t/4.4}$ in EC and $y = 0.058 - 0.013e^{-t/0.1}$ in EO. **(C,D)** show CoM and head backward-most position (all trials and all subjects collapsed). These only infrequently EC (gray bars) and never EO (white bars) bypass the position of the malleolus (backwards negative in the abscissa). **(E)** shows the direct relationship ($y = 0.04x + 0.08$; $r^2 = 0.3$; $p < 0.001$) between CoM position with respect to malleolus and the height of the marker placed on malleolus in a representative subject under EC condition. The white dot indicates the values of CoM position and malleolus height during quite stance. The mean slope across subjects of the regression line indicating the relationship between CoM position and malleolus height is reported in **(F)** for EC (gray bar) and EO (white bar).

Changes in the Temporal Relationship of the CoM Position With Respect to the Moving Base of Support

Figures 8A–C show the progressive time-shift of the CoM with respect to the support base in a representative subject (EC). For all subjects, the CC coefficient between the traces of CoM and platform (**Figure 8D**) was high from the beginning ($R = 0.77 \pm 0.2$, the average of the first cycle across subjects) and tended to increase and level off over time. The mean R of the last 5 cycles was 0.84 ± 0.07. The mean time-constant of this change in R over time was 11.9 ± 11.5 cycles. With EO (**Figure 8E**), the CC coefficient was high at the first cycle ($R = 0.84 \pm 0.11$) and increased slightly during the successive perturbation cycles ($R = 0.89 \pm 0.06$) with a mean time-constant across subjects of 4.8 ± 3.0 cycles. The time-constant of the changes in CC over time was not strongly affected by vision (EC and EO, paired *t*-test, $p = 0.08$).

Figures 8F,G show the average values over time of the CoM-platform time lags, under EC and EO conditions. At the beginning, the displacement of CoM trailed the platform displacement by about 0.16 s with EC and 0.1 s with EO (paired *t*-test, $p = 0.15$). The mean time-lag diminished with cycle repetition to about 0.1 s with EC and 0.07 s with EO (paired *t*-test, $p = 0.06$) with a mean time-constant **(F)** of

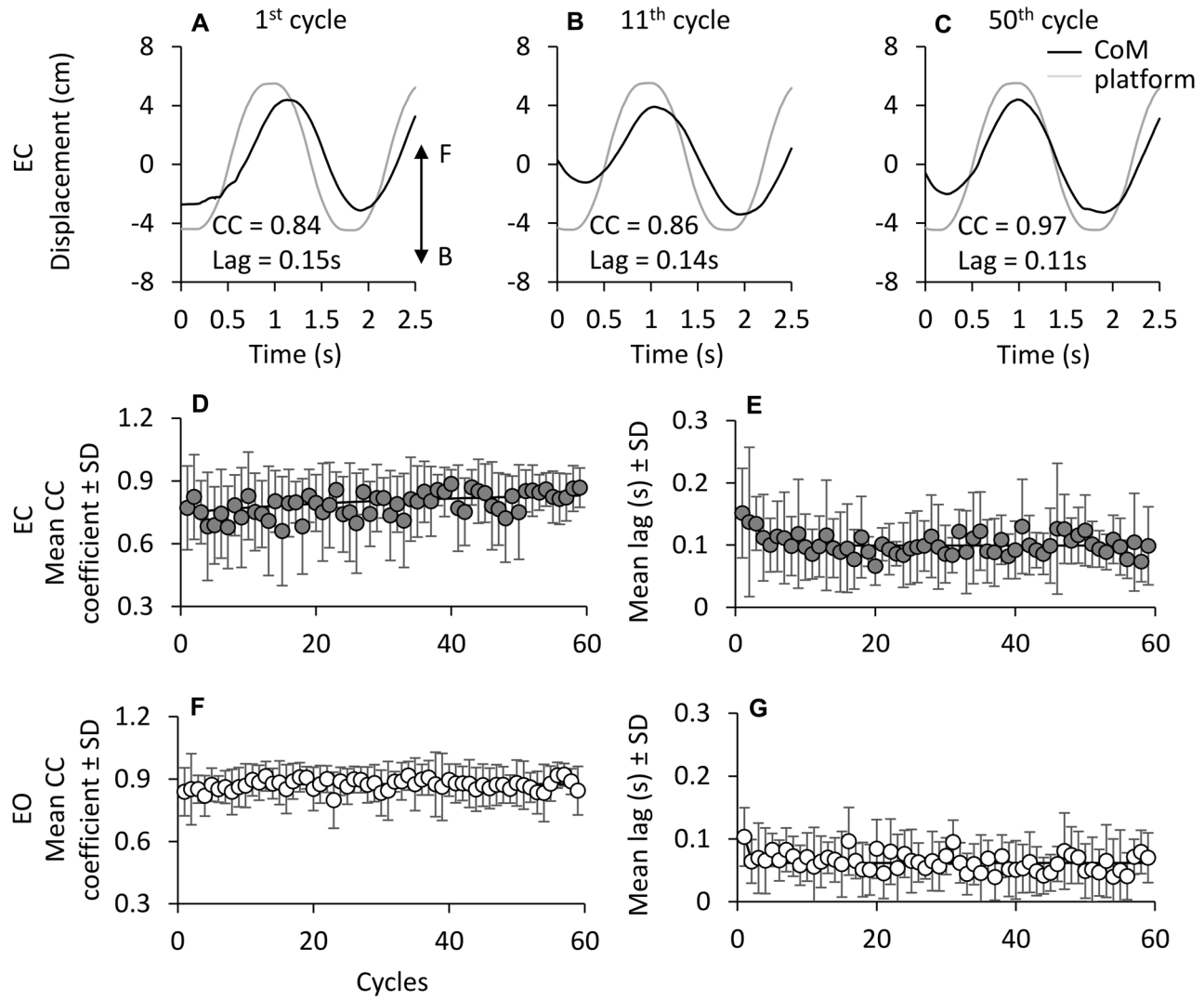

FIGURE 8 | Cross correlation (CC) between CoM and platform displacement. (A–C) show CoM (black line) and platform displacement (gray line; both referred to the laboratory space) during three non-consecutive cycles in one subject EC (F, forward; B, backward). **(D,E)** show the grand mean of the CC coefficient at time lag = 0 between CoM and platform displacement traces. CC values slightly increase with cycle repetition under both EC **(D)** and EO **(E)** condition. The exponential functions fitted to the mean CC coefficient data points are $y = 0.83 - 0.15e^{-t/36.3}$ in EC and $y = 0.87 - 0.04e^{-t/4.7}$ in EO. At the beginning of the oscillation cycles, CoM follows the platform with a lag of about 0.16 s EC, and 0.1 s EO. The time lag between CoM and platform diminishes with cycle **(F,G)** both EC and EO. The exponential function is $y = 0.10 + 0.05e^{-t/2.7}$ in EC and $y = 0.06 + 0.04e^{-t/0.5}$ in EO.

7.8 ± 9.7 cycles with EC, and of 4.6 ± 2.9 cycles with EO (paired *t*-test, $p = 0.33$). These lags were small, but significantly different from zero in most perturbation cycles of all subjects (EC, 83%; EO, 80%). Overall, the delay of the CoM with respect to the platform back-and-forth displacement was very limited, as a sign of effective synchrony of body to platform movements, but tended to become in-phase with the platform translation.

The regularity of the CoM cyclic displacement was at the expense of a presumably complex control. When the CoM back-and-forth displacement with respect to malleolus was plotted against ankle angle for each successive cycle (**Figure 9**), the coefficient of determination of the linear regression (r^2) was initially very low, and improved with time. Then, the "easy" balancing synergy (CoM moving forward when the ankle angle decreased and vice versa), featuring a coefficient of determination approaching unity, was reached with a time-constant of about 10 cycles (**J**). When the mean time course of r^2 was calculated for all subjects, this finding was replicated. This time-course proved to be much shorter with EO than EC (*post hoc*, $p < 0.001$), as shown in the bottom panel *(K)* of **Figure 9**, indicating a strong coupling between CoM displacement and ankle angular change with EO from the very beginning.

We note that both the time-constants of the coefficient of determination (r^2) and the time-constant of the co-contraction

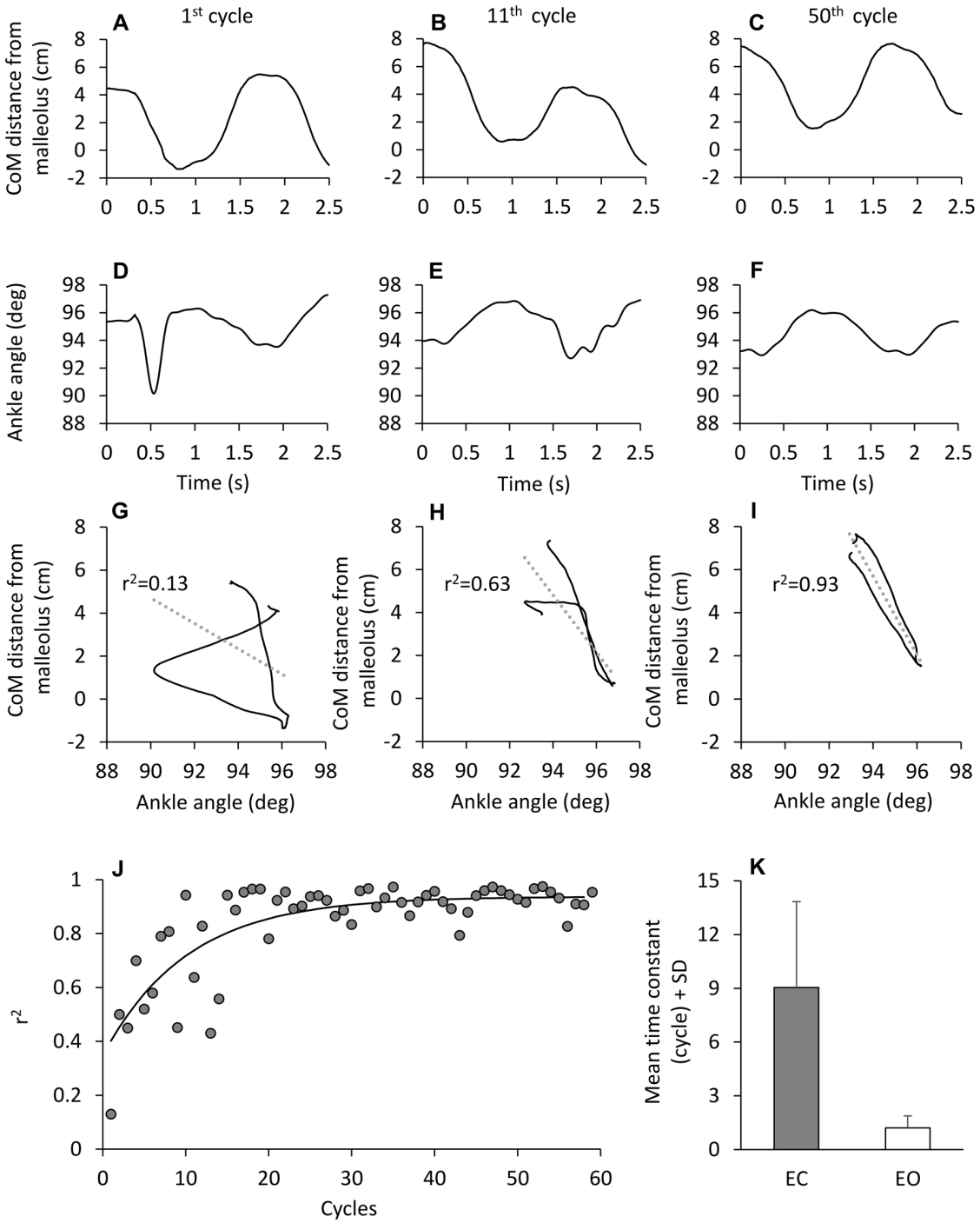

FIGURE 9 | Time-dependence of the correlation between CoM displacement and ankle angle variation. (A–F) CoM horizontal distance from malleolus **(A–C)** and ankle angle variation **(D–F)** in one subject during three different cycles of perturbation EC. When the CoM distance from malleolus is plotted against ankle angle **(G–I)**, the association between the two traces improves with cycle number. **(J)** show the value of the determination coefficient (r^2) calculated for each cycle EC. The r^2 values increase with cycle repetition with a time-constant of 10.1 cycles ($y = 0.93 + 0.6e^{-t/10.1}$). **(K)** show the mean time-constant across subjects, EC (gray bar) and EO (white bar).

index **(k)** (**Figure 3**) were not significantly different ($F_{(1,9)} = 4.19$, $p = 0.07$), suggesting a parallel time-course of both parameters. There was an effect of vision ($F_{(1,9)} = 28.52$, $p < 0.001$), since the time-course was much more rapid for EO than EC. There was no interaction between visual conditions and time-constants ($F_{(1,9)} = 3.44$, $p = 0.09$).

DISCUSSION

Progressive Decrease in Leg Muscle EMG Activity

Healthy young subjects underwent repeated and predictable perturbations of stance, featuring continuous A-P translations of the support base calling into action feedback responses and proactive postural adjustments related to the repetitive rhythmic platform displacements (Milner and Franklin, 2005; Franklin et al., 2008). Our aim was to confirm that: (a) leg muscle EMG activity decreases over the perturbation cycles (Schmid et al., 2011) and to assess whether; (b) adaptation is differently modulated for the reflex and anticipatory responses elicited in the leg postural muscles; (c) adaptation implies changes in both amplitude and latency of the response bursts; (d) a relationship exists between EMG response adaptation and critical kinematic variables; in addition, we addressed; and (e) the role of vision on adaptation. We will first discuss the no-vision data (EC), to later consider the effect of vision (EO) on the balancing behavior.

The TA muscle showed in all subjects a progressive decrease in activity, common to both legs (Vieira et al., 2014). The time-constant of this decrease with EC was such that the activity tended to level off to about 30% of its initial value after 15–20 cycles. The time course and the steady-state level of this decrease were not exactly the same in all the subjects, though, as indicated by the variance of the mean data. This could be connected with cycle-to-cycle differences in the balancing behavior, whereby some subjects kept their body straight, trying to counteract the platform displacement, while others allowed a moderate bending of their body by hip and ankle angle changes. In addition, since the stimulation pattern implied a fixed-support strategy and precluded the option of grasping (Maki and McIlroy, 1997), four subjects initially made a short step that was soon corrected. In other subjects, there was a transient phase wherein, after the initial smooth adaptation (Adi-Japha et al., 2008), the balancing performance was possibly disturbed by a gradual forward or backward body lean that required a corrective intervention by modulating the amplitude of the leg muscle bursts.

The Sol muscle also showed a progressive decrease in amplitude, with a time-constant just as like that of the TA, showing a contribution of the Sol to the general process of adaptation. However, contrary to TA, the steady-state EMG level remained elevated in the Sol (about 60% of the initial value). This is likely connected with the need to continuously counteract gravity, since in all subjects and cycles the CoM lay always in front of the malleolus, requiring a continuous plantar-flexor activity. The limited reduction of Sol activity could be also connected to the forward displacement of the CoM (about 1 cm) occurring during the first few initial cycles and persisting until the last cycles (Keshner et al., 1987), which would have increased the gravity torque (Schieppati et al., 1994). In addition, in the course of adaptation, TA activity progressively diminished. Overall, while CoM advancement requires a larger Sol activity to keep the body from falling, the diminishing TA force requires less counter-action by Sol so that, in the end, Sol activity may remain approximately constant.

The Timing of the Bursts Within Cycles, and the "First-Trial" Effect

Averaging the EMG traces across subjects and perturbation cycles gave a clear-cut profile of the time-varying muscle activity within a cycle. This presented a series of bursts that could be easily encompassed by distinct time-windows. The large TA bursts occurring during the first few cycles had the same latency as the corresponding smaller-amplitude bursts recorded during the following cycles. Hence, the latency of the bursts was independent from the process leading to the attenuation of burst amplitude over time. This was not necessarily predicted, since latency changes *can* occur under a continuous perturbation protocol similar to ours, as after deliberately produced fatigue of TA (Kennedy et al., 2012). One might argue that, in the latter case, the changes in latency take into account the smaller capacity of muscle force production, compelling the neural command to change its timing since changes in force recruitment would be less effective. Without fatigue, the strategy of reducing amplitude but not timing of activation would be adequate.

The latency of the first large TA burst is not different from that of the corresponding bursts of the following cycles. This reduces the probability that the first large burst is a startle reaction (Oude Nijhuis et al., 2010; Campbell et al., 2013), and suggests it to be a true stretch-induced balance-correcting response. McIlroy and Maki (1993) had already emphasized that a response to an unexpected perturbation can contain a compensatory reaction. The fact that subjects wore soundproof earphones also renders unlikely that they reacted with a startle reaction to the noise produced by the platform. The extent to which any "startling" effect of proprioceptive or vestibular origin (Bisdorff et al., 1994; Álvarez-Blanco et al., 2009; Sanders et al., 2015) might have contributed to the large amplitude of the first TA MLR and LLR bursts cannot be settled based on the present data. However, we would note that the body position was closer to the vertical at the time of the first perturbation cycle, as shown by the large ankle angle and the short distance between CoM and malleolus. The greater length of the TA at this time with respect to the subsequent cycles would favor a larger reflex response to the rapid TA stretch induced by the platform forward displacement. As to the bursts following the initial TA reflex responses, namely the so-called FPR and PAR, it seems even less likely that any startle reaction *per se* could have extended its effect to the muscle activity occurring later.

Adaptation of Reflex and Anticipatory Responses

For almost all cycles of the sequence, the TA burst occurring at the beginning of each platform forward translation had similar latency, in turn similar to the latency of the response

to the very first perturbation. This occurred in spite of the burst being triggered by "dynamic" consecutive perturbations, while the first perturbation started from the "neutral" static postural configuration. The amplitude of these TA bursts were always related to the velocity of the increase in ankle angle. These bursts were considered medium- and long-latency stretch reflexes (MLR and LLR), since the angular velocity is a variable appropriate for estimating the velocity of change in muscle length. The latter is the adequate stimulus for triggering the stretch reflex, given the velocity-dependence of the sensitivity of the muscle spindle receptors. The responses occurring at about the anterior platform turn-around points and during the backward translation periods bore instead no relation to the ankle angular velocity. For this reason, these were considered proactive activities and were named FPR and anticipatory PAR, respectively. In this connection, we would point out that continuous sinusoidal rather than single support surface perturbations were employed in this study, and that only leg muscle stretch was considered. Input from other muscles synchronous with some phase of the perturbation displacement might have produced phasic responses in the leg muscles triggered by changes in body segment movements that we have not examined. However, the similarity in the responses' latencies between EC and EO, two conditions producing different displacements of the body parts, would not readily favor that possibility. Of note, since the ankle angle *decreases* during the period where the PAR occurred (and the TA shortens accordingly), that burst might include the so-called "shortening reaction" (Katz and Rondot, 1978; Bathien et al., 1981; Berardelli and Hallett, 1984), the amplitude of which is known to depend on the central set (Miscio et al., 2001). This would be in keeping with the notion that, during adaptation, PAR can be modulated at cortical level, since the cortex is certainly involved in controlling critical postures (Taube et al., 2006; Maki and McIlroy, 2007; Nardone et al., 2008; Petersen et al., 2009; Tokuno et al., 2009; Bolton et al., 2011; Zwergal et al., 2012; Obata et al., 2014; Fujiwara et al., 2016). It has been recently suggested that the motor cortex confers sophisticated feedback to these responses, thereby potentially participating in their calibration (Pruszynski et al., 2011; Pruszynski and Scott, 2012).

The absolute decrease in amplitude of burst area from the second cycle (in order to exclude the "first-trial effect" from the computation) to steady state was larger for the reflex than for the anticipatory responses. Consequently, the weight of the anticipatory responses *relatively* increased over the series of perturbations. Hence, it can be inferred that adaptation does not prioritize reflex responses, but appropriately weights feedback and feed-forward control. This inference is not in contrast with the conclusion of previous studies (Cenciarini and Peterka, 2006) asserting that, during continuous perturbations, subject's reliance on information from the stimulus decreases, whereas a sensory reweighting mechanism ensues, tending to favor information that encode body orientation relative to vertical. A difference in the time course of the decrease in burst amplitude between reflex and PARs might potentially reside in muscle mechanical factors (Proske et al., 1993), such as thixotropy. This is dependent on the history of the changes in length and activation of muscle's extra- and intrafusal fibers. While we would not deny a contribution of these factors to the early adaptation phase, in particular for the ample decrease in amplitude of the reflex response at the 2nd cycle, we would note that the relatively low amplitude and high frequency of the changes in muscle length would not favor a history-dependent change in muscle fiber stiffness in active muscle (Gurfinkel et al., 1997; Altman et al., 2015, in rabbit in Ca^{++}-activated single fiber), which might contribute to the overall adaptation process. Further, the latency of the reflex responses did not change over time, whereas thixotropy would be expected to affect latency (Hagbarth et al., 1995). Besides, in our hands, similar changes in leg muscle length occurred during EC and EO perturbations, but the adaptation time course was very different.

Fast and Slow Adaptation

At first sight, both reflex and anticipatory TA responses decreased over successive cycles almost in parallel, as an indication of progressive general attenuation of the responsiveness of the TA motor pool to all converging excitatory inputs. However, their time-course (both reflex and anticipatory) was fitted by an equation with two exponential terms, in order to comply with the initial rapid decrease (τ_1) followed by a slower decrease (τ_2), and to better address possible differences in adaptation between bursts. The time-constant of the initial rapid decay was the shortest (albeit not significantly so) for the MLR, shaped by the vanishing of the "first-trial effect" (Oude Nijhuis et al., 2010) discussed above. The time-course of the other bursts was also best fitted by two time-constants. A difference was present between τ_1 and τ_2, since all bursts exhibited a rapid decrease during the initial few cycles and all slowly decreased with a similar time-course, until a steady state was reached after 20–30 cycles. We would argue that the first rapid adaptation produces a coarse adjustment of the corrective torques to promptly counteract the risk of falling (Peterka and Loughlin, 2004), while the second slow process would progressively fine tune muscle activity to the new sensory references (Assländer and Peterka, 2014). It is becoming clear that distinct processes can contribute to sensorimotor adaptation (Huberdeau et al., 2015). In a visuomotor adaptation paradigm requiring to overcome perturbation while reaching, one process learns rapidly and depends on an explicit component, the other learns slowly and in an implicit mode (Taylor et al., 2014). It would not be surprising if these processes also applied to balancing, whereby the early rapid and the later slow adaptation would be expression of an explicit and implicit process, respectively.

Parallel analysis of the Sol bursts allowed to identify stretch responses and anticipatory responses as well. As expected, the pattern of Sol EMG activity profile, as obtained by the same averaging procedure as for TA, showed a half-cycle delay with respect to that of TA. This was in keeping with the TA and Sol similar involvement in counteracting

oppositely directed platform translations (the Sol reflex burst appeared at the beginning of the backward displacement of the platform, in response to the rapid Sol muscle stretch, and so on for the other response bursts). For Sol, both reflex and anticipatory responses showed a rapid small reduction (τ_1) followed by a further slower reduction (τ_2). The decrease in amplitude from the second cycle to steady state was also similar for the feedback and PARs, but much less pronounced than for TA. It might be suggested that all Sol responses serve the main task of counteracting gravity by being less susceptible to *selective* adaptation. Also in a different context, task- and context-related changes were more clearly present in the TA than in the Sol muscle (Schieppati and Nardone, 1995).

Relationship Between Muscle Activity and Kinematics During Adaptation

The constant latencies of the response bursts matched the substantial invariance of the CoM, which is kept within safe margins from the beginning. Possibly, this consistency would be guided by the need to keep stable the CoM that is the important variable for balance control (Safavynia and Ting, 2013; Welch and Ting, 2014). The progressive decrease in muscle activity (particularly so in the case of TA) would not alter the critical time-relationships between biomechanical body parameters and instantaneous position of the continuously translating support base.

At the beginning of the perturbation cycles, the coordination between CoM and ankle joint angle was very poor, and gradually achieved larger determination coefficients. Other body muscles (not recorded here) must therefore be recruited to help keep CoM stable at the earliest cycles, compensating for the poorly controlled ankle angle. Cappa et al. (2008) attributed to the upper limbs (free to move) an anticipatory role in counteracting perturbations similar to ours. In our case, subjects' arms were deliberately kept crossed so that only small not-monitored motions would have minimally affected the CoM displacement (Assländer and Peterka, 2014). Maki and McIlroy (1997) have reviewed the role of limb movements in maintaining upright stance, and suggested that they are substantially finalized in spite of their apparently chaotic production (Corbeil et al., 2013). In a sense, our protocol "forced" the leg muscles to compensate for absence of assistance of the upper limb motion.

Co-contraction around the ankle joint occurs during tasks such as standing on one leg, balancing on an unstable platform or reacting to rotation of a support surface, or walking on a narrow beam (Diener et al., 1983; Keshner et al., 1987; Nielsen and Kagamihara, 1992; Geertsen et al., 2013) or after fatigue (Kennedy et al., 2012). However, co-contraction is not a rule under different critical postures (Sozzi et al., 2013). In our protocol, TA-Sol co-contraction was present during the initial few cycles, and then gradually vanished. Interestingly, the changes over time of the coefficient of determination of CoM displacement vs. ankle angle increased exponentially toward $r^2 \cong 1$ with a time-constant almost equal to that of the TA-Sol co-contraction index, suggesting that co-activation can be a major disturbing factor. This feature, whereby higher co-contraction is associated with poor performances, and lower co-contraction with good performances, seems to be a general phenomenon in motor adaptation (Thoroughman and Shadmehr, 1999; Osu et al., 2002; Cordo and Gurfinkel, 2004). Following Osu et al. (2002), we would suggest that increased stiffness is a sign of inaccurate knowledge of the task, and that this subsides as learning builds up. At steady state, co-contraction is almost absent, and riding the platform becomes smoother and more coordinated while stability of the CoM is maintained.

The slight surge in height of the malleolus (about 0.2 mm per cm of CoM advancement) gives evidence of a significant deformation of the foot arch as the CoM of the body moves forward. As shown by Wright et al. (2012), such deformation would contribute to a change in ankle joint angle ($<1°$) that accompanies CoM advancement. Regrettably, we are not in the position of dissecting out the role in this event of the change in torque over the ankle joint or of any potential activation of plantar foot muscles or toe-extensor muscle (Schieppati et al., 1994), since no electrodes were fixed to the foot plantar surface or dorsum as in Schieppati et al. (1995). On the one hand, we can only argue that plantar foot muscle activity likely occurred when the CoM moved ahead of the malleolus, and that its activity would parallel that of Sol given that these two muscles are agonist and co-active during backward platform translations (Schieppati et al., 1995). On the other hand, the strong similarity of the slopes of the lines best fitting malleolus height and CoM position with EC and EO (two conditions exhibiting large difference in TA activity) would point to a role for the mechanical constraint rather than for the TA EMG adaptation.

The Effect of Vision on the Adaptation of the Balancing Behavior

When the same perturbation protocol was administered with EO, clear-cut differences and invariances were observed with respect to EC. As a preliminary note, we would remind here that the EC and EO tests were not performed in a randomized order. The fact that subjects under EO condition were familiar with the protocol, having previously performed the same protocol with EC, might have influenced the adaptation pattern (Pai and Bhatt, 2007; Patel and Bhatt, 2015). However, in *ad hoc* experiments performed in a different group of matched subjects, EO administered first produced a very rapid adaptation, equivalent to that observed in the main subject group. For this reason, we are confident that the very rapid adaptation with EO did not depend critically on the earlier EC trial.

The time-constant τ_1 of the profile of the TA bursts with EO was very short and not significantly different from EC. This suggests that the proprioceptive control predominates for the responses to the first perturbation cycle also when vision is available. The time-constant τ_2 was also short with EO (significantly shorter than EC). In

some subjects and bursts (especially in the case of the FPR response), the fitting algorithm did not even converge to an exponential curve, since the EMG activity was low from the very beginning. Therefore, we would put forward the notion that the effect of vision does not only consist in speeding up the adaptation process. It would also consist in a generalized down-modulation of the excitability of the motor neurons of the postural muscles, which are the final common pathway for both reflex and proactive activation (Schieppati et al., 2002; De Nunzio et al., 2005; Schmid et al., 2011).

The time-constant τ_1 (EO) was about one cycle. Hence, with vision, experience of one single cycle is enough to reprogram the balancing behavior in the successive cycles. With EO, the adaptation rate may almost be the sole consequence of the vanishing of the "first-trial effect" (Allum et al., 2011). In a different study from this laboratory, an equally similar rapid adaptation in the balancing strategy and EMG activity was observed when passing from EC to EO condition *during* a series of perturbations similar to that used here (De Nunzio and Schieppati, 2007), generalizing the effect of vision beyond the first-trial effect. Also the stabilization of a standing posture (as measured by the reduction of body sway) on adding vision or haptic information is fast (Sozzi et al., 2011; Blouin et al., 2014). This suggests that addition of vision can very rapidly entrain a low-motion, low-activity balancing pattern.

The prediction that, with adaptation, the final level of TA activity with EC at steady state could have reached the level of activity observed with EO, signifying the attainment of a more energy-efficient mode of balancing, was not verified. The absolute level of TA activity at steady state was in fact substantially larger EC than EO. Therefore, even if TA activity *can* decrease to very low levels, absence of vision precludes what would seem an easily attainable task. On the contrary, Sol activity at steady state with EO remained almost similar to that recorded for EC, indicating major differences in the functional outcomes of adaptation according to muscles having different purposes, as mentioned above. With EO, the TA-Sol co-activation index was also low from the beginning and rapidly diminished further in the following cycles. Also, the coordination between CoM and ankle angle under EO promptly reached a high value. Moreover, the time lag between CoM and back-and-forth movement of the platform, which was just smaller for EO than EC, reached steady state very soon. Conversely, the mean position and the extent of back-and-forth displacement of the CoM were similar across cycles between EC and EO, both in amplitude and rapidity to attain a steady state. Therefore, vision does not confer any particular stability to the body' CoM. In contrast, the back-and-forth displacement of the head was remarkably reduced by vision, in keeping with previous findings (Buchanan and Horak, 1999; Corna et al., 1999; Schieppati et al., 2002; De Nunzio and Schieppati, 2007; Schmid et al., 2007). Therefore, we would interpret the head stabilization in space with EO as the direct consequence of vision, an input that critically helps defining the reference frame for balance control by conferring the nervous system information about the environment (Dokka et al., 2009; Isableu et al., 2010; Joseph Jilk et al., 2014). Since it is the head that bears the eyes, the rapid head stabilization in space with EO and minimization of its peak-to-peak displacement would mainly contribute to minimizing the changes in visual flow connected with the platform displacement (Schmid et al., 2008; Dokka et al., 2009; Kiemel et al., 2011). In the absence of the possibility of exploiting vision, our brain accepts some extra activity in the postural muscles.

Perhaps, minimization in the metabolic cost has a neural *computational* cost. While the process of adaptation put in action under EC seems to be insufficient for completing this minimization, the neural computation would be easily afforded with vision. Moreover, with clear perception of environment and body movement in space (Gresty and Bronstein, 1992), the brain need not previously experience repeated cyclic events, but uses sort of a "default" strategy as a substitute of a costly adaptation process. It is tempting to assume that the brain without vision undergoes a complex trial-and-error course, whereby balancing improvements are gained from repeated practice by processing down-up information, whereas vision allows an almost immediate shift from a down-up to a top-down control strategy. Admittedly, the possibility of generalizing these inferences is limited by the absence of concurrent recording of the EMG activity of other muscles, potentially relevant in the process of the bodily adaptation to the continuous perturbations. Further studies are needed for detailing the contribution of (rapid or slow) adaptation of other muscle groups in this task.

CONCLUDING REMARKS

Taken together, the findings show that adaptation occurs when a subject's balance is challenged by repeated perturbations. Under these circumstances, the underlying sensorimotor adaptive processes would include the initial collection of information about the task to handle (among others, from the moving support surface and the position of the CoM), determine how to improve the performance (e.g., reducing redundant muscle activity), to then implement these changes as enhanced motor control performance by repeated trial and error procedure. Contrary to what happens with a self-paced movement, under this balance task condition, the initiator of the process is the initial exposure to an external stimulus (the onset of the series of platform oscillation cycles). This implies reflexive stability-enhancing countermeasures at the same time as it produces an important volley of afferent information about the bodily events. Progressive improvements in balancing behavior, underscored by reduced postural muscle activity and better intersegmental coordination, supervenes from repeated practice.

The ensuing adaptation process selectively affects different neural circuits, since TA activity shows a rapid followed by a slow reduction, while Sol shows a rapid minor adaptation followed by no-reduction in activity (prioritizing antigravity action). Both feedback and feed-forward controls are gradually tuned: yet, the smallest reduction is observed for anticipatory responses

(featuring a partial shift from feedback to feed-forward control). Further, any initial TA-Sol co-contraction subsides with the repetition of successive cycles passing from a stiffening strategy to antagonist muscles reciprocal activation. With vision, almost no adaptation is observed after the first few cycles, and the head reduces its motion already at the 2nd perturbation cycle regardless of the persistent CoM back-and-forth displacement.

We therefore suggest that adaptation serves the purpose of: (a) reducing muscle activity and co-contraction while allowing continuous CoM back-and-forth displacement in compliance with the platform translations (*"effort-reducing" adaptation*); (b) improving body segment coordination, reducing over time the number of unnecessary movements (*"entropy-reducing" adaptation*); (c) diminishing head back-and-forth displacement when eyes are open, allowing stable vision (*"visual-field stabilizing" adaptation*). We would also note that standing and balancing on the continuously translating platform shares several features of voluntary control: subjects are aware of the critical stance condition particularly in the absence of visual input, clearly perceive the body displacements accompanying platform displacements, and produce anticipatory adjustments or react to it with correcting counter-movements (Ouchi et al., 1999). Hence, the role of the sensory input in maintaining equilibrium may not be different from the role sensory input plays in directing and correcting voluntary movements of the upper limb (Patla et al., 2002; Soto et al., 2006; Crevecoeur et al., 2012; Hemami and Moussavi, 2014). This ultimately suggests that the cerebral cortex may be the site of the sensorimotor integration and reweighting processes underlying balance control (Taube et al., 2007; Sumner and Husain, 2008; Honeine et al., 2015) and suggests that a similar repertoire of basic mechanisms lies behind skill acquisition in voluntary and postural tasks (Elion et al., 2015).

Postural adaptations occurring from day to day have been reported (Tjernström et al., 2010b; Nardone et al., 2015) and suggested to underpin the rehabilitation effects of repeated perturbations. Predictable balance perturbations by sinusoidal translations have been successfully employed for rehabilitation of balance in selected patient groups (Nardone et al., 2010, 2014) including vestibular patients (Corna et al., 2003), who may badly behave on the platform when not compensated (Buchanan and Horak, 2001–2002). Interestingly, the complex processes of adaptive behavior in a balancing task are able to produce true learning, the uniqueness of which would be to prepare the body to counteract more general features of platform motion (Van Ooteghem et al., 2008; Kanekar and Aruin, 2015). The analytical approach described here could be easily applied to patients with balance problems of different nature, as for instance patients with Parkinson's disease, who may well show adaptation problems contributing to their balance dysfunction (Schieppati and Nardone, 1991; De Nunzio and Schieppati, 2007; Weissblueth et al., 2008; Nanhoe-Mahabier et al., 2012; Paul et al., 2013; Schoneburg et al., 2013), and patients with stroke (Kitago and Krakauer, 2013) or spinal cord injury, in which co-activation of TA and Sol contribute to impaired balance and walking ability (Beauparlant et al., 2013; Manella et al., 2013).

AUTHOR CONTRIBUTIONS

MS and AN conceptualized the study and designed the experiments. SS performed the experiments. SS and MS performed the data analysis. All the authors made contributions in drafting the manuscript and have approved the final version.

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Accelerometer-Based Step Regularity Is Lower in Older Adults with Bilateral Knee Osteoarthritis

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Purpose: To compare the regularity and symmetry of gait between a cohort of older adults with bilateral knee osteoarthritis (OA) and an age and sex-matched control group of older adults with healthy knees.

Methods: Fifteen (8 females) older adults with knee OA (64.7 ± 6.7 years) and fifteen (8 females) pain-free controls (66.1 ± 10.0 years) completed a 9-min. walk at a self-selected, comfortable speed while wearing a single waist-mounted tri-axial accelerometer. The following gait parameters were compared between the two groups according to sex: mean step time, mean stride time, stride and step regularity (defined as the consistency of the stride-to-stride or step-to-step pattern) and the symmetry of gait (defined as the difference between step and stride regularity) as determined by an unbiased autocorrelation procedure that analyzed the pattern of acceleration in the vertical, mediolateral and anteroposterior directions.

Results: Older adults with knee OA displayed significantly less step regularity in the vertical ($p < 0.05$) and anteroposterior ($p < 0.05$) directions than controls. Females with knee OA were also found to have significantly less mediolateral step regularity than female controls ($p < 0.05$), whereas no difference was found between males.

Conclusion: The results showed that the regularity of the step pattern in individuals with bilateral knee OA was less consistent compared to similarly-aged older adults with healthy knees. The findings suggest that future studies should investigate the relationship between step regularity, sex and movement direction as well as the application of these methods to the clinical assessment of knee OA.

Keywords: knee osteoarthritis, accelerometry, gait regularity, gait symmetry

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INTRODUCTION

The ability to locomote is a fundamental activity for all humans, and is an essential component of maintaining independence and a healthy quality of life. However, it is understood that the physiological changes that accompany aging in the last decades of life increasingly challenge the neuromuscular system to maintain consistent levels of mobility. Often these changes are exacerbated by other disease mechanisms or processes in one or more systems, to the extent that gait function can be severely compromised. Osteoarthritis (OA) is a debilitating disease that involves the progressive degradation of articular cartilage in the body's major weight bearing joints

(Baliunas et al., 2002). It affects millions of people worldwide, with knee OA being the most common in terms of prevalence (6% of adults > 30 years of age) (Zhang and Jordan, 2008). It is widely reported that knee OA is associated with compromised gait function in that it exacerbates the altered spatiotemporal gait parameters caused by aging, such as reduced stride length and speed and increased stride time, stance phase duration and double support time (Al-Zahrani and Bakheit, 2002; Astephen et al., 2008; Mills et al., 2013a). In addition to changes in mean spatiotemporal gait parameters, other studies have shown that knee OA is associated with changes in the variability of these parameters and the basic movement patterns that comprise the gait cycle (Kiss, 2011; Tochigi et al., 2012).

Research that has investigated the variability of one or more aspects of the gait cycle defines the area of study known as gait variability. Numerous studies have shown that gait variability is particularly sensitive to differences between healthy individuals and those with mild to moderate gait impairments. Evidence suggests that too much or too little variability is disadvantageous to the stability of the system, as has been shown by studies that have found both increased and decreased gait variability in different populations (Hausdorff, 2009; Tochigi et al., 2012). Studies on gait variability have largely investigated the regulation and timing of the gait pattern in various pathological conditions, including Parkinson's disease (Hausdorff, 2009), multiple sclerosis (Kalron, 2016), Alzheimer's disease (Wittwer et al., 2013), ALS (Hausdorff et al., 2000) and the changes in gait associated with healthy aging (Hausdorff et al., 1997; Kobsar et al., 2014a). A variety of different methods (cameras, pressure-sensitive mats and accelerometry) have been used to investigate a range of parameters that typically include linear measures such as the standard deviation (SD) or coefficient of variation of mean spatiotemporal gait parameters (e.g., stride time SD), or more sophisticated non-linear methods that aim to quantify the complexity of the gait cycle across different time spans (e.g., sample entropy, fractal scaling index) (Hausdorff et al., 1997; Tochigi et al., 2012; Kobsar et al., 2014a; Alkjaer et al., 2015). The application of accelerometry for gait variability analysis is advantageous because it allows for the collection of large amounts of data (i.e., potentially thousands of gait cycles) using unobtrusive sensors under natural walking conditions (Kobsar et al., 2014a). Conducting a similar analysis using a lab-based 3D camera system (for example) requires the use of a treadmill, which potentially alters the participant's internal rhythm (and consequently their gait variability) due to the external pacing imposed by the constant speed of the belt. It also provides the opportunity to take advantage of advanced analytical methods such as autocorrelation analysis (Moe-Nilssen and Helbostad, 2004), which can be used to extract discrete parameters such as the stride time and step time, in addition to using the entire acceleration waveform to determine the regularity (consistency of the stride-to-stride or step-to-step pattern) and symmetry (difference between step and stride regularity) of the gait cycle (Moe-Nilssen and Helbostad, 2004; Kobayashi et al., 2014; Kobsar et al., 2014a).

In general, studies that have investigated gait variability have produced favorable results that have advanced the understanding of the effect of different pathologies on gait function; however, the majority of these studies have focused on the effects of neural pathology (Moon et al., 2016) as opposed to diseases that directly affect the musculoskeletal system such as hip and knee OA. Several studies have found differences in select measures of gait variability (Yakhdani et al., 2010; Kiss, 2011; Tochigi et al., 2012; Gustafson et al., 2015) and gait symmetry (Mills et al., 2013b) in patients with unilateral and bilateral knee OA, respectively, presumably because pathophysiologically-induced changes to the morphology of the joint (e.g., decreased joint space, decreased range of motion, and increased pain) produce altered gait patterns as a result of CNS-mediated compensation strategies that develop over time to avoid pain, re-distribute joint loads and/or maintain dynamic stability under adverse conditions. Other studies have shown that sex and laterality (i.e., unilateral vs. bilateral incidence) are important factors that should be considered when investigating step regularity and gait symmetry in older adults with and without knee OA. Recently, Kobayashi et al. (2014) found differences in step regularity between older adult males and females, while Kiss (2011) found differences in cadence and step length variability between males and females with knee OA. With respect to gait symmetry, Mills et al. (2013b) have shown that between-limb kinematic asymmetries are greater for individuals with bilateral knee OA as opposed to unilateral knee OA. Consequently, the purpose of this study was to use an accelerometry-based unbiased autocorrelation procedure to determine the stride regularity, step regularity and gait symmetry of individuals with bilateral knee OA, and to compare these values to a group of age and sex-matched pain-free controls. It was hypothesized that males and females with knee OA would display less step and stride regularity than control participants and that their gait would be less symmetric. Based on the results of Kobayashi et al. (2014), it was also hypothesized that male participants in both groups would have lower step regularity than females.

METHODS

Participants

Fifteen adults, 55 years of age or older (8 females, 7 males; 64.7 ± 6.8 years), with bilateral knee OA participated in the study. In addition, fifteen age and sex-matched older adults (8 females, 7 males; 66.1 ± 10.0 years) who presented with no knee pain or diagnosis of knee OA were recruited as control participants. **Table 1** provides further information concerning the participant demographics. Inclusion criteria for the knee OA group consisted of having received a medical diagnosis of knee OA in addition to being able to walk comfortably for at least 9 min without the use of an assistive device (e.g., cane or walker). The severity of knee OA (as determined by the Kellgren-Lawrence grading scale) varied across participants, in that five participants had a K-L grade of 4 (in the most severe knee), eight had a grade of 3, and two had a grade of 2. Participants in the control group were selected using the same criteria as those for the knee OA group except for the presence of knee OA. Participants in either group were excluded if they had any recent surgery that affected their legs or lumbar spine, if they possessed

TABLE 1 | Demographic and temporal gait parameter data for knee OA and control group participants.

Parameter	Control (Mean ± *SD*)			Knee OA (Mean ± *SD*)		
	Female ($n = 8$)	Male ($n = 7$)	Total ($n = 15$)	Female ($n = 8$)	Male ($n = 7$)	Total ($n = 15$)
Age (years)	66.8 ± 10.5	65.3 ± 10.2	66.1 ± 10.0	63.9 ± 8.7	65.6 ± 4.0	64.7 ± 6.8
Height (cm)	**159.3 ± 4.0**†	**176.8 ± 8.5**†	167.5 ± 11.0	**160.7 ± 7.6**†	**174.6 ± 5.4**†	167.2 ± 9.7
Mass (kg)	**61.9 ± 9.5**†	**84.3 ± 16.2**†	**72.4 ± 17.1***	**78.5 ± 10.0**†	**92.7 ± 6.6**†	**85.2 ± 11.0***
BMI (kg/m^2)	24.4 ± 3.9	26.8 ± 3.4	**25.5 ± 3.8***	30.5 ± 4.4	30.6 ± 3.8	**30.6 ± 4.0***
Stride time (ms)	979 ± 74	1029 ± 73	1002 ± 76	1055 ± 76	1046 ± 73	1051 ± 72
Step time (ms)	489 ± 37	515 ± 37	501 ± 38	527 ± 38	523 ± 37	525 ± 36

**Results of the two-way ANOVA (group × sex) indicating significant differences between groups ($p < 0.01$) in bold.* †*Significant differences between sexes ($p < 0.01$) are marked in bold.*

OA in any other lower extremity joint (e.g., hip), if they had any neuromuscular disorders (e.g., Parkinson's disease, multiple sclerosis, etc.), history of stroke, cardiovascular disease, or any other medical condition or physical impairment that would affect their gait, balance, and/or their ability to walk at a steady pace for 10 min. This study was carried out in accordance with the recommendations of the University of Regina Research Ethics Board (REB) with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the University of Regina Research Ethics Board (REB-71S112).

Apparatus and Procedure

The height and weight of each participant was recorded for the purpose of calculating the body mass index (BMI). The test procedure required the participants to walk around an oval 200-m indoor track at a consistent, self-selected speed for a period of 9 min. Self-selected speeds were chosen because they most accurately represent the natural gait pattern according to each participant's stature and other physical factors such as strength and flexibility (Clermont and Barden, 2016). A single triaxial accelerometer (GENEActiv, Cambridgeshire, UK) was attached to a belt that was located firmly at the lower back (L3) to approximate the total body center of mass (Moe-Nilssen and Helbostad, 2004; Kobsar et al., 2014b). For a depiction of the experimental setup please refer to Kobsar et al. (2014b). The accelerometer recorded continuous acceleration at a sampling rate of 100 Hz during the 9-min walking trial, which is consistent with sampling frequencies used by previous studies to determine measures of gait variability (Hartmann et al., 2009; Kobsar et al., 2014a).

Data Analysis

The data sets from the 9-min walking trials were reduced to 6 min by removing the first and last 90 s of each trial. The average number of steps for 6 min of walking was 682.1 (SD ± 45.1) for knee OA participants and 710.1 (SD ± 36.5) for control participants. This was done to ensure that the participants had sufficient time to achieve a steady-state walking speed prior to the analysis and to remove any potential gait irregularities associated with anticipating the termination of the trial (Lindemann et al., 2008). All data processing and gait parameter calculations were done using MATLAB version R2016A (The MathWorks Inc., Natick, MA). The signals from all three accelerometer axes were initially processed using a zero-lag, 4th order Butterworth low-pass filter with a cut-off frequency of 10 Hz. Subsequently, a negative peak-detection (local minima) method on the anteroposterior axis was used to identify each individual step to determine the step times for the 6-min time series (Terrier and Dériaz, 2011). From this series of step times, the mean step time and stride time were determined. Mean step time was defined as the average of all step times (i.e., right and left combined) and stride time was obtained by combining each set of subsequent left and right steps together. As per previous studies, a median filter was used to remove any potential outliers (defined as step times greater than three SDs from the median) in each subject's step time series (Hausdorff and Edelberg, 1997; Kobsar et al., 2014a).

To determine stride and step regularity, an unbiased autocorrelation procedure (see **Figure 1**) was used to measure the correlation of the acceleration signal for each step (first dominant period) or stride (second dominant period) at different periods of time (i.e., phase shifts) across each of the three accelerometer axes (Moe-Nilssen and Helbostad, 2004; Kobsar et al., 2014a). Step regularity was defined as the correlation between the original acceleration signal and the acceleration signal phase shifted to the average step time, whereas stride regularity was shifted to the average stride time (Kobsar et al., 2014a). These phase shifts were consistent with the first and second dominant periods of the unbiased autocorrelation coefficient, respectively (Moe-Nilssen and Helbostad, 2004; Kobayashi et al., 2014; Kobsar et al., 2014a). Gait symmetry (*Sym*) was defined as the percent difference between the regularity of steps (*StpReg*) and the regularity of strides (*StrReg*) for each of the three axes, with zero being perfect symmetry and larger values depicting greater levels of asymmetry (the difference between the consistency of strides and the consistency of steps) in the accelerometer waveform (Kobsar et al., 2014a).

$$Symmetry = \left\{ \frac{|StpReg - StrReg|}{(StpReg + StrReg)/2} \right\} * 100$$

Consequently, the accelerometer waveforms in the vertical (V), anteroposterior (AP), and mediolateral (ML) directions were

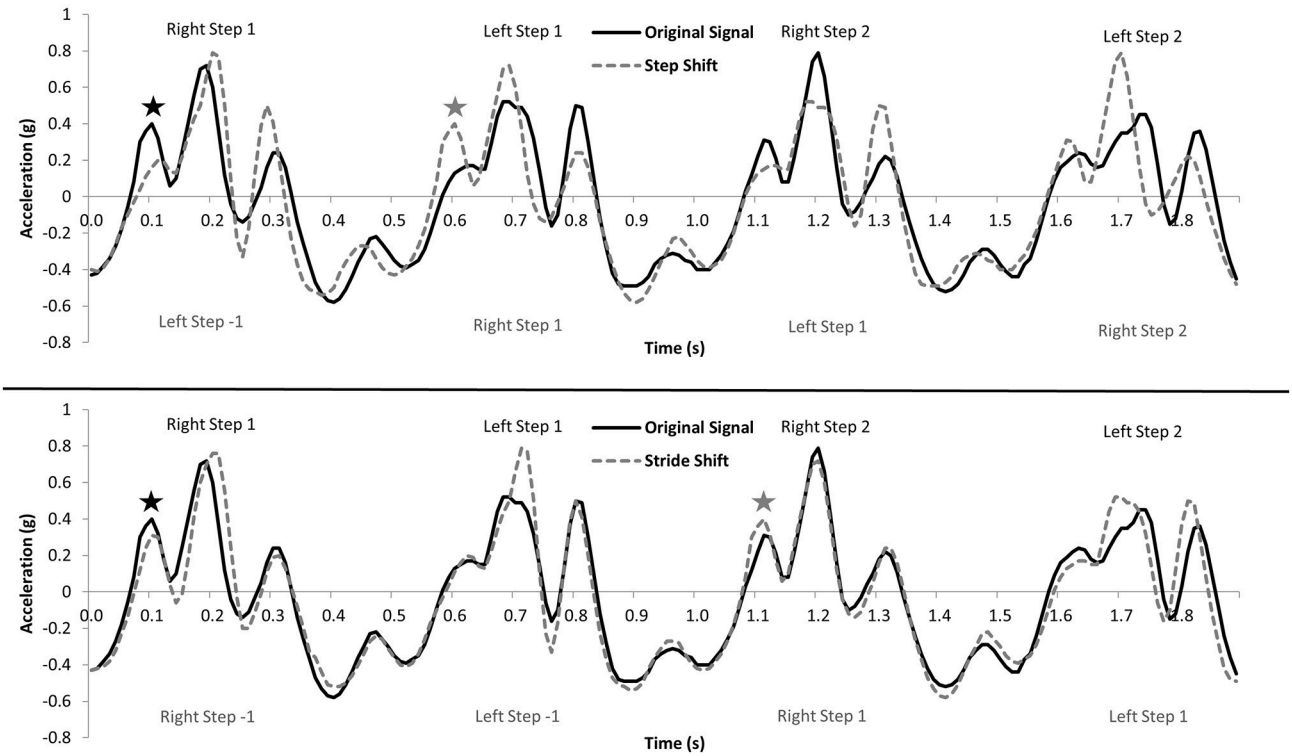

FIGURE 1 | Visual representation of the autocorrelation procedure for a series of four steps. The top panel shows the correlation between the original signal and the signal shifted equivalent to the average step time, which defines step regularity. The bottom panel shows the correlation between the original signal and the signal shifted equivalent to the average stride time, which defines stride regularity. The ⋆ shows the original and step/stride shifted waveforms in the top and bottom panels, respectively. Adapted from Kobsar et al. (2014a), with permission from Elsevier.

phase-shifted using the autocorrelation procedure to determine the step regularity (*StpV, StpAP, StpML*), stride regularity (*StrV, StrAP, StrML*) and symmetry (*SymV, SymAP, SymML*) of knee OA and control group participants.

Statistical Analysis

Separate two-way (group × sex) ANOVAs were used to compare dependent variables for participant demographics (age, height, mass, and BMI), temporal gait parameters (stride time and step time) as well as stride regularity (*StrRegV*, *StrRegAP*, *StrRegML*), step regularity (*StpRegV*,*StpRegAP*, *StpRegML*) and gait symmetry (*SymV*, *SymAP*, *SymML*). *Post-hoc* comparisons using Fisher's LSD test were used to further identify any significant interaction effects. Effect sizes (partial η^2) were determined for all comparisons according to the following categories: small (<0.06), moderate (0.06–0.14) and large (>0.14) (Cohen, 1988). All statistical analyses were performed using IBM SPSS Statistics 19.0 (SPSS Inc., Armonk, NY) with the significance level set to $p < 0.05$.

RESULTS

Mean values for age, height, mass, and BMI along with the temporal gait variables (step and stride time) for both groups are presented in **Table 1**.

Significant between group differences were found for mass [$F_{(1, 26)} = 9.65$, $p = 0.005$, $\eta_p^2 = 0.271$], and BMI [$F_{(1, 26)} = 12.01$, $p = 0.002$, $\eta_p^2 = 0.317$], indicating that participants with knee OA had a higher mass and a greater BMI than control group participants. Significant differences were also found between males and females of both groups for height [$F_{(1, 26)} = 43.00$, $p = 0.000$, $\eta_p^2 = 0.623$] and mass[$F_{(1, 26)} = 20.61$, $p = 0.000$, $\eta_p^2 = 0.442$], demonstrating that male participants were heavier and taller than their female counterparts. Mean differences between groups for stride time [$F_{(1,26)} = 2.91$, $p = .100$, $\eta_p^2 = 0.101$] and step time [$F_{(1, 26)} = 2.91$, $p = 0.100$, $\eta_p^2 = 0.101$] approached significance with moderate effect sizes, suggesting that the strides and steps of knee OA participants took longer, which is indicative of slower walking speeds.

The two-way ANOVA results for stride regularity, step regularity and gait symmetry are summarized in **Table 2**. The mean values for stride regularity, step regularity and gait symmetry for participants in both groups (for each axis) are presented in **Figure 2**. Significant group main effects were found for step regularity in the vertical [$F_{(1,26)} = 5.28$, $p = 0.030$, $\eta_p^2 = 0.169$] and anteroposterior directions [$F_{(1,26)} = 5.77$, $p = 0.024$, $\eta_p^2 = 0.182$], indicating that the steps of both males and females with knee OA were completed with less regularity (i.e., were associated with less similar waveforms) than control participants. No significant main or interaction

TABLE 2 | ANOVA results for stride regularity, step regularity and gait symmetry based on accelerometer axis (i.e., direction).

Factor	Stride regularity						Step regularity						Gait symmetry					
	V		AP		ML		V		AP		ML		V		AP		ML	
	p	η_p^2	p	η_p^2	p	η_p^2	p	η_p^2	p	η_p^2	p	η_p^2	p	η_p^2	p	η_p^2	p	η_p^2
Group	0.06	**0.13**†	0.79	0.00	0.93	0.00	**0.03***	0.17	**0.02***	0.18	0.17	0.07	0.22	0.06	0.07	**0.12**†	0.22	0.06
Sex	0.62	0.01	0.86	0.00	0.46	0.02	0.60	0.01	0.79	0.00	0.52	0.02	0.38	0.03	0.14	0.08	0.52	0.02
Group*Sex	0.99	0.00	0.57	0.01	0.24	0.05	0.83	0.00	0.60	0.01	**0.03***	0.18	0.96	0.00	0.65	0.01	0.08	**0.12**†

*V, vertical; AP, anteroposterior; ML, mediolateral. *Significant differences ($p < 0.05$) are indicated in bold. Effect sizes (partial η2) were determined for all comparisons according to the following categories: small (<0.06), moderate (0.06–0.14) and large (>0.14) (Hartmann et al., 2009). †Differences approaching significance with moderate effect sizes are indicated in bold.*

effects were found for stride regularity or gait symmetry in any of the three directions. A significant interaction effect [$F_{(1,26)} = 5.50$, $p = 0.027$, $\eta_p^2 = 0.175$] was also found for step regularity in the mediolateral direction. *Post-hoc* comparisons revealed that mediolateral step regularity was significantly higher for female controls than for females with knee OA ($p < 0.05$), whereas the difference between males was non-significant. Further, mediolateral step regularity was significantly higher for female controls than for males ($p < 0.05$), whereas the difference between males and females in the knee OA group was not significant. All significant differences were associated with large effect sizes ($\eta_p^2 > 0.14$). **Table 2** also shows that several additional comparisons (specifically, group *StrRegV,* group *SymAP,* and group*sex *SymML*) were associated with moderate effect sizes ($\eta_p^2 = 0.06$–0.14) and p-values that approached significance ($p < 0.06$, $p < 0.07$, and $p < 0.08$, respectively).

DISCUSSION

The purpose of this study was to compare the stride regularity, step regularity and gait symmetry of individuals with knee OA to age and sex-matched control participants, using an unbiased autocorrelation procedure based on data obtained from a triaxial accelerometer. It was hypothesized that males and females with knee OA would display less step and stride regularity than control participants and that their gait would be less symmetric. It was also hypothesized that male participants in both groups would have lower step regularity than females. Participants with knee OA had a higher mass and a greater BMI than control group participants ($p < 0.01$), which is consistent with the findings of other studies on knee OA (Landry et al., 2007). More importantly, the hypothesis with respect to step regularity was supported in that significant differences were found between knee OA and control group participants in the vertical and anteroposterior directions. Significant differences were also found for mediolateral step regularity between females with and without knee OA, and between males and females in the control group. To the best of our knowledge, this is the first study to have investigated stride and step regularity in individuals with knee OA using accelerometry-based autocorrelation analysis. Two other studies have investigated step and stride regularity in healthy older adults and the current findings are consistent with those results (Kobayashi et al., 2014; Kobsar et al., 2014a).

This study found significant differences in vertical and anteroposterior step regularity between participants with and without knee OA. This finding demonstrates that the similarity of step-to-step trunk acceleration waveforms was less regular (more variable) for individuals with knee OA compared to similarly-aged older adults with healthy knees. Only a limited number of studies have investigated gait variability in knee OA, and the findings of this study are generally consistent (in terms of increased variability) with the study by Kiss (2011) who found that knee OA participants demonstrated greater variability in step length, stance time, cadence, and double-support time than controls. However, these findings conflict with the results of Tochigi et al. (2012) and Yakhdani et al. (2010), who found that participants with knee OA possessed reduced variability of leg and knee motion compared to controls. In relation to this difference, it is important to note that Tochigi et al. (2012) and Yakhdani et al. (2010) not only used different methods (Sample Entropy and Lyapunov exponents, respectively), but more importantly quantified the variability of the affected limb as opposed to the variability of the approximate total body center of mass as was the case in this study. From a dynamical systems perspective, the variability of an injured limb may be inherently different from that of the center of mass during gait (Hamill et al., 2012). It is also important to note that significant differences in mass and BMI were found between knee OA and control group participants. To our knowledge, no studies have investigated the effect of body mass on step and stride regularity in older adults (or in younger adults), and as such it is not possible to know whether this had any effect on the results. Given that body mass and BMI are both important risk factors for knee OA (and are therefore common in this population), it is important that future studies take these factors into account. Further research is also needed to investigate the effect of knee OA on joint specific (knee) and total body variability to provide further insights into gait coordination and stability in this population. Additionally, a study by Lewek et al. (2006) found no difference in knee motion variability between unilateral knee OA participants and controls, but an increase in variability of the unaffected limb within the knee OA group. These mixed results demonstrate that additional research is needed to determine the relationship between knee OA and the various measures of gait variability.

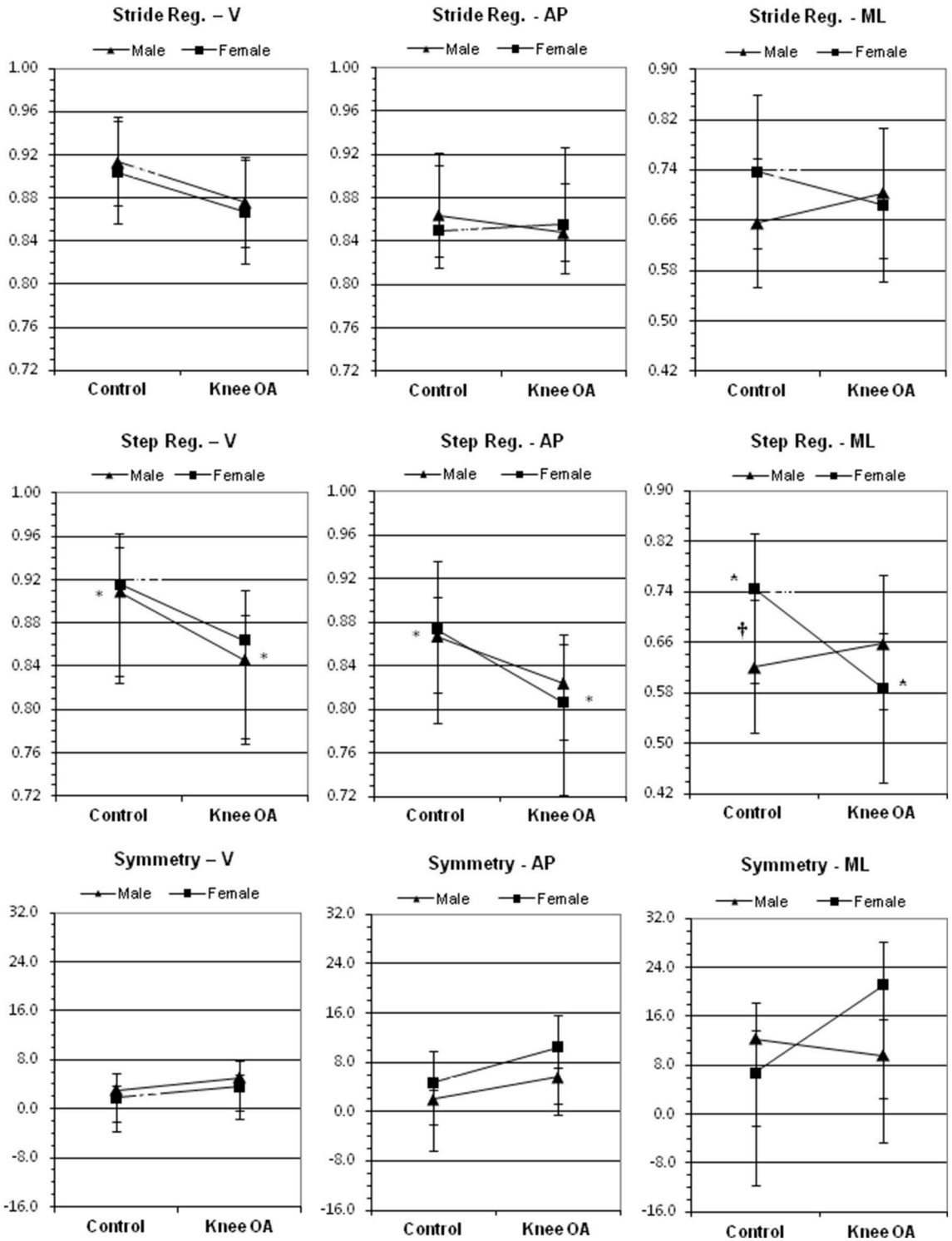

FIGURE 2 | Effects of group (control vs. knee OA) and sex (male vs. female) on stride regularity (top), step regularity (middle) and gait symmetry (bottom) in the vertical (V), anteroposterior (AP) and mediolateral (ML) directions. The * indicates a significant difference ($p < 0.05$) between groups whereas the †indicates a significant difference ($p < 0.05$) between male and female controls. Error bars = ± 1 standard deviation of the mean.

With respect to the current findings, it is important to interpret the differences in anteroposterior step regularity in combination with the differences in stride regularity (Moe-Nilssen and Helbostad, 2004). Specifically, anteroposterior stride regularity was essentially the same for both groups, whereas step regularity was significantly less for the knee OA group. Low values for step regularity in combination with similarly low values for stride regularity indicate low regularity for both steps and strides, whereas low step regularity with a higher stride regularity indicates better regularity for strides than steps, which suggests bilateral asymmetry between left and right steps (Moe-Nilssen and Helbostad, 2004). This difference between step and stride regularity is also reflected in the gait symmetry measure, which in the case of the anteroposterior direction was associated with a moderate effect size ($\eta_p^2 = 0.12$) that approached significance ($p < 0.07$). Together these findings suggest that individuals with knee OA possessed greater bilateral step asymmetry than individuals with healthy knees. This indicates that the variability of the anteroposterior trunk acceleration pattern on a step-to-step basis was greater than normal in individuals with knee OA. It is possible that this may have occurred because of differences in knee OA severity between the two limbs, resulting in a less consistent pattern of motion between right and left steps. In relation to this point, it should be noted that the participants in this study possessed bilateral knee OA, and while it might seem reasonable to speculate that a similar study on unilateral knee OA participants would find an even more pronounced difference in anteroposterior step regularity, a recent study by Mills et al. (2013b) demonstrated that bilateral joint kinematic asymmetries were more prevalent in individuals with bilateral knee OA than unilateral knee OA. Mills et al. suggested that this may occur because individuals with unilateral disease maintain kinematic symmetry further into the knee OA process than those with bilateral disease (Mills et al., 2013b). Concerning the importance of the anteroposterior direction, it has also been suggested that differences in anteroposterior stride and step regularity may reflect differences in the control of the propulsion and braking phases of gait (Kobsar et al., 2014a), whereas Moe-Nilssen et al. (2010) found that anteroposterior step autocorrelation (i.e., anteroposterior step regularity) was highly associated (negatively correlated) with step length variability. Consequently, in addition to bilateral asymmetry, it is possible that reduced anteroposterior step regularity indicates a diminished capacity to control step length in individuals with bilateral knee OA.

With respect to the difference in vertical step regularity, it is important to note that the vertical stride regularity of knee OA participants was also lower than that of the control group (which approached significance at $p < 0.06$ with a moderate effect size of $\eta_p^2 = 0.13$), suggesting that a more general lack of regularity for both steps and strides existed in this direction for those with knee OA. This is supported by the fact that the gait symmetry values for the knee OA group were lower for the vertical direction (indicating greater symmetry between steps and strides) than for the anteroposterior direction. Consequently, the findings for the vertical direction suggest a more general lack of consistency in the overall pattern of gait for individuals with knee OA. In terms of what these results might signify, it is conceivable that they could reflect inconsistencies in loading and/or differences in step time variability. Evidence exists to suggest the latter as Moe-Nilssen et al. (2010) have shown that vertical step autocorrelation (i.e., step regularity) is highly related to step time variability. Therefore, in addition to greater bilateral step asymmetry, it is conceivable that the differences in anteroposterior and vertical step regularity together indicate that individuals with knee OA possess greater step length and step time variability than participants with healthy knees. If supported by future research, these findings suggest that waist-mounted accelerometry and autocorrelation analysis could be used to conduct clinical assessments of gait variability in individuals with knee OA using a simple, non-invasive, self-paced walking test. Such assessments have the potential to evaluate differences in gait between individuals with different levels of knee OA severity, to evaluate individuals before and after knee replacement surgery and to evaluate the functional outcomes of post-surgical physical therapy. Given the advantages of using accelerometers to determine measures of gait variability (i.e., small size, low cost, collection of large amounts of data and easily placed on the body in multiple locations, not to mention their ubiquity in most modern smart phones), the potential for clinical application is substantial. This potential will be realized if future studies can demonstrate that gait variability parameters, such as step and stride regularity, have practical value as clinical outcome measures that can be applied to the assessment and treatment of knee OA.

This study also found a significant interaction effect for mediolateral step regularity, such that females with knee OA had significantly lower mediolateral step regularity than female controls, while females within the control group had significantly higher mediolateral step regularity than males. These findings were surprising because it was not hypothesized that group differences in step regularity, stride regularity or gait symmetry would be dependent on sex. For control participants, the data clearly shows that an important difference exists between males and females for both mediolateral step and stride regularity, such that males had lower step and stride regularity than females. This is in contrast to the vertical and anteroposterior directions in which the mean values were quite similar. It is interesting to note that a recent study by Kobayashi et al. (2014), which investigated step and stride regularity in young and older adults, found differences in step regularity for the vertical and anteroposterior directions between males and females in the older adult group, but not for the young group. Unfortunately, Kobayashi et al. (2014) did not provide data for the mediolateral direction, but the findings for step regularity are consistent with the current study in terms of older adult males displaying lower step regularity than females, albeit for different directions. This study did not find any differences in vertical and anteroposterior step regularity between older adult male and female controls as Kobayashi et al. (2014) did; however, it is possible that this could be the result of the small number of steps that were used to determine step and stride regularity in the Kobayashi et al. (2014) study (participants walked the length of a 7 m walkway twice, which likely amounted to approximately 20–30 steps, as opposed to the approximately 700 steps used in this study).

Given that Moe-Nilssen et al. (2010) found no relationship between mediolateral step regularity and other gait variability parameters such as step time and step length variability, it is possible that mediolateral trunk variability may serve a different purpose in locomotor control compared to the other two directions. This is consistent with the observations made by Kobsar et al. (2014a), who suggested that mediolateral step regularity may be indicative of dynamic balance control. Regardless of what the difference signifies, to our knowledge this is the first study to have found a significant difference in mediolateral step regularity between older adult males and females and between females with and without knee OA. If this parameter is representative of dynamic balance control, it suggests that older adult females have better postural stability in the mediolateral direction than men. This may occur because men on average tend to be taller than women, and in theory maintaining dynamic stability with an aging neuromuscular control system should be more challenging for those individuals with a higher center of mass. However, it is also interesting that the relationship between male and female mediolateral step regularity appears to be negated in the presence of knee OA. Given that no previous research exists on step or stride regularity in knee OA it is difficult to speculate about what the cause of this might be. Nevertheless, it can be inferred that knee OA appears to affect the consistency of mediolateral trunk acceleration patterns more for women than for men, suggesting that women with knee OA may experience a greater loss of dynamic balance control than men. It is also conceivable that mediolateral step regularity might be associated with fall risk and/or the etiology of knee OA (given that knee OA is more common in women than in men), and as such this is an important finding that should be investigated further, both in healthy older adults and in adults with knee OA.

While the main strength of this study is the use of an accelerometer-based approach to investigate step/stride regularity and gait symmetry in older adults with knee OA, there were several limitations that should be considered. First, the participants were not matched according to body mass or BMI, and given that significant differences existed between the groups for these parameters, it is conceivable that these differences may have affected the results. Second, the sample size was relatively small and limited to participants with bilateral knee OA. The sample was also heterogeneous with respect to knee OA severity (i.e., K-L grade range of 2–4), both between limbs and between participants, and as such these factors may have also affected the results. Given that this study provides preliminary evidence to suggest a relationship between knee OA and step regularity, future studies should attempt to stratify participants according to severity.

CONCLUSION

This study found that males and females with knee OA possessed significantly less vertical and anteroposterior step regularity than similarly-aged control group participants with pain-free knees. The findings suggest that the presence of knee OA affects the control of gait such that the consistency of the step pattern (more than the stride pattern) is compromised. Based on these results, it is not possible to know whether this is a direct consequence of the effects of knee OA itself (for e.g., pain and reduced range of motion), or if the increased variability is reflective of one or more compensation strategies employed by the CNS to manage the pathomechanics caused by the structural deficiencies of the joint. The study also found that mediolateral step regularity was lower for females with knee OA and lower for males than for females in the control group, suggesting that the relationship between mediolateral step regularity and knee OA is different in males and females. To our knowledge this is the first study to investigate stride regularity, step regularity and gait symmetry in individuals with knee OA, and the findings suggest that future research is needed to determine the specific aspects of gait control that are represented by these parameters (for e.g., is there a relationship between mediolateral step regularity and step width variability or dynamic balance control?). Given that this study found differences in step regularity with a relatively small number of bilateral knee OA participants, future studies (with larger sample sizes) should investigate unilateral knee OA and the effect of knee OA severity on step and stride regularity. The application of accelerometry-based gait regularity analysis for the assessment and treatment of knee OA in the clinical setting should also be investigated.

AUTHOR CONTRIBUTIONS

JB authored the manuscript and was involved with all aspects of the study, CC was involved with the data collection and analysis, DK conducted the data analysis and OB assisted with manuscript preparation and revision.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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METHODS
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Computerized Dual-Task Testing of Gait and Visuospatial Cognitive Functions; Test-Retest Reliability and Validity

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The common occurrence of age decline in mobility and cognition does cause a decrease in the level of physical activity and an increased falls risk. Consequently, dual -task (DT) assessment that simultaneously addresses both mobility skills and cognitive functions are important because, continued difficulties and fall injuries will have a sizable impact in this population. The first objective of the present study was to assess test-retest reliability of a computerized DT treadmill walking protocol and concurrent outcome measures of gait and visuospatial executive function in a group of healthy older adults. Secondly, discriminative validity was evaluated by examining the effect of DT conditions (single task vs. dual-task) on; (a) spatiotemporal gait measures (average and coefficient of variation) and (b) visuomotor and visuospatial executive performance measures. Twenty-five community-dwelling individuals median age 65 (range 61–67) were recruited from a Fitness Facility. Participants performed a computerized visuomotor tracking task and a visuospatial executive game task in standing and while treadmill walking. Testing was conducted on two occasions, 1 week apart. Moderate to high test-retest reliability (ICC values of 0.65–0.88) were observed for spatiotemporal gait variables. No significant differences between the group means were observed between test periods in any gait variable. Moderate test-retest reliability (ICC values of 0.6–0.65) was observed for measures of visuomotor and visuospatial executive performance during treadmill walking. Significant DT effects were observed for both spatiotemporal gait variables and visuospatial executive performance measures. This study demonstrates the reliability and reproducibility of the computer-based assessment tool for dual task treadmill walking. The high to moderate ICC values and the lack of systematic errors in the measures indicate that this tool has the ability to repeatedly record reliable data from community-dwelling older adults. The present computerized dual-task protocols broaden the types of standardized visuomotor and visuospatial executive activities for use with DT treadmill walking that has previously been reported.

Keywords: treadmill walking, spatiotemporal gait variables, cognitive performance, Dual-task performance, intra-class correlation coefficient

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INTRODUCTION

The frequent occurrence of mobility limitations and falls with age can arise due to singular events (e.g., stroke, peripheral vestibular dysfunction) or can have an insidious onset, with the problem source found in multiple predisposing factors, such as, the gradual decline of musculoskeletal and/or neural fitness (sensory, cognitive, motor; Santos-Eggimann et al., 2008). Walking problems and falls, in particular outdoors, become evident when compensatory strategies have failed, or where certain tasks and environmental conditions cannot be avoided (Shumway-Cook et al., 2007; Santos-Eggimann et al., 2008).

For older adults, community ambulation is strongly associated with the preservation of skills for independent living, community participation, and healthy aging (Simonsick et al., 2005). Safe, independent community walking outdoors requires both mobility skills and cognitive flexibility to address threats to balance while attending to a range of environmental demands and concurrent executive tasks. Mobility limitations and executive impairments common to aging often coexist and are prognostic of adverse health events, including falls (Santos-Eggimann et al., 2008; van Iersel et al., 2008; Herman et al., 2010; Ijmker and Lamoth, 2012). Consequently, dual- task screening and training programs that simultaneously address both mobility and cognition are important to consider in the promotion of healthy aging and in rehabilitation (Pichierri et al., 2011; Diamond, 2015; Gregory et al., 2016).

The application of digital media and computer technologies provides a number of promising approaches for dual task (DT) assessments and training. For example, a Virtual reality (VR) environments viewed during treadmill walking have been used to provide a more ecological and task-oriented approach to mobility training. Preliminary results suggest that mixed, augmented VR environments that incorporate both treadmill walking and executive tasks have the potential as a rehabilitation tool. (Mirelman et al., 2013; Park et al., 2015) The application of computer games has also received considerable interest from researchers and clinicians as a method to challenge and train many different aspects of executive functions (Anguera et al., 2013; Wolinsky et al., 2013; Rebok et al., 2014; Strenziok et al., 2014). These emerging rehabilitation technologies have the potential to improve clinical outcomes by making therapies and exercise more engaging more motivating and more effective. For this purpose, an engaging, Game-Based Rehabilitation Platform (GRP) for dual-task training with embedded assessment was developed (Szturm et al., 2013a,b). The platform provides an integrated approach to decline in balance, mobility, visuomotor and gaze control, and visuospatial executive function. The GRP consists of a standard treadmill instrumented with a pressure mapping system to record center of foot pressure, and an interactive computer game subsystem (Betker et al., 2008; Szturm et al., 2015a). The treadmill is equipped with a standard LED monitor, and thus, a broad range of visuomotor and visual-spatial executive game activities can easily be managed concurrently while treadmill walking. The GRP includes a monitoring application which uses advanced data logging and analysis method to record the client's actions and choices while playing designed rehabilitation assessment games. The game activities involve visual attention, visual search and tracking of moving visual targets, and the ability to select and interact with relevant targets and ignore/avoid distracter objects. Visuospatial processing is an important aspect of cognition to explore as a factor involved in age decline in mobility and increased fall risk (Santos-Eggimann et al., 2008; van Iersel et al., 2008; Nagamatsu et al., 2009; Murray et al., 2010). With this method both gait and visuospatial executive performance can be quantified during steady state walking at a constant velocity and over durations of 1–2 min or more, as tolerated (i.e., 40 to hundreds of consecutive steps).

Many over ground walking studies examine how information processing load affects gait rhythm or stability, (i.e., spatiotemporal gait variables (Al-Yahya et al., 2011). However, gait speed is a confounding variable, as spatiotemporal gait variables are sensitive to changes in gait speed (Kang and Dingwell, 2008; Stoquart et al., 2008; Szturm et al., 2013a; Keene et al., 2016). Most of over ground walking studies use an instrumented walkway, which records only 4–6 consecutive steps. This method may reliably measure gait speed, but is not sufficient for measures of gait variability or periodicity, particularly during dual-task walking (Bruijn et al., 2009; Hollman et al., 2010; Galna et al., 2013).

The purpose of this study is to establish the psychometric properties of the test protocols and the dual-task outcome measures of the GRP during treadmill walking. This is an important initial step before it can be routinely used clinically or in community centers for screening, fall risk assessment, and rehabilitation, as well as for preventative measures. Although, the test-retest reliability of mean values of spatiotemporal gait parameters has been assessed for reliability while walking alone, little is known about the test-retest reliability of gait variability while performing concurrent executive tasks (Brach et al., 2008; Paterson et al., 2008; Beauchet et al., 2011; Faude et al., 2012).

The first objective was to establish test-retest reliability of outcome measures that represent gait performance, visuomotor (VM) performance, and visuospatial executive function when tested during dual-task conditions. The second objective was to examine the discriminative validity of the computerized outcome measures. Specifically to examine the influence that information processing load has on gait function, and vice versa to examine the influence that physical demands of walking have on visuospatial cognition. A better understanding of the interactions between physical demands of walking and visuospatial cognition will be important for identifying high-risk scenarios that people might encounter outside the lab, and for designing effective, personalized exercise programs suitable for community applications.

METHODS

Participants

Twenty-five adults participated, 19 male and 6 female, the median age of 65 years (range 60–67) who attended a Medical Fitness Facility. The participants were able to walk outside without any walking aids and had no self-reported history of falling. Exclusion

criteria included histories of neurological or musculoskeletal disorders (e.g., stroke, hip/knee joint surgery). All participants provided written consent. The study was approved by the University of Manitoba research ethics committee. Prior to testing, each participant completed a 6-min walk test on a 300-m track, and the average walking speed was determined over a 25-m distance.

Tests and Instrumentation

Figure 1A presents the components of the treadmill platform. Participants stood on a treadmill at a viewing distance of 100 cm from an 80 cm computer monitor. The following tasks were performed while walking on a treadmill at 0.9 m/s: for 1 min:

a) Walk only (single task condition),
b) Walk while performing a Visuomotor (VM) task,
c) Walk while performing a Visuospatial Executive Game (VEG) task.

As presented in **Figure 1** the treadmill is instrumented with a pressure mat (Vista Medical, Canada) which was used to record vertical foot contact forces and to compute spatiotemporal gait variables (Betker et al., 2008). At a walking speed of 0.9 m/s, and duration of 1 min, then data for 30 consecutive steps were obtained. Before starting the tests participants walked for 5 min to acclimate to treadmill walking. Test 2 was conducted 1 week after test 1.

Visuospatial Executive Tasks

A custom computer application with the following two assessment modules was used for this study: (a) a Visuomotor (head tracking) module and (b) a Visuospatial Executive game (VEG) module (Szturm et al., 2013a, 2015a). An inexpensive, commercial motion sense mouse (Gyrations, SMK-Link, USA) was used to control and interact with the visuospatial executive games. The motion-sense mouse is small with inertial sensors which are used to derive instantaneous angular position. The motion sense mouse allows head angular rotation to be translated and interpreted as a standard USB computer mouse. Velcro secures the wireless motion mouse to a headband, and with this simple method, the head rotation is used as the pointing device

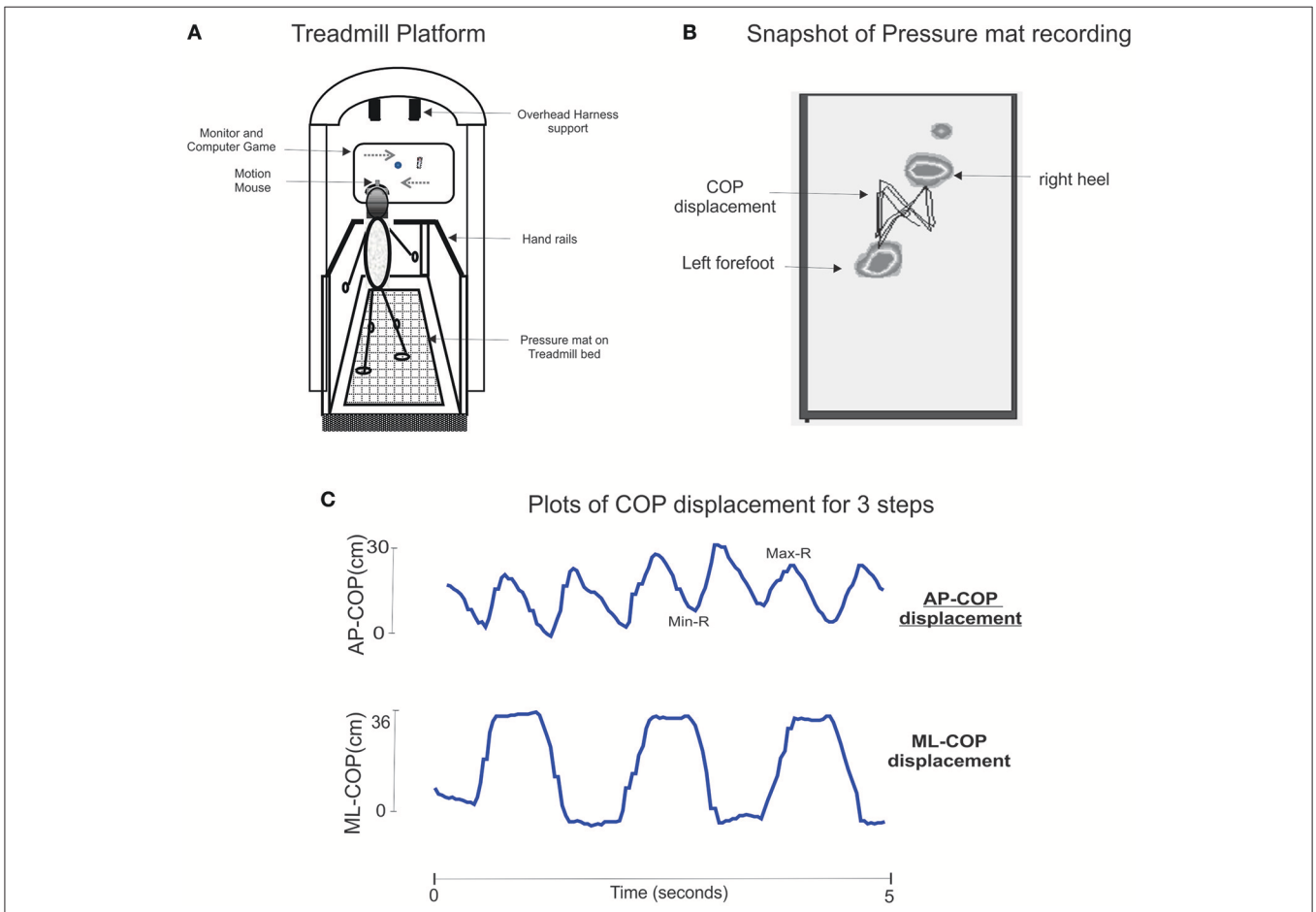

FIGURE 1 | Panel (A) is an illustration of the treadmill platform and experimental set-up. Participant is walking on the instrumented treadmill while viewing a computer monitor. Head rotation (via motion mouse) is used to interact with the visuospatial executive task. Panel **(B)** presents a snapshot of the recorded treadmill pressure mat and the trace of center of foot pressure displacement for a complete gait cycle. Panel **(C)** presents AP and ML COP time-series data for 3 steps. Maxima and minima of COP excursion for right and left steps are quantified, and use to compute swing and step times and step length.

to control the position and motion of the computer game sprite. Therefore, a hands-free computer/game controller to interact with the game activities of the assessment software is introduced. Head pointing movements are among the most natural and can easily be performed with minimal instruction and by most people.

Visuomotor (VM) Task

The goal is to align two moving objects. One object, a bright circular object, is computer controlled and moved horizontally, left and right (cyclic motion) on a computer display for 45 s. Motion frequency was 0.5 Hz and amplitude was 70% of monitor width. The second object, a square, was slaved to head rotation using the head-mounted motion sense mouse (Szturm et al., 2015a). The goal of the task is to maintain an overlap of the two objects for 45 s. The computer application generates a logged data file to record the coordinates of the circle (target) and square (head rotation) at 100 Hz. The data file is processed off-line to quantify visuomotor performance as described below. Participants were tested in one direction, (a) horizontal motion (left/right).

Visuospatial Executive Game (VEG) Task

The goal was to move a paddle (the game sprite) to interact with moving game objects. Head rotation via the motion sense mouse was used to move the game paddle and catch the target objects while avoiding distractor objects. See **Figure 2A** for illustration of the game function. The target object was a brightly colored circle and the distractor object was an oval shaped object. The target and distractor objects appear at random locations at the top of the monitor and moves to the bottom in a time period of 1.5 s and then disappear. For each game event (target appearance) the participant moves a game paddle along the bottom of the display to catch the target object and avoid any distractor objects. The game was played for 60 s or 45 game events. The software indexes the "times" for the appearance and disappearance of each target game object and logs the position coordinates of the game objects and game paddle (participant's head rotation) at a

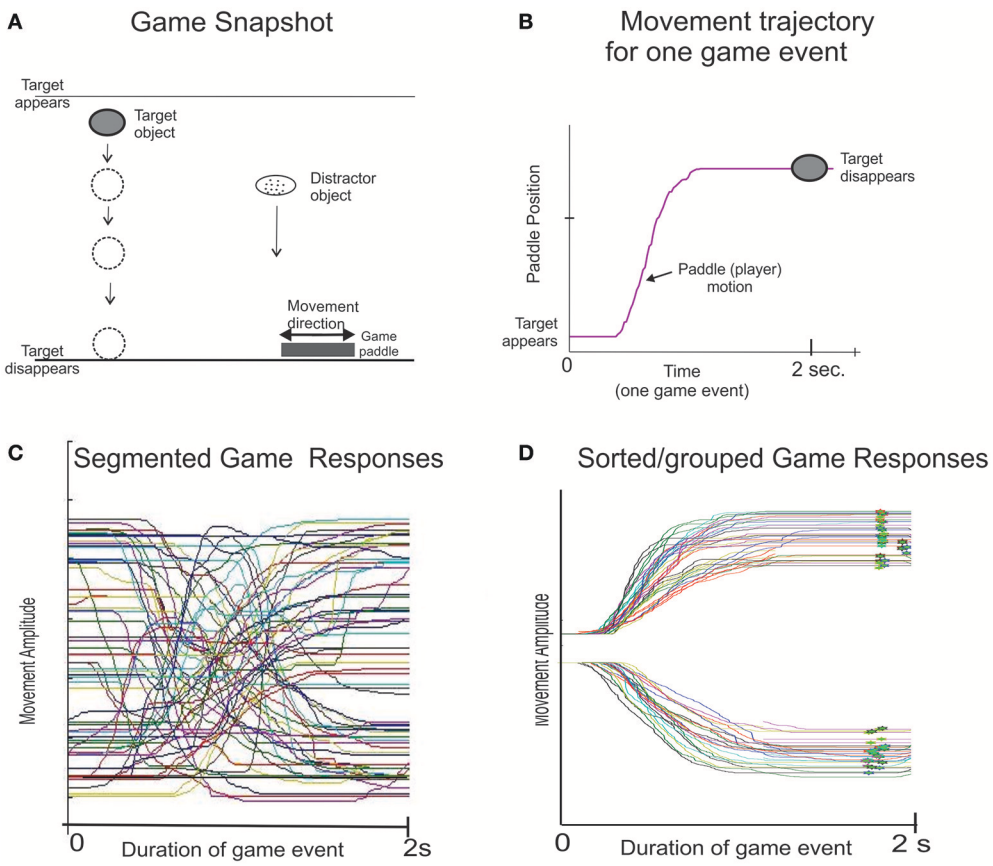

FIGURE 2 | Illustration of the game objects and motions of the visuospatial executive game. Panel **(A)** Screenshot of the VEG game software. The target appears at the top of the screen at a random location and the participant interacts with the target. Panel **(B)** presents the trajectory for one game movement response from target appearance to target disappearance panel **(C)** presents overlay trajectories of all game movement responses (as shown in panel **B**) for one game session of 60 s duration. Some game movements are upward and some downward (i.e., different movement directions), and some game movements are medium and some large amplitudes. Panel **(D)**, the game movement responses of panel **(C)** are sorted and grouped in bins, which in this case represent medium amplitude movement responses for both directions; leftward game movements (upward trajectories), and rightward game movements (downward trajectories).

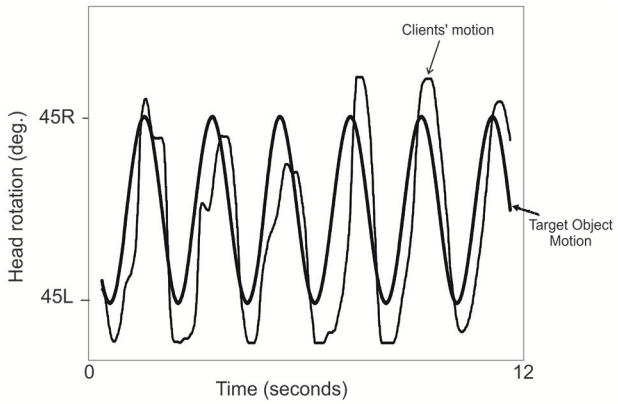

FIGURE 3 | Presents Synchronous plots of the target cursor motion and user movement trajectories (head rotation) for a typical VM tracking task. Maxima are the left most position and minima the right most position.

sampling rate of 100 Hz. The data file is processed off-line to quantify visuospatial executive performance as described below.

The visuomotor and visuospatial executive game tasks were performed in standing (baseline and during treadmill walking (dual-task condition).Prior to testing, the participants were allowed to play the tracking and game tasks while sitting for a few minutes to become familiar with each task.

The treadmill walking tasks were difficult when performing the concurrent game tasks. The treadmill was equipped with safety side rails in easy reach, and participants were fitted with a safety harness secured above to a support system. Also during all test a Physical Therapist stood behind the participants to provide assistance if required.

DATA ANALYSIS

Spatiotemporal Gait Variables

The average and coefficient of variation (COV) over 30 consecutive steps were determined for (a) right step time, (b) right single support times, and (c) right step length. Step time is defined as the time from a right foot off (beginning of left single support) to left foot off. Note analysis was also performed for left steps. Since the statistical analysis showed no significant difference in means of right and left gait variables, only the right gait variables will be presented.

Visuomotor Performance

Figure 3 presents synchronous plots of the target motion (circle) and user head rotation (square) for a typical visuomotor task. A sine-wave function of the reference target cursor waveform was determined, Head rotation trajectories were fit to the sine-wave function, and the coefficient of determination (COD) was computed based on total and the average residual difference between the position (pixel coordinates) of the target and head cursor for all sampled data points. The first two cycles of the tracking tasks were excluded to allow the participants' time to acquire the moving target and begin tracking. MATLAB (The Math Works, Natick, MA, version 2010a) was used to compute the COD.

Visuospatial Executive Performance Measures

Figure 2B presents the trajectory of an individual game movement response. Each game event was 1.5 s in duration from target appearance to target disappearance. **Figure 2C** Presents overlay trajectories of individual game movement responses in one game session. Based on time indices of target appearance and disappearance the software segments all game movement traces for each direction and game movement amplitude. The software then sorts these movement traces by direction and for medium amplitude movements (**Figure 2D**). Thus, the software produces multiple, standardized contextual movement events (Players actions) for each direction. For a detailed description of the game movement indexing and segmentation see (Lockery et al., 2011; Szturm et al., 2015a). The following variables were quantified; (a) success rate determined as the percentage of target objects that were caught, (b) average Response Time: the time from target appearance to the start of the game paddle movement and (c) average Movement Time, the time from start of the game paddle movement to the time it reaches its plateau at the point the target disappears Response Time and Movement Time were averaged over all game movement responses separately for leftward and rightward directions. Statistical analysis (paired t-test) revealed no significant difference in average response time or average movement time between leftward and right game movement responses, and therefore only averages for leftward game movements are presented in the present study.

Statistical Analysis

Relative reliability was assessed using a fixed model intra-class correlation coefficient (ICC) (Weir, 2005). The ICC scores were interpreted as high when equal to or greater than 0.70, as moderate between 0.5 and 0.69, and as low when less than 0.50 (Lexell and Downham, 2005). Absolute reliability was analyzed using standard error of measurement (SEM). Systematic errors between the test periods were evaluated using a paired t-test. Normality of data was assessed using the Shapiro-Wilks test ($n < 50$). This test revealed a normal distribution for all variable ($p > 0.1$).

Discriminative validity was evaluated using a paired t-test to examine the effect of dual-task conditions on; (a) gait performance and (b) visuomotor and visuospatial executive performance. For the VM and VEG performance measures, the single task condition is when performed in standing on a fixed surface and the DT condition is when performed during treadmill walking.

SPSS software for Windows, version 20.0 (SPSS Inc. Chicago) was used for all statistical analysis procedures.

RESULTS

Nineteen females and six males participated. The median age was 65, range 61–68 years. Group average gait speed was 1.1 m/s

and a standard deviation (SD) of 0.14, and the average distance walked in 6 min was 532 m and SD of 87. All participants walked outdoors on a regular basis, and none had reported a fall in the last year.

Table 1 presents the results of the test-retest reliability analyses for the temporal and spatial gait variables. With a few exceptions, high ICC values of 0.71–0.85 were observed for both averages and COV. Moderate ICC values were observed for average step length (0.65) during the visuomotor task, and for SL COV (0.65) when performing the executive game task. The standard error of measurement (SEM) as a percentage of the group mean values ranged from 4 to 15% and was less than 10% in the majority of cases. Based on a paired *t*-test analyses, no systematic errors in the average or COV variables were observed between the two test sessions for either the single or the two DT walk conditions. As presented in **Table 2**, moderate ICC values of 0.6–0.65 were observed for visuomotor and executive game performance measures. The SEM as a percentage of the group mean values for the visuomotor task was 15%, and for the executive game performance measures, it ranged from 5 to 11%. The results of the paired *t*-tests revealed no significant difference in visuomotor or executive performance measures between the two test periods.

Group means and 95% CI for average and COV of spatiotemporal gait variables obtained during walk only and dual-task walk conditions are presented in **Figures 4**, **5** respectively. As presented in **Table 3** all temporal and spatial gait variables did demonstrate a significant change when performing the visuospatial executive tasks (DT condition) as compared to walk alone (single task condition). Average swing time ($p < 0.01$) and average step length ($p < 0.001$) significantly decreased from single to dual-task conditions, whereas average single support time significantly increased ($p < 0.001$) from single to dual-task conditions. Group means and 95% confidence intervals (CI) are presented in **Table 1**. There was a significant increase in COV for all gait variables when performing the visuospatial executive game task as compared to walk alone ($p < 0.01$). As presented in **Table 3** the majority of gait variables did not demonstrate a significant change when performing the visuomotor task. There were two exceptions; a significant decrease in Average step length ($p < 0.001$) and a significant increase in single support time COV ($p < 0.001$) as compared to walk alone.

Figure 6 presents the group means and 95% CI for the visuomotor performance measure obtained during walk only and dual-task walk conditions. As presented in **Table 4** there was a significant decrease in visuomotor performance when tested during treadmill walking as compared to standing; ($p < 0.001$). Group means and 95% confidence intervals (CI) are presented in **Table 2**. When tested in standing visuomotor performance was 0.78 and decreased to 0.65 during walking.

Figure 7 presents the group means and 95% CI for the visuospatial cognitive performance measures obtained during walk only and dual-task walk conditions. As presented in **Table 4** there was a significant decrease in visuospatial executive performance when tested during treadmill walking as compared to standing. There was a significant decrease in success rate ($p < 0.04$), but no significant change in Response time or Movement Time when tested during treadmill walking as compared to standing. Success rate, when tested in standing, was 94%, as compared to 82% during walking.

TABLE 1 | Results of statistical analysis, ICC scores, standard error of measurement (SEM), group means and 95% confidence interval (CI) for the spatial and temporal gait parameters during the three walking conditions.

Task conditions	Test 1 Mean (95%CI)	Test 2 Mean (95%CI)	ICC	SEM
WALK ALONE				
Avg-SsT, ms	376 (359.6–392.4)	386 (369.3–402.7)	0.8	19.1
Avg-SwT, ms	457 (429.6–484.4)	478 (450.6–505.4)	0.7	40.7
Avg-SL, cm	40.4 (38.1–42.7)	41.6 (39.7–43.5)	0.8	2.9
COV-SsT	10.4 (9.48–11.3)	10.7 (9.9–11.5)	0.8	1.1
COV-SwT	12.1 (10.6–13.6)	11.5 (10–13)	0.9	0.5
COV-SL	14.7 (13.1–16.2)	15.3 (13.9–16.8)	0.8	1.6
DT-VM				
Avg-SsT, ms	401 (379.6–422.4)	393 (376.2–409.4)	0.8	30.3
Avg-SwT, ms	437 (409.6–464.4)	421 (393.6–448.4)	0.8	36.1
Avg-SL, cm	32.5 (30.7–34.3)	31.8 (30.3–33.3)	0.7	2.6
COV-SsT	13.2 (12–14.4)	13.7 (12.2–15.2)	0.7	1.5
COV-SwT	12.7 (11.5–13.9)	11.5 (10.3–12.7)	0.7	1.7
COV-SL	16.2 (14.7–17.7)	16.3 (15.2–17.4)	0.9	1.2
DT-VEG				
Avg-SsT, ms	445 (422.2–467.8)	436 (419.7–452.4)	0.7	35.1
Avg-SwT, ms	294 (281.2–306.8)	302 (288.1–315.9)	0.7	18.3
Avg-SL, cm	32.5 (30.7–34.3)	32.5 (30.8–34.2)	0.8	4.1
COV-SsT	16.2 (14.3–18.1)	19.4(17.3–21.5)	0.8	2.1
COV-SwT	19.8 (18.9–20.7)	20.0 (17.7–22.3)	0.7	1.3
COV-SL	23.9 (22.3–25.5)	23.1 (21–25.2)	0.8	2.1

SsT, single support time; SwT, swing time; SL, step length; Avg, Average; COV, coefficient of variation (%).

DISCUSSION

High ICC values (greater than 0.8) have been reported for average gait variables during overground and treadmill walking (Brach et al., 2008; Paterson et al., 2008). In the present study comparable

TABLE 2 | Results of statistical analysis, ICC scores, standard error of measurement (SEM), group means and 95% confidence interval (CI) for visuomotor and Visuospatial Executive Game tasks during treadmill walking.

Outcome measures	Test 1 Mean (95%CI)	Test 2 Mean (95%CI)	ICC	SEM
VISUOMOTOR				
COD	0.6 (0.6–0.7)	0.7 (0.6–0.7	0.7	0.1
VISUOSPATIAL EXECUTIVE GAME				
Success Rate, %	82.5 (79.5–85.5)	84 (83.3–88.7)	0.7	3.6
Avg-Response Time, ms	502 (475.5–528.5)	493 (465.9–508.1)	0.6	41
Avg-Movement Time, ms	526 (505.7–552.3)	514 (482.5–535.5)	0.6	56

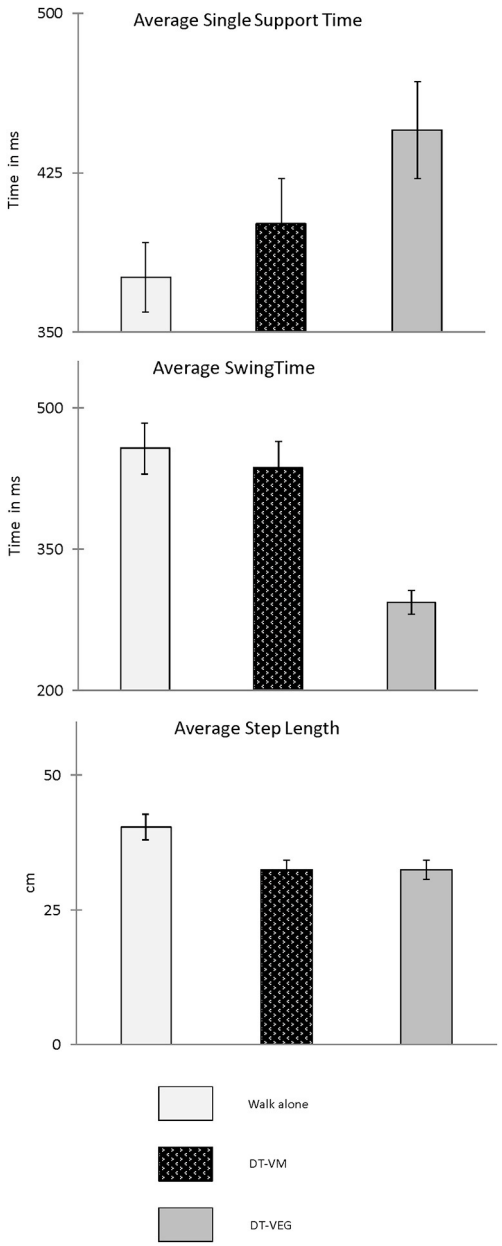

FIGURE 4 | Presented are group means and 95% confidence intervals (CI) for the average spatiotemporal gait variables (SsT, SwT, SL) obtained during walk only and dual-task walk conditions.

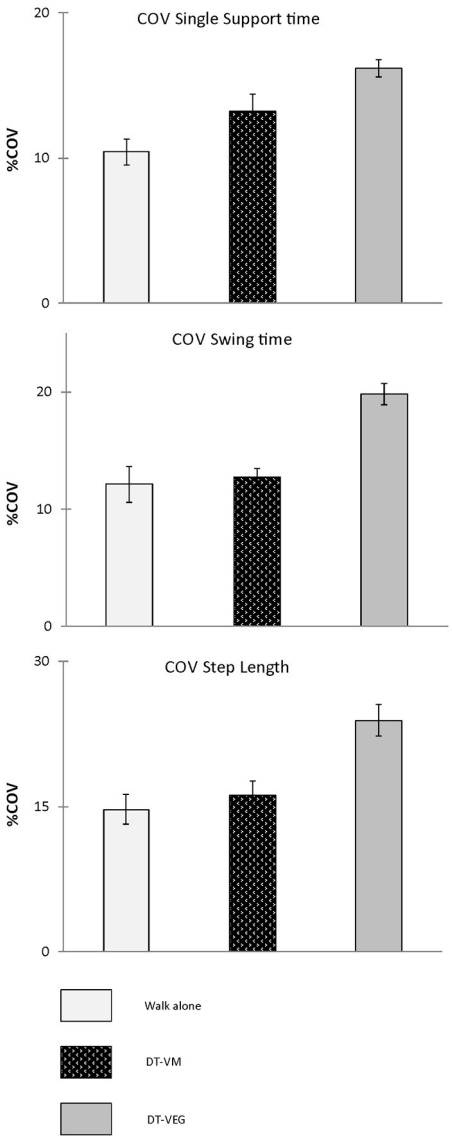

FIGURE 5 | Presented are group means and 95% CI for COV of the spatiotemporal gait variables (SsT, SwT, Sl) obtained during walk only and dual-task walk conditions.

high to moderate ICC values were observed for all average gait variables during walk alone trials. The present results extend reliability analysis to include DT treadmill walking involving computerized visuomotor and visuospatial executive tasks. A number of studies have reported low ICC values (less than 0.4) for measures of gait variation (Brach et al., 2008; Paterson et al., 2008; Faude et al., 2012). Immediate test re-test reliability was examined in older adults (mean age of 75.5 years) during an over ground DT walking test consisting of counting backward (Beauchet et al., 2011). Low ICC values of 0.28 for stride variability were observed. In contrast, the present results show modest to high ICC values for COV of gait variables during DT treadmill walking. There are a few important differences between the present study and the studies using over ground walking. In the present study participants viewed a computer monitor and performed standardized visual-spatial executive tasks for a duration of 60 s. The VEG tasks employed in the present study were executively demanding, requiring timely responses (less than 1 s) to identify a moving object as the target or a distractor, to estimate its final position, and to move the game sprite using head rotation in order to intercept the moving target, i.e., accuracy requirement. Secondly, walking speed was controlled and over 30 consecutive steps were recorded, as opposed to recordings of

TABLE 3 | Effect of dual-tasking on spatiotemporal gait variables (Average and COV).

Gait variables	Walk alone vs. Walk + visuospatial task	Walk alone vs. Walk + visuomotor task
	t-statistics, *p*-value	*t*-statistics, *p*-value
Avg-SsT	4.5, 0.01	1.9, 0.07
Avg-SwT	10.1, 0.01	1.0, 0.3
Avg-SL	8.5, 0.01	6.8, 0.01
COV-SsT	5.4, 0.01	3.7, 0.01
COV-SwT	8.1, 0.01	0.6, 0.5
COV-SL	7.8, 0.01	1.4, 0.18

Degrees of Freedom (df) = 24.

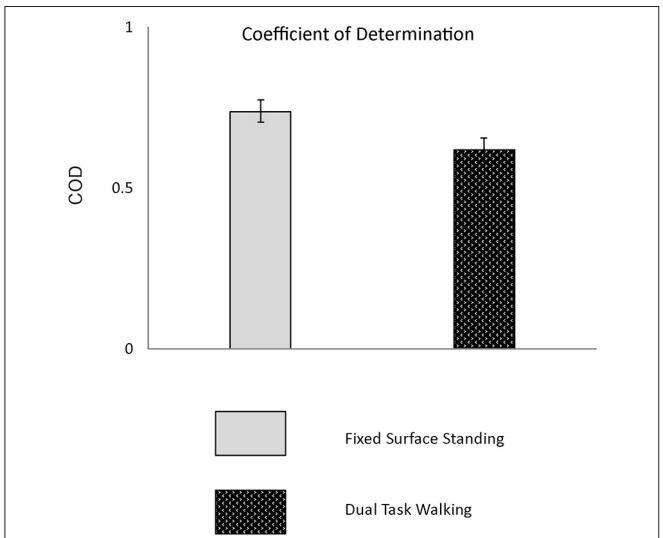

FIGURE 6 | Presented are group means and 95% CI for the visuomotor performance measure obtained during fixed surface standing and dual-task walk conditions.

TABLE 4 | Effect of dual-tasking on Visuomotor and Visuospatial executive game performance measures.

Outcome measures	*t*-statistics, *p*-value
VISUOMOTOR TASK	
Coefficient of Determination (COD)	4.5, 0.01
VISUOSPATIAL EXECUTIVE TASK	
Success Rate, %	2.3, 0.04
Avg-Response Time, ms	0.1, 0.9
Avg-Movement Time, ms	0.9, 0.4

Degrees of Freedom (df) = 24.

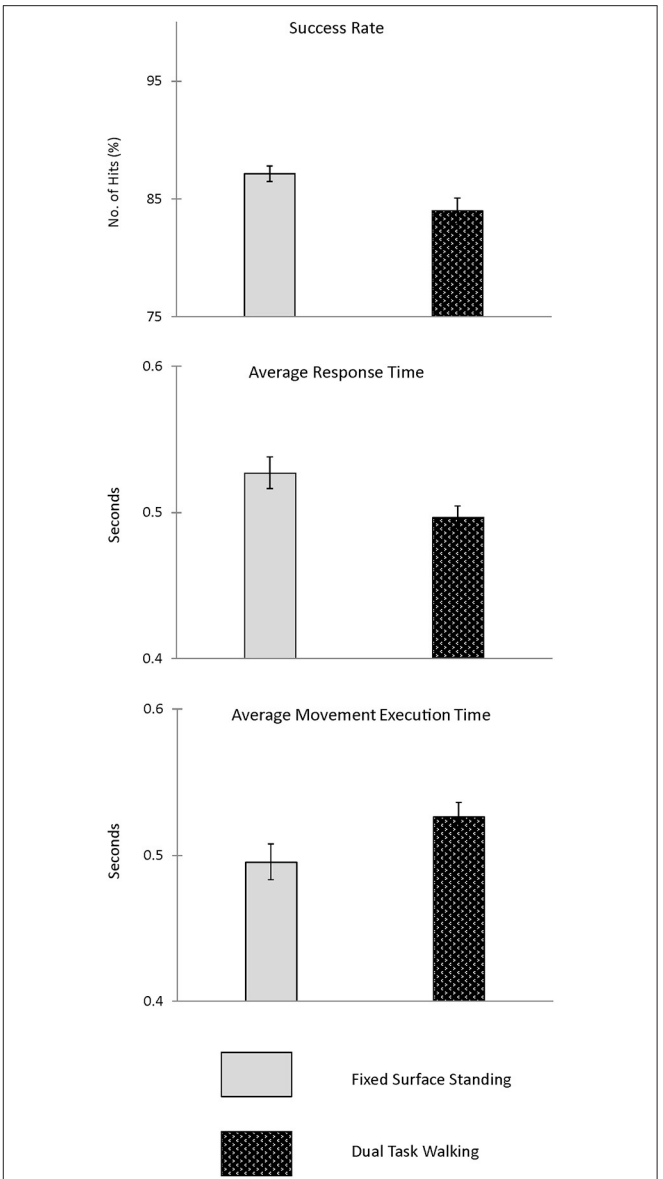

FIGURE 7 | Presented are group means and 95% CI for the visuospatial executive performance measures obtained during fixed surface standing and dual-task walk conditions.

a small number of consecutive steps on a short walkway (i.e., 3–5 m). Many studies have demonstrated that spatiotemporal gait variables are influenced by walking speed (Kang and Dingwell, 2008; Stoquart et al., 2008; Keene et al., 2016). Furthermore, it has been shown that using a continuous walking protocol instead of short intermittent walks, and collecting more than 30 steps improved reliability, in particular for measures of gait variability (Galna et al., 2013). Low between day ICC values (less than 0.4) for gait variation has been reported for active, healthy older adults (mean age of 64 years) when tested on a treadmill (Faude et al., 2012). It is not clear why this large difference (during walk alone condition) is observed between the present study and the results of (Faude et al., 2012). One difference is the walking speed of the two studies; 1.3 vs. 0.9 m/s. A lower speed was used in the present study because the addition of the visuospatial executive activities did make the walking more difficult.

The present results show a small absolute variability; SEM ranged from 4 to 15% of the mean scores and the majority were less than 10%. Taken together the moderate to high ICC values

and the small measurement error indicate that this tool has the ability to repeatedly record reliable data from active older adults, and would serve as acceptable outcome measures to examine effects of preventative measures and targeted interventions on dual-task walking performance.

Ability to recover from a sudden loss of balance is only part of the equation that governs the probability of falling; also important is what causes the instability. Besides large physical disturbances, performing a concurrent executive task can lead to a sudden change in locomotor rhythm and even falls. A number of studies have examined the interaction among physical and information processing load as a function of aging using a DT paradigm (Plummer-D'Amato et al., 2012; Xiangde, 2014). In the present study where speed is held constant all gait variables tested (average and COV) except one case were significantly affected when performing the visuospatial executive task as compared to walk alone. Average Single support time did increase when the information processing load was added. These findings for average gait variables would indicate the main effect of visuospatial processing load on locomotor rhythm. There was also a significant increase in COV for all gait variables when the visuospatial load was increased. These results are consistent with other studies which have examined dual-task effects on gait variation during overground walking in healthy young and older adults (Ijmker and Lamoth, 2012; Montero-Odasso et al., 2012). Variation of gait variables has often been used to index gait stability (Baltadjieva et al., 2006; Herman et al., 2010; Lord et al., 2011). Herman et al. (2010) reported swing time variability to be nearly 20% higher in fallers compared to non-fallers. Unlike the dual-task visuospatial trials, there was little change in gait performance during the dual-task visuomotor trials. The VM task has very simple executive demand, overlap two visible objects. This may explain why the dual-task VM trials had little effect on spatiotemporal gait variables.

A significant decrease in the Success Rate of the visuospatial tasks was observed during treadmill walking. However, Response Time and Movement Time were not affected by the increased processing demands of treadmill walking. Motor planning and temporal parameters of precision movements would not be the only factors that contribute to movement accuracy of the visuospatial task. The estimation of the final target position and control requirements of the head rotations would also contribute to movement accuracy. This is an area that will receive further investigation. The performance of the visuomotor task also decreased during treadmill walking as compared to standing. The VM task required continuous visual attention and foveation to determine the relative positions (overlap error) of 2 moving objects, and this spatial feedback would be required to maintain or restore their overlap. The significant decline in VM performance is likely due to the increase in the amount of passive head movement between standing vs. treadmill walking. There is a considerable increase in the magnitude of passive head velocity during walking, as much as 10 times of that seen during standing (Szturm et al., 2015b). Passive head motion will cause increased retinal image slip, and thus affects the ability to stabilize gaze during continuous fixation tasks, such as, tracking and interacting with moving targets (Scherer et al., 2008; Lambert et al., 2010).

Most commonly dual-task studies have utilized executive tasks, like walking while talking, verbal fluency or number subtraction that is typically only assessed qualitatively, do not involve visuospatial processing, and are limited in what individual brain areas are recruited (Al-Yahya et al., 2011).Visual attention, tracking, choice responses and the processing of object locations/trajectories and their spatial relations with respect to other objects are key aspects to consider in locomotor control and are important factors in fall risk (Bagurdes et al., 2008; Nagamatsu et al., 2009; Murray et al., 2010). The present computerized dual-task protocols broaden the types of standardized executive activities for use with treadmill walking that has previously been reported.

Study Limitations

Treadmill walking does constrain gait, for example, by the belt width, and does not reflect all aspects of over ground walking behavior (Hollman et al., 2016). The present visuospatial computer task involves both head rotation and information processing, and at this point we cannot rule out any intersegmental mechanical effect of the head rotation as a cause of the gait changes observed between the walk alone and the DT walk trials. Head rotations during the VEG task were relatively small and slow i.e., the majority of the head rotations for game responses were less than 20° and movement duration was in the order of 500 ms. Therefore, every 2 s the participant produced these small ramp head rotations. The head movements were rotations so the mass center of the head segment would not change relative to body center of mass. Duysens et al. examined COP migration during an open-loop tracking tasks (up to 30° of visual target motion) while treadmill walking (Duysens et al., 2008). Three tasks were performed; tracking with eye movements only (head stationary), tracking by rotating the head in synchrony with the moving visual target (open-loop tracking task), and tracking while rotating the trunk in synchrony with the moving visual target. The results demonstrated no significant deviation of the COP migration when participants performed the tracking task with eye or head rotation, whereas, trunk rotations led to a doubling of ML-COP deviation. The mechanical effect of head rotation on gait rhythm pacing and variation will receive further investigation.

CONCLUSION

This study demonstrates the reliability and reproducibility of the computer-based assessment tool for DT treadmill walking. The high to Moderate ICC values, the small standard errors of measurement and the lack of systematic errors in the measures indicate that this tool has the ability to repeatedly record reliable data from community-dwelling older adults Improved and affordable methods of screening and fall risk assessment in the community particularly are important because continued difficulties and fall injuries will have a sizable impact in this population.

ETHICS STATEMENT

Bannatyne Campus Health Research ethics board at the University of Manitoba (Ethics Reference number H2011:284) approved the study "Computerized Dual-task testing of gait and visuospatial cognitive functions; Test-retest reliability and validity." A written informed consent was acquired from all participants before the screening process by blind assessors. This study was carried out in accordance with the recommendations of "University of Manitoba, Bannatyne campus Health Research Ethics Board" with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the "University of Manitoba, Bannatyne campus Health Research Ethics Board."

AUTHOR CONTRIBUTIONS

TS and VS: study concept and design; acquisition, analysis, and interpretation of data; preparation of the manuscript. AK: Acquisition, analysis, and interpretation of data; preparation of the manuscript. MN: Analysis, and interpretation of data; preparation of the manuscript.

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METHODS
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Guidelines for Assessment of Gait and Reference Values for Spatiotemporal Gait Parameters in Older Adults: The Biomathics and Canadian Gait Consortiums Initiative

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Background: Gait disorders, a highly prevalent condition in older adults, are associated with several adverse health consequences. Gait analysis allows qualitative and quantitative assessments of gait that improves the understanding of mechanisms of gait disorders and the choice of interventions. This manuscript aims (1) to give consensus guidance for clinical and spatiotemporal gait analysis based on the recorded footfalls in older adults aged 65 years and over, and (2) to provide reference values for spatiotemporal gait parameters based on the recorded footfalls in healthy older adults free of cognitive impairment and multi-morbidities.

Methods: International experts working in a network of two different consortiums (i.e., Biomathics and Canadian Gait Consortium) participated in this initiative. First, they identified items of standardized information following the usual procedure of formulation of consensus findings. Second, they merged databases including spatiotemporal gait assessments with GAITRite® system and clinical information from the "Gait, cOgnitiOn & Decline" (GOOD) initiative and the Generation 100 (Gen 100) study. Only healthy—free of cognitive impairment and multi-morbidities (i.e., ≤ 3 therapeutics taken daily)—participants aged 65 and older were selected. Age, sex, body mass index, mean values, and coefficients of variation (CoV) of gait parameters were used for the analyses.

Results: Standardized systematic assessment of three categories of items, which were demographics and clinical information, and gait characteristics (clinical and spatiotemporal gait analysis based on the recorded footfalls), were selected for the proposed guidelines. Two complementary sets of items were distinguished: a minimal data set and a full data set. In addition, a total of 954 participants (mean age 72.8 ± 4.8 years, 45.8% women) were recruited to establish the reference values. Performance of spatiotemporal gait parameters based on the recorded footfalls declined with increasing age (mean values and CoV) and demonstrated sex differences (mean values).

Conclusions: Based on an international multicenter collaboration, we propose consensus guidelines for gait assessment and spatiotemporal gait analysis based on the recorded footfalls, and reference values for healthy older adults.

Keywords: gait, aged, guidelines, reference values

INTRODUCTION

Gait—the medical term used to describe the human locomotor movement of walking in healthy adults—is simple in terms of execution, but complex in terms of biomechanics and motor control (Nutt et al., 1993; Zajac et al., 2002; McCann and Higginson, 2008; Dicharry, 2010; Kuo and Donelan, 2010). Gait is usually considered as a dynamic balance condition in which the body's center of gravity is maintained within a slight base of support while moving (Farley and Ferris, 1998; Dicharry, 2010; Kuo and Donelan, 2010). During the past decade, it has been highlighted that even the simplest walking condition, such as straight-line walking at a comfortable steady-state pace without any disturbance, involves important cortical networks and cognitive functions (Alexander and Crutcher, 1990; Seidler et al., 2010; Zwergal et al., 2012; Beauchet et al., 2015b, 2016).

Numerous studies show that gait changes over an individual's lifetime (Nutt et al., 1993; Hausdorff et al., 1996; Nutt, 2001; Verghese et al., 2006; Montero-Odasso et al., 2012). Although, gait disorders are common in older (i.e., >65 years) adults, they are not unavoidable. With aging, there are physiological changes in the sensorimotor systems, which when combined with adverse effects of chronic diseases, may cause gait disorders (i.e., a deviation of normal gait performance leading to gait instability and related adverse health consequences; American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Nutt, 2001). Gait disorders in old age are a risk factor for falls and are associated with increased morbidity, mortality, loss of independent living, disability, altered quality of life, and as such can lead to increased health care expenditures (Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011). The prevalence of gait disorders can be as high as 80% in the oldest-old (i.e., >85 years) age category and gait disorders represent a major worldwide concern based on their expanding prevalence (American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Verghese et al., 2006; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011).

The assessment of gait characteristics in older adults has enhanced our understanding of the mechanisms of gait disorders, which have been helpful in developing preventive and curative interventions (Nutt, 2001; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011). Clinical gait assessment has typically been based on visual observation (Nutt, 2001). However, this approach has two main limitations. First, visual observation depends on the background and experience of the clinician who performs the gait assessment, which explains the poor inter-rater reliability of this approach (Eastlack et al., 1991; Kressig et al., 2006). Second, a limited amount of information is collected, which limits the possibility of detecting gait impairments at an early stage as well as understanding the disorganization of gait control (Kressig et al., 2006; Montero-Odasso et al., 2012). The use of quantitative

and standardized clinical tests, such as the Timed Up & Go (TUG) test has been shown to be useful as a complement to visual gait observation (Podsiadlo and Richardson, 1991). Indeed, it improves the inter-rater reliability of gait assessment and provides a common objective language that facilitates exchanges between clinicians and researchers. However, it is insufficient in detecting relevant subtle gait abnormalities like changes in gait variability (Kressig et al., 2006; Beauchet et al., 2014a). For instance, an increase in stride time variability (STV) has been identified as the best motor phenotype of cognitive decline in older adults, suggesting that increases in STV could be used to improve the prediction of dementia such as Alzheimer Disease (AD; Montero-Odasso et al., 2012; Beauchet et al., 2014a). It has been proposed that subclinical gait changes may be used as a surrogate marker of development of future diseases or adverse clinical outcomes, such as falls or disability (Verghese et al., 2009; Rao et al., 2011; Ayers et al., 2014; Beauchet et al., 2014a; Artaud et al., 2015).

Currently, advanced technology has changed the practice of gait analysis because it surpasses the limits of clinical observation (i.e., visual observation and standardized test) of gait and is easily accessible and feasible (Webster et al., 2005; Beauchet et al., 2008). The initial trade-off between the accuracy of gait measuring systems and their clinical use due to cost, labor-intensity, and time consumption has disappeared. There are numerous validated and user-friendly portable gait analysis systems, like electronic gait mats, insole footswitch systems and body worn inertial sensor systems that allow objective gait parameters to be easily obtained at low cost (Kressig et al., 2006; Beauchet et al., 2008). Gait analysis systems may be separated into three categories: the first includes non-wearable sensors and consists of devices based on image processing and pressure-sensitive floor sensors, such as the GAITRite® system, which provided all spatiotemporal parameters based on the recorded footfalls. The second category includes wearable sensors such as pressure-sensitive insoles and body worn accelerometers/inertial measurement units (IMUs), with this last category providing the opportunity to analyse gait outside the laboratory and obtain information about gait during the individual's everyday activities. The third category of devices includes a combination of both previous systems. Though promising, the research on gait characteristics derived from wearable sensors in free living situations is still in its infancy. It is therefore too early to give strong recommendations on gait assessment and on the protocols that should be used to derive reliable and valid information about gait from these systems.

While this is an important advancement for researchers, as well as for patients and clinicians, it presents a new challenge based on a combination of different issues: (1) the lack of consensus on which gait parameters to assess and their clinical relevance; (2) the lack of a consensus concerning data acquisition; (3) the lack of standardized data from a large number of people to correctly define reference values related to healthy aging; (4) the excessive fragmentation, dispersion and confinement of data, skills, and knowledge of teams of researchers and/or clinicians; (5) and finally the lack of sufficient research funding in science and medicine. The successful future of scientific and medical research in the field of gait disorders mainly depends on sharing and/or pooling of resources, research and databases between teams. Hence, there is an emergence of networks with a common interest to provide mutual assistance and useful information. Recently, two networks have been formalized, with the aim of helping clinicians and researchers to increase their knowledge and improve the field of age-related gait disorders by sharing knowledge and data sets: these are (1) the Biomathics (Beauchet et al., 2014c) and (2) the Canadian Gait Consortium. Both consortiums connect academic research teams working on age-related gait changes, and share their databases in order to compound a larger, more comprehensive and representative database. This provides fast and comprehensive answers to research questions with minimal additional financial resources and large population-based samples. Furthermore, it is likely that some objectives identified in a specific study may be relevant to other teams, and at the very least the initial investigators can respond to queries of a secondary team. In such cases, the requesting team launches an initiative within the consortium and contacts all team members who may be able to help. Willing researchers are included in the initiative to participate in the research, contribute to the collaborative publication and be included in the list of co-authors depending on their contribution to the study and the number of included participants. For instance, the Biomathics consortium recently focused on gait disorders in older individuals with cognitive decline: the objective was to compare spatiotemporal gait parameters based on the recorded footfalls in cognitively healthy individuals (CHIs), individuals with amnestic (aMCI) and non-amnestic mild cognitive impairment (naMCI), and individuals with mild and moderate stages AD and non-Alzheimer's disease (non-AD; Allali et al., 2016). They merged databases for a first initiative called "Gait, cOgnitiOn & Decline" (GOOD), which involved 2717 participants and represented the largest database in this field of research. The GOOD study demonstrated that spatiotemporal gait parameters are more disturbed in the advanced stages of dementia with worse performance in the non-AD dementias than in AD. These results suggest that quantitative gait parameters may be used for improving the accuracy of classifying dementia (Allali et al., 2016), as well as supporting clinical follow-ups that try to prevent adverse events such as falls or disability.

This first initiative underscored the requirement of utilizing standardized assessment when performing spatiotemporal gait analysis. Although, some reference values for gait parameters in older adults already exist (Oberg et al., 1993; Oh-Park et al., 2010; Bohannon and Williams Andrews, 2011; Hollman et al., 2011; Hass et al., 2012), this first initiative demonstrated that there is a need for quantitative reference values of spatiotemporal gait parameters for large numbers of healthy older adults. Importantly, older adults are considered to be healthy when they are free of cognitive deficits and comorbidities. Combining and integrating evaluations performed in populations from different countries is crucial for the development of future research on gait disorders. Indeed, the definition of gait disorders requires comparisons with quantitative reference values for spatiotemporal gait parameters in healthy older adults with diverse social, cultural, ethnic, and demographic backgrounds. Based on this first experience of the GOOD initiative, the Biomathics and Canadian Gait Consortiums decided to launch

an initiative with the following aims: (1) to give consensus guidance for clinical and spatiotemporal gait analysis based on the recorded footfalls in older adults aged 65 years and over, and (2) to provide reference values for spatiotemporal gait parameters based on the recorded footfalls in healthy older (i.e., >65 years) adults free of cognitive impairment and multimorbidities.

METHODS

Guidelines for Clinical and Spatiotemporal Gait Analysis Based on the Recorded Footfalls in Older Adults Aged 65 Years and Over

The guidelines for clinical and spatiotemporal gait analysis based on the recorded footfalls in older adults followed the usual procedure of formulation of a consensus finding, consisting of a three-step process (Annweiler et al., 2015). In the first step, between May and October 2015, the lead author (OB) invited members of the Biomathics and Canadian Gait Consortiums composed with experts of gait disorders in aging, to form a group. The members of both consortiums are experts in gait and/or movement and are presented in **Table 1**. In a second step from July 2015 to May 2016, all experts communicated by email, phone calls or videoconferencing with the first author to identify items required for spatiotemporal gait analysis in older adults. The first author, as the leader of both consortiums, contacted each member to explain the initiative, obtain their agreement to the consensus procedures, and propose an initial version of the guidelines. Each member of the consortium formulated changes and/or proposed additional information. The first author merged all changes and wrote the second version of the guidelines. All experts reviewed this version and finally a consensual

TABLE 1 | Composition of Biomathics and Canadian Gait Consortiums.

Country/Canadian province	Town	University	Centre	Reference person
BIOMATHICS CONSORTIUM				
Australia	Hobart	University of Tasmania	Menzies Institute of Medical Research	Michele L Callisaya; PhD
	Melbourne	University of Melbourne & Western Health	Australian Institute for Musculoskeletal Science	Gustavo Duque; MD, PhD
	Victoria	Monash University	Department of Medicine	Velandai Srikanth; PhD
Belgium	Antwerp	University of Antwerp	Department of geriatrics and department of primary and interdisciplinary care (ELIZA)	Anne-Marie De Cock; MD
	Liege	University of Liege	Department of Geriatrics	Sylvie Gilain; MD
France	Angers	University of Angers	Department of Neuroscience, Geriatrics division	Cyrille P Launay; MD, PhD
Japan	Chiba-ken	University of Health and Welfare	Department of Physical Therapy, School of Health Sciences at Narita International	Ryuichi Sawa; PhD
Luxembourg	Luxembourg-city	Zitha Senior	Centre for Memory and Mobility	Jean-Paul Steinmetz; PhD
Norway	Trondheim	Norwegian University of Science and Technology	Department of Neuromedicine and Movement Science	Jorunn L. Helbostad; PT, PhD
USA	New York	Yeshiva University	Department of Neurology, Division of Cognitive & Motor Aging	Joe Verghese; MD, MBBS
Switzerland	Basel	University of Basel	Basel University Center for Medicine of Aging	Reto W. Kressig; MD
	Geneva	University of Geneva	Department of Neurology	Gilles Allali; MD, PhD
CANADIAN GAIT CONSORTIUM				
Alberta	Edmonton	University of Alberta	Department of Medicine, Division of Neurology	Richard Camicioli; MD, PhD
British Columbia	Vancouver	University of British Columbia	Aging, Mobility, and Cognitive Neuroscience Lab Djavad Mowafaghian Centre for Brain Health	Teresa Liu-Ambrose; PT, PhD
Manitoba	Winnipeg	University of Manitoba	College of Rehabilitation Sciences	Tony Szturm; PT, PhD
Quebec	Montreal	University of Concordia	Perform institute	Louis Bherer; PhD
		University of McGill	Department of Medicine, Division of Geriatrics, Jewish General Hospital	Olivier Beauchet; MD, PhD
		University of Montreal	Institut universitaire de gériatrie Montreal Heart Institute Research Center and Departement of Medicine	Sébastien Grenier; PhD Louis Bherer; PhD
	Sherbrooke	University of Sherbrooke	Research Centre on Aging	Léonard Guillaume; PhD
New Brunswick	Fredericton	University of New Brunswick	Richard J. Currie Center	Victoria L. Chester; PhD
Saskatchewan	Regina	University of Regina	Neuromechanical Research Centre, Faculty of Kinesiology and Health Studies	John M. Barden; PhD

agreement was obtained. A dataset of common items divided into three categories was selected: demographic characteristics, clinical characteristics, and gait characteristics. Furthermore, a standardized procedure for spatiotemporal gait analysis based on the recorded footfalls was defined and two types of datasets were individualized: a minimum dataset corresponding to items required for all gait analysis in older individuals, and a full dataset corresponding to items of the minimum dataset plus additional items recorded when possible and for specific purposes. All selected items are shown in **Table 2**.

Quantitative Reference Values for Spatiotemporal Gait Parameters Based on the Recorded Footfalls

Participant Selection

Data were extracted from two databases: the GOOD initiative (Clinical trials registration number: NCT02350270) (Allali et al., 2016) and the Generation 100 (Clinical trials registration number: NCT01666340) (Stensvold et al., 2015). The GOOD initiative was based on a cross-sectional design such that the main objective was to compare spatiotemporal gait characteristics based on the recorded footfalls of CHIs, and participants with MCI or dementia. Data collection, study procedures and criteria for categorization of participants have been described in detail elsewhere (Allali et al., 2016). In brief, data from seven countries (Australia, Belgium, France, India, Luxembourg, Switzerland, and the United States) were merged. Data sources were the "Tasmanian Study of Cognition and Gait" (TASCOG) (Tasmanian), the Mechelen memory clinic database (Belgium), the "Gait and Alzheimer Interactions Tracking" (GAIT) study (France), the "Kerala-Einstein Study" (KES) (India), the Center for Memory and Mobility (Luxembourg), the "Central Control of Mobility in Aging" (US), and the Basel mobility center (Switzerland).

The Generation 100 study is a population-based large randomized controlled clinical trial (Stensvold et al., 2015). The primary aim of this study is to examine the effects of 5 years of exercise training on mortality in the elderly (Stensvold et al., 2015). The data collection and study procedures have been described in detail elsewhere (Stensvold et al., 2015). In summary, it is an ongoing phase IIb clinical trial. The participants are stratified by sex and marital status and randomized 1:1 into an exercise training group or a control group. They are assessed at baseline and at follow-up after 1, 3, and 5 years. For this analysis, we used the data collected at baseline.

Exclusion criteria for the present study were age <65 years, non-Caucasian, cognitive decline (i.e., MCI and dementia), walking with personal assistance, polypharmacy defined as more than 3 therapeutic drug classes taken daily, history of falls in the past 12-month period, the presence of depressive and/or anxiety symptoms, moderate or severe distance vision impairment (when information was accessible), and absence of spatiotemporal gait data. From the 2,717 participants initially recruited in the GOOD initiative, 548 (20.2%) healthy older adults met the inclusion criteria. A total of 457 (29.7%) participants from the 1,541 participants who had a gait assessment at baseline in the Generation 100 study met the inclusion criteria. Fifty-one of the 1005 (19.7%) identified participants were excluded because of incomplete gait data. Finally, 954 participants were included in the analysis.

Assessment

Age, sex, and anthropometric measures (i.e., height in metres and weight in kilograms) were recorded. Body mass index (BMI, in kg/m^2) was also calculated. Spatiotemporal gait parameters based on the recorded footfalls were measured during steady-state walking using the GAITRite®-system. This gait system is an electronic walkway with an integrated pressure-sensitive electronic surface connected to a portable computer via an interface cable. The GAITRite®-system is a well-established method of quantifying gait and provides reliable and accurate measures of spatiotemporal gait parameters. Spatiotemporal gait parameters have shown excellent test-retest reliability in clinical and research settings in community-dwelling older people when using the GAITRite®-system (Brach et al., 2008). During the past decade over 100 manuscripts have been published using data collected and processed with the GAITRite® system.

The active recording area of the gait mats ranged from 4.6 m (TASCOG study) to 7.9 m (GAIT study). Participants completed one (GAIT, CCMA, and KES studies; the Mechelen memory clinic, the Centre for Memory and Mobility of Luxembourg-city, The Basel mobility center), two (Generation 100 study) or six (TASCOG study) trials at their usual self-selected walking speed in a quiet, well-lit environment, wearing their own footwear. The mean of the 2 (the Generation 100) or 6 trials (the TASCOG studies) was used to calculate the gait variables. The mean value and coefficient of variation [CoV = (standard deviation/mean) × 100] of the spatiotemporal gait parameters were used as outcomes. For a list of the included spatiotemporal variables, see **Table 2**.

Standard Protocol Approvals and Registrations

Each site involved in this study obtained approval from their local ethics committee to conduct site-specific assessments: the Southern Tasmanian Health and Medical Human Research Ethics Committee for the TASCOG study (Australia), the ethics committee of Angers University hospital for the GAIT study (France), the ethics committee of Emmaus—St Maarten General Hospital Mechelen for the Mechelen memory clinic database (Belgium), the institutional ethics committee of Baby Memorial Hospital for KES study (India), the ethics committee of Luxembourg for the Center for Memory and Mobility database (Luxembourg), the ethics committee of Albert Einstein College of Medicine for the "Central Control of Mobility in Aging" (US) study, and the ethics committee of Basel for the Basel mobility center database (Switzerland). The ethics committee of Angers (France) University hospital approved the GOOD initiative (2014/17). The regional committee of Mid Norway for Medical and Health Research Ethics approved the transfer and the merging (number 2015/1797) of the Generation 100 database with the GOOD database.

TABLE 2 | Selected items for gait analysis in the elderly.

Items for the minimum dataset	Additional items for the full dataset
DEMOGRAPHIC CHARACTERISTICS	
Age (year)	
Sex	
Ethnicity coded as follows: 1, Black; 2, Caucasian; 3, Asian; 4, Other	
CLINICAL CHARACTERISTICS	
Height (m)	
Weight (kg)	
Medication; Number of therapeutic classes used per day >3 (coded yes vs. no)	
	Number of therapeutic classes taken daily
	Use of psychoactive drugs (i.e., benzodiazepines, antidepressants, neuroleptics) (coded yes vs. no)
History of falls (i.e., defined as an event resulting in a person coming to rest unintentionally on the ground or at another lower level, not as the result of a major intrinsic event or an overwhelming hazard) in the previous 12-month period (coded yes vs. no)	Recurrent falls (i.e., ≥2) (coded yes vs. no) Severe falls (i.e., fractures, cranial trauma, large and/or deep skin lesions, post-fall syndrome; inability to get up; time on ground ≥1 h; hospitalization) (coded yes vs. no). Fear of falling (Are you afraid of falling? Never, almost never, sometimes, often, and very often)
Neurological diseases:	
• Dementia (coded yes vs. no)	• Cognitive complaint (coded yes vs. no)
	• Mild cognitive impairment (coded yes vs. no)
	• Dementia (coded yes vs. no), if yes stage (i.e., mild, moderate, severe) and etiology (i.e., AD, non-AD neurodegenerative, non-AD vascular, mixed)
	• Global cognitive performance: MoCA score (Nasreddine et al., 2005)
• Other (coded yes vs. no)	• Parkinson's disease or parkinsonian syndromes (coded yes vs. no)
	• Idiopathic normal pressure hydrocephalus (coded yes vs. no)
	• Cerebellar disease (coded yes vs. no)
	• Myelopathy (coded yes vs. no)
	• Peripheral neuropathy (coded yes vs. no)
Depressive symptoms (coded yes vs. no)	4-item Geriatric Depression Scale score (Shah et al., 1997)
Anxiety symptoms (coded yes vs. no)	5-item Geriatric Anxiety Inventory (Byrne and Pachana, 2011)
Major orthopedic diagnoses (e.g., osteoarthritis) involving the lumbar vertebrae, pelvis or lower extremities (coded yes vs. no)	
Vision disorders (coded yes vs. no)	Distance binocular vision measured at 5 m with a standard scale, vision assessed with corrective lenses if needed
Lower limb proprioception disorders (coded yes vs. no)	Lower limb proprioception evaluated with a graduated tuning fork placed on the tibial tuberosity: The mean value obtained for the left and right sides (/8)
Muscle strength impairment (coded yes vs. no)	Hand grip strength: mean value of the highest value of maximal isometric voluntary contractions (3 trials) measured with computerized dynamometers expressed in Newtons per square meter
Use of walking aid (coded yes vs. no)	
GAIT CHARACTERISTICS	
Clinical analysis	
Subjective self-reported difficulties (coded never, almost never, sometimes, often, and very often)	
Clinical gait abnormalities (coded yes vs. no)	
Timed Up & Go score (s) (Podsiadlo and Richardson, 1991)	Timed Up & Go imagined form score (s) (Beauchet et al., 2010)
Walking speed: time to walk 4 m at steady-state walking	

(Continued)

TABLE 2 | Continued

Items for the minimum dataset	Additional items for the full dataset
Spatiotemporal analysis	
• Conditions	
✓ In a quiet, well-lit environment	
✓ Steady state walking (acceleration and deceleration phase of 1 m each)	
✓ Wearing participant's own footwear	
✓ Usual self-selected walking speed	
	• Fast walking speed
	• Dual tasking:
	✓ Backward counting by ones from 50
	✓ Verbal fluency task (animal names)
• Parameters	
✓ Walking speed [mean value (cm/s)]	
✓ Stride time [mean value (ms) and coefficient of variation (%)]	
✓ Swing time [mean value (ms) and coefficient of variation (%)]	
✓ Stride width [mean value (cm) and coefficient of variation (%)]	
	• Stride length [mean value (cm) and coefficient of variation (%)]
	• Stance time [mean value (ms) and coefficient of variation (%)]
	• Single support time [mean value (ms) and coefficient of variation (%)]
	• Double support time [mean value (ms) and coefficient of variation (%)]
	• Stride velocity [mean value (cm/s) and coefficient of variation (%)]

m, meter; kg, kilogram; s, second; cm, centimeter.

Statistics

Participants' baseline characteristics were summarized using means and standard deviations or frequencies and percentages. Participants were separated into three age groups (65–74 years, 75–84 years, and $\geq$85 years), and each group was dichotomized by sex. First, between-group comparisons were performed using unpaired *t*-test or Mann–Whitney tests, as appropriate. $P < 0.0006$ were considered as statistically significant after adjustments for multiple comparisons ($n = 79$). Second, multiple linear regressions showing the association of each spatiotemporal gait parameter (dependent variable) with age and sex (independent variable), adjusted for BMI and test center were performed. $P < 0.05$ were considered as statistically significant. All statistics were performed using SPSS (version 15.0; SPSS, Inc., Chicago, IL).

RESULTS

Guidelines for Clinical and Spatiotemporal Gait Analysis Based on the Recorded Footfalls

Two complementary sets of standardized information were identified: a minimal data set and a full data set. All items of both sets are shown in **Table 2**. They have been separated into three categories: demographic, clinical, and gait characteristics. This last category has been divided into clinical and spatiotemporal gait analysis based on the recorded footfalls.

Demographic and Clinical Characteristics

Demographic (i.e., age in years, sex and ethnicity) and anthropometric items [height in meters (m), weight in kilograms (kg), body mass index (BMI) in kg/m^2], are required because each may influence spatiotemporal gait parameters (American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Kressig et al., 2006; Verghese et al., 2006; Beauchet et al., 2008; Dicharry, 2010; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011). Given that the burden of disease can influence gait performance, it was decided to record this information as well (American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011). Different scales have been developed to score the burden of morbidity, but they remain difficult to use in older adults, especially because of possible recall bias when reporting chronic disease among individuals with cognitive disorders, and lack of feasibility in clinical practice (due to their complexity and value for physicians, physiotherapists, or other health care professionals; Linn et al., 1968; Parmelee et al., 1995; Salvi et al., 2008; de Decker et al., 2013). Recently, an independent association was found between the Cumulative Illness Rating Scale Geriatric form (CIRS-G), which provides a morbidity score, and the number of drug classes taken daily (de Decker et al., 2013). The results showed that an increase of three drug classes corresponds to a one-point increase on the CIRS-G (de Decker et al., 2013). This result is consistent with previous studies in the general population, which reported that pharmacy data using the Anatomical Therapeutic Chemical Classification (ATCC) system might be used to provide reliable prevalence estimates of several common comorbid conditions (Von Korff et al., 1992;

Maio et al., 2005; Chini et al., 2011). In addition, it has been demonstrated that pharmacy data provide a stable measure of morbidity status, and are associated with physician-rated disease severity as well as with individual-rated health status (Von Korff et al., 1992). Hence, the decision was made to record the use of drugs in the clinical assessment. Polypharmacy is defined as the use of more than three drugs per day, which was used as the item for the minimum data set, and was combined with the exact number of therapeutic drug classes taken daily and the use of psychoactive drugs (i.e., benzodiazepines, antidepressants, neuroleptics), which was coded as yes or no in the full dataset.

Information about falls, with a fall being defined as an event resulting in a person coming to rest unintentionally on the ground or at another lower level, not as the result of a major intrinsic event or an overwhelming hazard, in the previous 12 month-period before the assessment, is also proposed (American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011). For the minimum data set, only the existence (or not) of a fall(s) history is required, while for the full data set information on recurrence (i.e., $\geq$2 falls) and severity (defined as fractures, cranial trauma, large, and/or deep skin lesions, post-fall syndrome including an association of fear of falling (FOF), postural instability with absence of postural reflexes, inability to get up, time on ground $\geq$1 h, and hospitalization) are proposed for the data collection. Recently, a systematic review and meta-analysis reported that FOF might increase gait instability (Ayoubi et al., 2015). Thus, it was determined to measure FOF using the single question: "Are you afraid of falling?" with a graded answer (i.e., never, almost never, sometimes, often, and very often) for the full dataset.

In addition to FOF, collecting information on disorders or diseases that directly influence gait performance is also advised. First, information on neurological diseases (limited to the existence or non-existence of dementia) and other diseases (coded as yes or no) are collected for the minimal data set. Information on memory complaints, MCI, nature of dementia (i.e., AD, non-AD neurodegenerative, non-AD vascular, mixed), Parkinson disease, idiopathic normal pressure hydrocephalus, cerebellar disease, stroke, myelopathy, and peripheral neuropathy are also proposed for the full dataset (Alexander and Crutcher, 1990; Nutt et al., 1993; Nutt, 2001; Verghese et al., 2006; Montero-Odasso et al., 2012). A quantification of global cognitive functioning is also recommended, using for example the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005). In addition, among the neuropsychiatric disorders, it is important to collect information about depression symptoms because they can lead to gait instability and falls. This is limited to a simple binary question in the minimum data set and the score for the 4-item geriatric depression scale in the full data set (Shah et al., 1997). A measure of anxiety is also proposed using the 5-item Geriatric Anxiety Inventory (Byrne and Pachana, 2011).

Information on major orthopedic diagnoses (e.g., osteoarthritis) involving the lumbar vertebrae, pelvis, or lower extremities, coded yes vs. no, as well as the use of a walking aid, should also be recorded (American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011).

Information on sensory and motor subsystems such as muscle strength, lower-limb proprioception and vision are required because the age-related impairment in the performance of these subsystems may affect gait performance (Beauchet et al., 2014a). For the minimal data set, impairments were coded as binary (i.e., yes or no), while in the full dataset standardized measures are required. First, the Maximum isometric Voluntary Contraction (MVC) of handgrip strength must be measured with a computerized hydraulic dynamometer. The test should be performed three times with the dominant hand. The mean value of MVC over the three trials should be used as the outcome measure. Second, distance binocular vision should be measured at a distance of 5 m with a standard scale (Lord et al., 1994). Vision needs to be assessed with corrective lenses, if used regularly. Third, lower extremity vibration sense should be measured, using a graded tuning fork placed on a bony area, such as the tibial tuberosity, medial malleolus or big toe. This is correlated with proprioception, which is critical to balance (Beauchet et al., 2014a).

Gait Characteristics

Before conducting a spatiotemporal gait analysis based on the recorded footfalls, a standardized clinical evaluation is advised. First, the individual's subjective perception of gait difficulties is registered using a single question: "Do you have any difficulty walking?" with a graduated answer (i.e., never, almost never, sometimes, often, and very often). Second, a visual observation of gait during habitual walking is proposed with a binary answer (yes vs. no) to the question "are there gait abnormalities during physical examination?"

Third, the TUG test score and gait speed (distance divided by ambulation time) when walking a distance of 4 m at a steady-state pace is suggested (Podsiadlo and Richardson, 1991; Goldberg and Schepens, 2011). These measures are proposed for the minimal dataset, while for the full data set an additional measure is proposed; that being the time to achieve the imagined TUG (iTUG) (Beauchet et al., 2015a). Exploring the higher levels of gait control may be more difficult in clinical practice. There are two alternatives: using a dual-task paradigm (i.e., walking while simultaneously executing an attention-demanding task), or using motor imagery of gait (i.e., the mental simulation of gait without its actual execution; Beauchet et al., 2015a). Recently, interest in the latter alternative has been underscored using the mental chronometry approach applied to the TUG, a well-known motor test used in clinical practice (Beauchet et al., 2010, 2014b, 2015a). The TUG is a standardized assessment of a basic functional mobility task of relevance to daily living and records the time needed to stand up, to walk 3 m, to turn back and sit down (Podsiadlo and Richardson, 1991). It has been reported that

cognitive performance, and in particular executive functioning, contributes to the temporal correspondence between executing and imaging gait in individuals with neuropsychiatric conditions like dementia, schizophrenia or multiple sclerosis (Linn et al., 1968; Von Korff et al., 1992; Oberg et al., 1993; Lord et al., 1994; Parmelee et al., 1995; Shah et al., 1997; Maio et al., 2005; Nasreddine et al., 2005; Brach et al., 2008; Salvi et al., 2008; Beauchet et al., 2010, 2014a,b, 2015a; Bohannon and Williams Andrews, 2011; Byrne and Pachana, 2011; Chini et al., 2011; Goldberg and Schepens, 2011; Allali et al., 2012; Hass et al., 2012; Lallart et al., 2012; de Decker et al., 2013; Annweiler et al., 2015; Ayoubi et al., 2015; Stensvold et al., 2015). It has also been shown that older individuals with cognitive impairment executed the iTUG more rapidly than they performed it (Allali et al., 2012; Beauchet et al., 2015a). On the contrary, there has been no significant difference between the two conditions in healthy younger adults (Lallart et al., 2012). This difference in terms of performance between pTUG and iTUG, called "delta TUG," can be interpreted as the awareness of movement and physical performance, and thus may be used as a biomarker of the disorders of higher levels of gait control (Beauchet et al., 2010, 2014b, 2015a; Allali et al., 2012; Lallart et al., 2012).

It is necessary to underscore that the spatiotemporal gait analysis based on the recorded footfalls should be performed in a reproducible, quiet, well-lit environment, with patients wearing their own footwear (walking shoes, no slippers) with heel height not exceeding 3 cm and comfortable and non-restrictive clothing. Depending on the participant's fall risk, the use of safety support systems is recommended, such as a safety belt around the participant's waist. We recommend assessing the normal walking condition for the minimal data set, and for the full dataset we recommend three additional walking conditions; a fast walk at a maximum speed, and two dual-task conditions, in which the patient is instructed to walk normally while (a) counting backwards by ones starting from 50 and (b) to enumerate animal names (Kressig et al., 2006; Beauchet et al., 2012; Montero-Odasso et al., 2012). For the dual task condition, no prioritization should be given to a single task and the trial should be performed to the best of the participant's ability. Steady-state gait and gait trials in the same walking direction are required for all conditions and may be achieved by instructing participants to start walking at least 1 m prior to the data recording zone and stopping at least 1 m beyond it. It is also advisable to use simple, clear and standardized walking instructions to explain the various tasks to the participants.

Regardless of the type of category of devices used to assess gait, we recommend using a validated system that provides reliable measures. For the minimum data set, four gait parameters during normal walking including the mean value of walking speed, and mean values and coefficient of variation of stride time, swing time and stride width need to be reported. We suggest adding more stressful walking conditions (i.e., fast speed and dual tasking conditions) and reporting mean values and coefficients of variation of stride length, stance time, single and double support, and stride velocity for the full dataset. This choice is based on the fact that in terms of control of gait, gait variability has been identified as a biomarker for cortical control of gait in normal aging individuals and in individuals with dementia (Beauchet et al., 2010, 2012, 2014b, 2015a; Allali et al., 2012; Lallart et al., 2012). In addition, higher (i.e., worse) STV during normal walking has been associated with lower cognitive performance in non-demented older community-dwellers (Beauchet et al., 2012). This result has been confirmed by a meta-analysis underscoring that higher STV during normal walking was related to both MCI and dementia (Beauchet et al., 2014a). In terms of gait variability, a certain level of "healthy" variability of the motor control system is necessary to adapt to unexpected instability. Indeed, both high and low gait variability during habitual walking have been reported in younger and older CHIs with safe gait, depending on the type of gait parameters being examined (Beauchet et al., 2009). In particular, safe gait has been characterized by a low STV, an intermediate swing time variability and a high stride width variability in CHIs (Beauchet et al., 2009). These results can be explained by the fact that temporal and spatial gait parameters appear to reflect different constructs of gait control (Gabell and Nayak, 1984; Newell and Corcos, 1993; Nutt et al., 1993; Nutt, 2001; Launay et al., 2013). Stride time and stride width variability provide an indication of control of the rhythmic stepping mechanism and dynamic postural control, respectively, while swing time is indicative of both mechanisms (Gabell and Nayak, 1984; Beauchet et al., 2009). Furthermore, it is important to consider the number of steps recorded. Indeed, the accuracy of gait variability measures are highly dependent on obtaining a sufficient number of steps, with a study suggesting that a minimum of 400 steps are needed to obtain valid measures of gait variability during treadmill walking (Faude et al., 2012). However, even if it is recommended to have the highest number of gait cycles possible from a practical standpoint to assess gait variability of spatiotemporal parameters, it has been suggested that a minimum of three consecutive gait cycles should be obtained for both the left and right sides (i.e., a total of six gait cycles; Kressig et al., 2006). Furthermore, including steps from several shorter walks is recommended when obtaining the number of steps over a long walking distance is not possible.

For the collection of gait data, we suggest that gait should be assessed without assistive devices whenever possible. When a device is required it is important to describe the type of device used by the individual. Given that there are no established reference values for assistive devices, the first assessment should be used as the reference point for individuals who repeatedly use the same device.

The operational definitions of spatiotemporal gait parameters, based on GAITRite® software are as follows: (1) Stride length (in cm): anterior-posterior distance between the heel strikes of two successive placements of the same foot; stride width (in cm): lateral distance between the midlines of the right and left heels; stride time (in ms): time elapsed from the first contact of two consecutive footsteps of the same foot; swing time (in ms): time elapsed from the last contact of the current footstep to the first contact of the next footstep on the same foot; stance time (in ms): time elapsed from the initial contact and the last contact of consecutive footstep of the same foot; single support time (in ms): time elapsed from the last contact of

the opposite footfall to the initial contact of the next footstep of the same foot; double support time (in ms): time elapsed during which both feet are in ground contact; stride velocity (in cm/s): stride length divided by the stride time; and walking speed (in cm/s): distance walked divided by the ambulation time.

Procedure for Clinical and Spatiotemporal Gait Analysis Based on the Recorded Footfalls

All adults aged 65 and over should be systematically interviewed or examined for gait disorders at least once per year. In addition, those who report a fall or have an acute medical condition should be asked about difficulties with gait and should be examined for gait disorders.

Clinical assessment should be separated into two main parts: global and analytic clinical assessment. The global assessment detecting gait difficulties begins with watching individuals as they walk into the examination room. The use of a walking aid and its nature (i.e., cane, walker, personal assistance, and supervision) should be noticed and the individual should be asked about his/her subjective perception of gait difficulties. This visual observation should be completed with one of the two standardized motor tests to provide an objective measure of gait performance: the TUG score and the gait speed value. After this clinical assessment and if an abnormality is recorded, a spatiotemporal gait analysis based on the recorded footfalls (collection of all information described in **Table 2**) in laboratory setting is suggested. If necessary and based on abnormalities recorded during the clinical and clinical and spatiotemporal gait analysis, an analysis outside the laboratory using wearable sensors may be propose to obtain information about gait during the individual's everyday activities. The role of other laboratory testing and diagnostic evaluation for gait and balance disorders has not been well-studied, and there is no recommended systematic investigation to perform. However, the following complementary investigations are recommended: (1) Bone radiography in the event of acute pain, joint deformation and/or functional disability, (2) Standard 12-lead ECG in case of dizziness, 3) Blood glucose level in patients with diabetes, and (4) Serum 25OHD concentration if there is no vitamin D supplementation. Cerebral imaging in the absence of specific indications based on a clinical examination may not be necessary.

Quantitative Reference Values for Spatiotemporal Gait Parameters

Table 3 shows the group mean values, standard deviations and CoV of spatiotemporal gait parameters separated by age groups and sex. In most cases, men demonstrated greater performance for mean values (i.e., less difference relative to normal values for healthy young adults) than women, but not for CoV. This effect was observed in the total sample as well as for the 65–74 year age category. Interestingly, walking speed and stride velocity were similar in both males and females when considering the total sample and each age strata separately.

The results of multiple linear regression analyses exploring the effects of age and sex on spatiotemporal gait parameters, adjusted for BMI and test center are shown in **Table 4**. Increasing age was associated with significant lower performance for mean values and CoV for all gait parameters, except for the mean value of stride width ($P = 0.861$) and CoV of double support time ($P = 0.186$). Women demonstrated lower mean values for all temporal gait parameters compared to men, except for the mean value of double support time ($P = 0.059$) CoV of spatial parameters were significantly greater in women compared to men. In addition, both mean and CoV of stride velocity were significantly worst with increasing age in women.

DISCUSSION

Standardized systematic assessment of three categories of information, which included demographics, clinical features and gait characteristics were selected for the development of gait assessment guidelines. Two complementary sets of guidelines have been proposed: a minimal data set and a full data set. Concerning the quantitative reference values, we observed lower values in several spatiotemporal gait parameters with age as well as differences between men and women. Age had a negative effect on mean values and CoV, while sex was mainly associated with mean values. Stride velocity parameters were affected both by age and sex.

Our study provides quantitative normative values for widely used and clinically relevant spatiotemporal gait parameters. Compared to previous studies on this topic, the strategy of recruiting participants through an intercontinental initiative provides access to probably the highest number of participants involved in a study exploring reference values until now. Furthermore, we chose to select "very healthy" older participants to avoid any interaction with morbidities or cognitive impairments that can affect gait performance. Previous studies have controlled for the potential effects of morbidities using statistical analysis (Oberg et al., 1993; Oh-Park et al., 2010; Bohannon and Williams Andrews, 2011; Hollman et al., 2011; Hass et al., 2012). However, it has recently been suggested that the strategy of statistical adjustment may be limited and does not take into consideration the complex interplay and potential effects of morbidities (Kressig et al., 2006; Byrne and Pachana, 2011; Montero-Odasso et al., 2012). For instance, a recent study reported the results of the independent and combined effects of impairments of muscle strength, distance vision, lower-limb proprioception, and cognition on gait performance using pTUG and iTUG (Byrne and Pachana, 2011). It was shown that cognitive impairment, considered either separately or in combination with any other subsystem decline, notably muscle strength, was strongly associated with decreased performance on the pTUG and delta TUG scores. In contrast, lower-limb proprioceptive impairment was associated with worse performance (i.e., lower) on the iTUG. The subsystem's impairment has been associated with worse (i.e., greater) delta TUG scores; the highest impact being reported when combining muscle strength and cognition. In our study, all participants were free of morbidities, and thus

TABLE 3 | Quantitative reference values (i.e., mean ± standard deviation) for spatiotemporal gait parameters by age group (65–74 years, 75–84 years and ≥ 85 years) and sex ($n = 954$).

	Total population ($n = 954$)			*P*-value*	Age											
	Total	Female ($n = 437$)	Male ($n = 517$)		65–74 years ($n = 711$)			*P*-value*	75–84 years ($n = 207$)			*P*-value*	≥85 years ($n = 36$)			*P*-value*
					Total	Female ($n = 312$)	Male ($n = 399$)		Total	Female ($n = 101$)	Male ($n = 106$)		Total	Female ($n = 24$)	Male ($n = 12$)	
Age (years), mean ± *SD*	72.8 ± 4.8	73.2 ± 5.1	72.4 ± 4.5	0.006	70.6 ± 2.4	70.7 ± 2.4	70.5 ± 2.3	0.649	77.6 ± 2.6	77.8 ± 2.5	77.4 ± 2.6	0.274	87.7 ± 2.8	87.2 ± 2.0	88.6 ± 4.0	0.585
BMI (kg/m^2), mean ± *SD*	26.2 ± 4.1	26.0 ± 4.8	26.4 ± 3.3	0.105	26.0 ± 3.8	25.6 ± 4.4	26.2 ± 3.2	0.094	26.6 ± 4.1	26.2 ± 4.7	27.0 ± 3.4	0.171	28.0 ± 7.2	28.2 ± 8.4	27.6 ± 3.8	0.379
STRIDE TIME																
Mean value (ms)	1123.7 ± 122.4	1095.5 ± 109.8	1147.6 ± 127.4	**<0.001**	1118.5 ± 122.3	1081.5 ± 104.3	1147.3 ± 127.5	**<0.001**	1132.7 ± 117.0	1124.3 ± 109.4	1140.7 ± 123.7	0.314	1176.1 ± 140.9	1155.7 ± 139.2	1216.9 ± 141.1	0.177
CoV (%)	2.2 ± 1.1	2.2 ± 1.1	2.1 ± 1.0	0.244	2.1 ± 1.1	2.1 ± 1.0	2.1 ± 1.0	0.520	2.3 ± 1.1	2.4 ± 1.1	2.2 ± 1.0	0.053	2.8 ± 1.3	3.1 ± 1.3	2.3 ± 1.3	0.067
SWING TIME																
Mean value (ms)	414.1 ± 40.2	402.1 ± 36.5	424.2 ± 40.5	**<0.001**	416.3 ± 40.0	403.4 ± 36.2	426.3 ± 40.0	**<0.001**	409.6 ± 39.6	401.2 ± 36.7	417.5 ± 40.8	0.003	396.7 ± 43.1	388.6 ± 37.5	413.1 ± 50.2	0.188
CoV (%)	4.2 ± 1.8	4.2 ± 2.0	4.2 ± 1.6	0.863	4.0 ± 1.7	3.9 ± 1.9	4.1 ± 1.6	0.063	4.5 ± 1.7	4.7 ± 1.8	4.4 ± 1.6	0.199	6.0 ± 2.7	6.5 ± 2.7	4.9 ± 2.3	0.020
STANCE TIME																
Mean value (ms)	706.6 ± 91.2	689.3 ± 87.3	721.2 ± 92.0	**<0.001**	700.9 ± 88.1	677.6 ± 79.0	719.0 ± 90.6	**<0.001**	713.5 ± 91.6	706.6 ± 90.3	720.1 ± 92.7	0.291	779.4 ± 114.9	767.0 ± 122.6	804.0 ± 97.9	0.212
CoV (%)	3.1 ± 1.4	3.1 ± 1.3	3.1 ± 1.4	0.309	3.1 ± 1.3	3.1 ± 1.3	3.1 ± 1.4	0.743	3.2 ± 1.5	3.3 ± 1.4	3.0 ± 1.5	0.124	3.5 ± 1.7	3.8 ± 1.8	2.9 ± 1.4	0.029
SINGLE SUPPORT TIME																
Mean value (ms)	414.3 ± 39.8	401.5 ± 35.5	425.2 ± 40.0	**<0.001**	417.2 ± 39.5	403.4 ± 36.2	427.4 ± 39.6	**<0.001**	407.8 ± 38.7	396.8 ± 34.3	418.3 ± 39.8	**<0.001**	396.7 ± 43.1	388.6 ± 37.5	413.1 ± 50.2	0.188
CoV (%)	4.0 ± 1.8	4.1 ± 2.0	4.0 ± 1.6	0.453	3.9 ± 1.7	3.9 ± 1.9	3.9 ± 1.5	0.154	4.3 ± 1.7	4.5 ± 1.8	4.2 ± 1.6	0.102	6.0 ± 2.7	6.5 ± 2.8	4.9 ± 2.3	0.062
DOUBLE SUPPORT TIME																
Mean value (ms)	292.6 ± 71.0	288.1 ± 74.1	296.4 ± 68.2	0.072	284.2 ± 64.5	274.5 ± 62.1	291.8 ± 65.4	**<0.001**	305.7 ± 74.2	308.8 ± 77.3	302.9 ± 71.4	0.569	381.4 ± 100.2	376.4 ± 115.3	391.3 ± 63.1	0.398
CoV (%)	6.6 ± 2.8	6.8 ± 2.7	6.5 ± 2.8	0.079	6.8 ± 2.9	7.0 ± 2.8	6.6 ± 2.9	0.117	6.3 ± 2.5	6.5 ± 2.8	6.1 ± 2.2	0.273	6.0 ± 2.1	6.2 ± 2.8	5.5 ± 2.6	0.177
STRIDE LENGTH																
Mean value (cm)	134.1 ± 18.9	126.5 ± 17.1	140.7 ± 18.0	**<0.001**	138.0 ± 16.6	131.1 ± 14.8	143.3 ± 15.9	**<0.001**	126.5 ± 19.7	118.2 ± 15.1	134.4 ± 20.4	**<0.001**	102.9 ± 15.3	100.7 ± 16.2	107.3 ± 13.0	0.166
CoV (%)	2.3 ± 1.2	2.7 ± 1.3	2.2 ± 1.1	0.005	2.2 ± 1.1	2.2 ± 1.2	2.1 ± 1.0	0.087	2.6 ± 1.3	2.7 ± 1.3	2.6 ± 1.3	0.743	3.6 ± 2.1	4.1 ± 2.4	2.7 ± 1.0	0.026
STRIDE WIDTH																
Mean value (cm)	9.9 ± 3.1	9.4 ± 33.1	10.2 ± 3.0	**<0.001**	9.9 ± 3.1	9.5 ± 3.1	10.3 ± 3.0	0.001	9.6 ± 3.2	9.0 ± 3.4	10.1 ± 2.9	0.010	10.0 ± 3.2	9.9 ± 2.5	10.2 ± 4.3	0.804
CoV (%)	26.6 ± 49.0	30.9 ± 69.8	23.0 ± 17.2	0.013	24.6 ± 34.7	27.4 ± 48.5	22.5 ± 17.2	0.057	33.0 ± 82.6	43.4 ± 116.9	23.0 ± 12.8	0.075	28.2 ± 23.4	22.5 ± 9.1	39.5 ± 36.8	0.934
WALKING SPEED (CM/S)																
mean ± *SD*	121.5 ± 23.4	120.2 ± 23.8	122.7 ± 23.0	0.103	125.4 ± 21.7	126.1 ± 21.7	124.9 ± 21.6	0.488	113.9 ± 23.5	109.7 ± 21.3	118.0 ± 24.9	0.011	88.5 ± 17.8	88.3 ± 19.4	88.9 ± 14.9	0.934
STRIDE VELOCITY																
Mean value (cm/s)	119.9 ± 22.5	118.8 ± 23.2	120.8 ± 21.8	0.175	122.9 ± 21.1	123.6 ± 21.2	122.3 ± 21.0	0.426	114.8 ± 22.8	111.1 ± 22.7	118.5 ± 22.5	0.020	89.0 ± 17.8	88.9 ± 19.4	89.3 ± 15.0	0.251
CoV (%)	43.5 ± 1.7	3.5 ± 1.7	3.4 ± 1.6	0.244	3.4 ± 1.6	3.4 ± 1.7	3.4 ± 1.6	0.983	3.7 ± 1.7	3.8 ± 1.8	3.6 ± 1.6	0.280	4.2 ± 2.0	4.6 ± 2.0	3.5 ± 1.9	0.084

*SD, standard deviation; m, meter; s, second; ms, millisecond; CoV, coefficient of variation; *Comparison based on unpaired t-test; P significant (i.e., $P < 0.0006$) indicated in bold.*

TABLE 4 | Multiple linear regression showing the association of spatiotemporal gait parameters (dependent variables) with age and sex (independent variables) adjusted for body mass index and test center among participants (n = 954).

Spatiotemporal gait parameters* (Dependent variables)	Independent variables					
	Age			Sex		
	β	[95%CI]	*P*-value	β	[95%CI]	*P*-value
STRIDE TIME						
Mean value (ms)	3.14	[1.55; 4.73]	**<0.001**	−50.62	[−65.85; −35.38]	**<0.001**
CoV (%)	0.04	[0.02; −0.05]	**<0.001**	00.13	[−0.00; 0.25]	0.056
SWING TIME						
Mean value (ms)	−0.52	[−1.03; −0.00]	**0.049**	−21.69	[−26.62; 16.76]	**<0.001**
CoV (%)	0.10	[0.07; 0.12]	**<0.001**	−0.02	[0-0.25; 0.21]	0.880
STANCE TIME						
Mean value (ms)	3.51	[2.34; 4.69]	**<0.001**	−31.11	[−42.38; −19.83]	**<0.001**
CoV (%)	0.03	[0.01; 0.05]	**0.004**	0.14	[−0.04; 0.31]	0.122
SINGLE SUPPORT TIME						
Mean value (ms)	−0.59	[−1.10; −0.09]	**0.021**	−22.66	[−27.50; −17.82]	**<0.001**
CoV (%)	0.10	[0.08; 0.13]	**<0.001**	−0.00	[−0.23; 0.22]	0.992
DOUBLE SUPPORT TIME						
Mean value (ms)	−4.03	[3.14; 4.92]	**<0.001**	−8.22	[−16.73; 0.30]	0.059
CoV (%)	−0.03	[−0.06; 0.01]	0.186	0.34	[−0.01; 0.70]	0.057
STRIDE LENGTH						
Mean value (cm)	−1.49	[−1.68; −1.29]	**<0.001**	−14.48	[−16.34; 12.62]	**<0.001**
CoV (%)	0.07	[0.06; 0.09]	**<0.001**	0.22	[0.08; 0.36]	**0.002**
STRIDE WIDTH						
Mean value (cm)	0.00	[−0.04; −0.04]	0.861	−0.95	[−1.33; −0.57]	**<0.001**
CoV (%)	0.77	[0.11; 1.44]	**0.023**	8.09	[1.71; 14.47]	**0.013**
STRIDE VELOCITY						
Mean value (cm/s)	−1.47	[−1.75; −1.20]	**<0.001**	−2.62	[−5.23; −0.01]	**0.049**
CoV (%)	0.05	[0.03; 0.07]	**<0.001**	0.27	[0.08; 0.46]	**0.005**

ms, millisecond; s, second; cm, centimeter; *CoV, coefficient of variation*; *CI, confidence interval*; *β, coefficient of regression corresponding to a decrease or increase in value of gait parameters*; **Used as dependent variable in the multiple linear regression. P-value significant (i.e., <0.05) indicated in bold; each linear Model is adjusted for Body mass index and test center.*

provided the opportunity to report real normative quantitative reference values by age category from 65 to 85 years and above. The decline in gait performance with age is consistent with the literature and supports the validity of the reported values.

Some limitations, however, need to be acknowledged. First, the number of participants in the 85 and over age category was low, probably because healthy individuals only represent a low percentage of this age group. More effort needs to be made to explore this population, as they currently represent the fastest growing age group in many countries and have the highest prevalence and incidence of gait disorders (American Geriatrics Society and British Geriatrics Society and American Academy of Orthopedic Surgeons Panel on Falls Prevention, 2001; Panel on Prevention of Falls in Older Persons and American Geriatrics Society and British Geriatrics Society, 2011). Second, because this initiative merged data from clinical and research centers in different countries and different clinical settings, assessment was not strictly uniform even if the same procedures and equipment were used.

CONCLUSIONS

The past decade has been characterized by an acceleration of knowledge in medicine and science, particularly in the area of neuroscience. Considerable efforts have been (and continue to be) made in developing accessible and practical technology-based assessment tools aiming at providing accurate measurements of spatiotemporal gait parameters. These advances challenge researchers and clinicians, pushing them to develop new ways of thinking and working. Currently, new opportunities exist as the result of working as part of an internationally structured consortium. The GOOD initiative (Allali et al., 2016) underscores the fact that there is still a lot of work to do, but significant progress has been made and the future is optimistic with respect to the development of the Biomathics and Canadian Gait Consortiums. This work represents an important first step in the development of guidelines for clinical and spatiotemporal gait analysis based on the recorded footfalls in laboratory setting and the definition of quantitative reference values in healthy older adults. These

guidelines facilitate the ability to work together and think broadly and effectively in the field of gait disorders and aging.

AUTHOR CONTRIBUTIONS

Study concept and design: OB, GA and JH; acquisition of data: OB, JV, JS, RK, CL, MC, VS, AD, and JH; analysis and interpretation of data: OB, GA, and JH; drafting of the manuscript: OB, GA, CL, and JH; critical revision of the manuscript for important intellectual content: HS, JV, SGu, JS, RK, JB, TS, CL, SGr, LB, TL, VC, MC, VS, GL, AD, RS, GD, and RC; obtained funding: OB, JV, and JH; statistical expertise: OB; administrative, technical, or material support: OB and JH; study supervision: OB and JH. All the authors have participated in the research reported, have seen and approved the final version of the manuscript, and have agreed to be an author of the paper.

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Multi-Trial Gait Adaptation of Healthy Individuals during Visual Kinematic Perturbations

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Optimizing rehabilitation strategies requires understanding the effects of contextual cues on adaptation learning. Prior studies have examined these effects on the specificity of split-belt walking adaptation, showing that contextual visual cues can be manipulated to modulate the magnitude, transfer, and washout of split-belt-induced learning in humans. Specifically, manipulating the availability of vision during training or testing phases of learning resulted in differences in adaptive mechanisms for temporal and spatial features of walking. However, multi-trial locomotor training has been rarely explored when using visual kinematic gait perturbations. In this study, we investigated multi-trial locomotor adaptation in ten healthy individuals while applying visual kinematic perturbations. Subjects were instructed to control a moving cursor, which represented the position of their heel, to follow a prescribed heel path profile displayed on a monitor. The perturbations were introduced by scaling all of the lower limb joint angles by a factor of 0.7 (i.e., a gain change), resulting in visual feedback errors between subjects' heel trajectories and the prescribed path profiles. Our findings suggest that, with practice, the subjects learned, albeit with different strategies, to reduce the tracking errors and showed faster response time in later trials. Moreover, the gait symmetry indices, in both the spatial and temporal domains, changed significantly during gait adaptation ($P < 0.001$). After-effects were present in the temporal gait symmetry index whens the visual perturbations were removed in the post-exposure period ($P < 0.001$), suggesting adaptation learning. These findings may have implications for developing novel gait rehabilitation interventions.

Keywords: locomotor adaptation, visuo-motor adaptation, gait symmetry, human locomotion, motor adaptation

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NEW AND NOTEWORTHY

This study deployed a novel gait adaptation paradigm in which healthy subjects learned to move their lower limbs to control a cursor in response to visuo-motor perturbations (i.e., gain change). Our findings suggest that, with practice, the subjects learned, albeit with different strategies, to reduce the tracking errors and showed faster response time in later trials. Moreover, we observed differential effects of adaptation to the kinematic perturbation on the temporal and spatial symmetry (i.e., after-effects were only observed in the temporal domain of gait symmetry, indicating its adaptation). Overall, these findings may have implications for the development of novel gait interventions for people with lower-limb disabilities.

INTRODUCTION

Motor adaptation can be defined as an error-driven process that allows humans to adjust sensorimotor mappings of well-learned movements to adapt to new, predictable demands (Bastian, 2008; Malone et al., 2011). Thus, motor adaptation mechanisms are generally engaged in response to changing intrinsic (e.g., muscle fatigue, aging, and neurological disease) and/or extrinsic (e.g., visual kinematic or dynamic perturbations) conditions. Motor adaptation to extrinsic perturbations has been investigated in the context of gait rehabilitation for people with walking disabilities (Torres-Oviedo et al., 2011). Both visual and dynamic disturbances induce sensorimotor errors, which initiate motor adaptation. Indeed, experimental studies of motor adaptation have been performed by applying extrinsic perturbations including introducing abnormal visual feedback (Contreras-Vidal and Kerick, 2004; Krakauer et al., 2005; Cheng and Sabes, 2007; Wei and Kording, 2009; Izawa and Shadmehr, 2011; Luu et al., 2015, 2016), manipulating physical dynamics (split-belt treadmill; Scheidt et al., 2001; Choi and Bastian, 2007; Emken et al., 2007; Izawa et al., 2008; Malone et al., 2012), or both (Kim et al., 2010).

Helm and Reisman have reviewed the split-belt walking paradigm, which has been widely used to explore motor learning and spatiotemporal asymmetry for post-stroke conditions (Helm and Reisman, 2015). The locomotor adaptation to split-belt treadmill training can improve walking symmetry in post-stroke patients (Reisman et al., 2007), and the persistence of improved gait symmetry on a treadmill partially transfers to over-ground walking (Reisman et al., 2009). Moreover, the temporal and spatial control for symmetric gait can be adapted separately, which suggests we could potentially develop interventions targeting either temporal or spatial domain of gait deficits (Malone et al., 2012). However, split-belt treadmill is not the only way to disrupt normal gait patterns. In some cases, this purpose can also be achieved by altering the visual-motor representation of locomotion.

Prior studies have examined the effect of altering visual feedback in walking adaptation. Torres-Oviedo and Bastian showed that removing vision via blindfolds improved the transfer of split-belt treadmill adaptation to natural walking (Torres-Oviedo and Bastian, 2010). This agreed with a prior study that reported the transferring of motor learning occurs in the intrinsic coordinates (Imamizu et al., 1998; Malfait et al., 2002). Prisms are used in many studies to distort vision and interrupt the visuo-motor neural pathway (Morton and Bastian, 2004; Alexander et al., 2013; Nemanich and Earhart, 2015). On the other hand, visual cues can be provided and manipulated in rehabilitation. Kim et al. used a cursor on a screen to represent the sagittal position of a subject's foot when walking with a robotic system (Kim et al., 2010). They suggested that combining both dynamics (interaction force between subjects and robot) and visual perturbations to the gait pattern retained the gait adaptation for longer than training with either dynamics or visual perturbation alone. Statton et al. used bars on a screen to show subjects the amount of their knee flexion (Statton et al., 2016). By manipulating the height of the bars, they created illusions in subjects that they had to over-correct their gait. Long et al. showed the position of steps on a screen so that the subjects would know where their feet landed (Long et al., 2016). Although the effect induced in the gait pattern from these studies vary greatly, they can usually be labeled as either spatial (Long et al., 2016; Statton et al., 2016) or temporal (Hussain et al., 2013; Finley et al., 2014) gait patterns but not both, partially limited by the paradigm of interruption to the visual-motor system.

In this study, we proposed a novel method to explore multi-day gait adaptation of human treadmill walking under visual kinematic perturbations. Participants were instructed to control a moving cursor, representing the heel position in the sagittal plane, to follow a specific trajectory displayed on a screen. Visual kinematic perturbations were introduced by scaling the lower limb joint angles (factor of 0.7) therefore distorting the mapping of the actual heel position on the screen, resulting in mismatch between the moving cursor and the prescribed heel path. Participants adapted their locomotor patterns to visual perturbations as demonstrated by a reduction of tracking errors across trials. After-effects were present when the visual perturbations were removed in the post-exposure period suggesting adaptation learning had taken place. We also found that individual subjects are idiosyncratic in which joints they use to control the heel positions during the adaptation. The modifications in the spatial and temporal symmetry of gait induced by the visual kinematic perturbations were also investigated. These findings have implications for developing novel effective gait rehabilitation interventions.

METHODS

Experimental Setup and Procedure

Ten healthy individuals (six males, four females; aged from 22 to 30) with no history of neurological disease or lower limb pathology participated in this study. All participants provided written and informed consent as approved by the Institutional Review Board at the University of Houston. Each subject participated in two sessions (two consecutive days, two trials per session). There were two phases in each day at trial 1 and trial 3 (**Table 1**). In the first phase, the subjects were instructed to walk normally and consistently for 3 min on a treadmill at a fixed speed of 1 mile per hour (mph), or 0.45 meter per second (m/s). A 52-inch TV monitor was placed in front of the treadmill at eye level and it showed a black screen in this phase. The subjects were also instructed to look at the screen during the entire protocol. Heel path profiles of their normal walking were computed for each session from the goniometer data using Matlab 2016a (The MathWorks, Inc.). Details of the calculation are provided in Section Forward Kinematic Model. In the second phase, the subjects first stood still (rest) on the treadmill for 2 min, then started walking at 1 mph without visual feedback on the screen for 5 min, following by a walking period with visual feedback. The subjects stood still for another 2 min at the end of each trial. The walking period without the

TABLE 1 | The experimental procedure for 4 trials in 2 consecutive days.

Phase 1			Phase 2					
Template generation			Rest	Without visual feedback	With visual feedback			Rest
					Pre-	Exposure	Post-	
Day 1	Trial 1	3	2	5	8	8	–	2
	Trial 2	–	2	5	–	8	–	2
Day 2	Trial 3	3	2	5	–	8	–	2
	Trial 4	–	2	5	–	8	5	2

Heel path profiles (template generation) were generated in Phase 1. In Phase 2, subjects stood for 2 min in the beginning and the end (rest) and walked in periods without and with visual feedback. Small dash "–" represents periods that were excluded in a trial. All values are in minutes.

visual feedback serves as a baseline to normalize gait symmetry indices. The visual feedback to the subjects included a moving cursor, which was linked to their right heel position in the sagittal plane, and a desired heel path. During the entire visual feedback period, the subjects were instructed to control a moving cursor to follow prescribed right heel path profiles displayed on the screen. The tracking task was mainly spatial because the subjects performed the task without considering the time to reach a specific point. In the pre-exposure phase (8 min) in Trial 1, the moving cursor was driven by the goniometer data (right hip, knee, and ankle). In the exposure period (8 min), a visual kinematic perturbation was introduced by scaling the goniometer data of the right leg by 0.7 and the moving cursor departed from the prescribed heel profiles. The subjects controlled the moving cursor to follow the prescribed heel profiles by adapting their gait patterns. A gain of 0.7 was chosen because the visual perturbation is detectable with this gain and the physical demand to compete the task at this gain is not so high. In the post-exposure period (5 min), the perturbations were removed and the moving cursor was driven by the goniometer data again. We defined early- and late- exposure phases in each trial as the first and the last 30 gait cycles (∼1 min), respectively. Similarly, early post-exposure phase was defined as the first 30 gait cycles in the post-exposure period. For safety purposes, all subjects were instructed to hold onto a front handle bar while walking on the treadmill.

Data Collection

Lower limb joint angles (hip, knee, and ankle) in the sagittal plane were recorded by goniometers (SG150 & SG110/A Gonio electrodes, Biometrics Ltd., UK) at 100 Hz using our customized C++ program. We visually estimated the joint locations and placed six sensors on both legs. To improve the consistency of sensor placement across days, we used the same sensor for each joint, 3D-printed a tool to hold the two pieces of a goniometer in place, and recorded the distance (from the ground) of each goniometer after the sensors were attached. Details for the goniometer sensor setup are provided in the Supplementary Material. Three wireless inertial motion sensors (OPAL, APDM Inc., Portland, OR) were mounted on the head, left heel, and right heel of the subject. Each sensor included accelerometer, gyroscope, and magnetometer sampled at 128 Hz. Electroencephalography (EEG) signals were also collected but will be reported elsewhere. **Figure 1** shows raster plot of these signals and illustrates the movements of the right leg in a full gait cycle during pre- and early-exposure phases.

Data Analysis

Data analysis and statistical analysis were performed using custom software written in Matlab R2016a (The MathWorks, Inc.). Joint angle data were low-pass filtered at 6 Hz by using a second order Butterworth filter. Because subjects walked at a slow speed (1 mph), the 0–6 Hz band covers most power of joint angle signals (Antonsson and Mann, 1985; Luu et al., 2014). Heel position in sagittal plane was calculated using a forward kinematic model (Section Forward Kinematic Model).

Forward Kinematic Model

The forward kinematic model of human treadmill walking (in sagittal plane) and the definitions of lower limb joint angles are shown in **Figure 2**. In this model, the hip joint position is assumed to be fixed. The prescribed heelpaths and trajectories of moving circle displayed on a screen during experiment were calculated by using the following equations:

$$\begin{aligned} z_{heel} &= l_1 \sin(\theta_h) + l_2 \sin(\theta_h + \theta_k) + l_3 \sin(\theta_h + \theta_k + \theta_a) \\ &\quad + l_4 \cos(\theta_h + \theta_k + \theta_a) \\ y_{heel} &= -l_1 \cos(\theta_h) - l_2 \cos(\theta_h + \theta_k) - l_3 \cos(\theta_h + \theta_k \\ &\quad + \theta_a) + l_4 \sin(\theta_h + \theta_k + \theta_a) \end{aligned} \quad (1)$$

where z_{heel} and y_{heel} are horizontal and vertical heel position in sagittal plane, respectively; θ_h, θ_k, θ_a are hip, knee, and ankle joint angles, respectively; l_1 is the length from the greater trochanter to the lateral epicondyle of the femur, l_2 is the length from the lateral epicondyle of the femur to the lateral malleolus of the fibula, l_3 is the perpendicular distance from the lateral malleolus of the fibula to the plantar surface of the foot, and l_4 is the distance from the posterior aspect of the calcaneus (heel) to the projection of ankle onto the foot.

To assess the rate of change of y_{heel} with respect to the changes of each lower limb joint angle, the gradient of y_{heel} was also

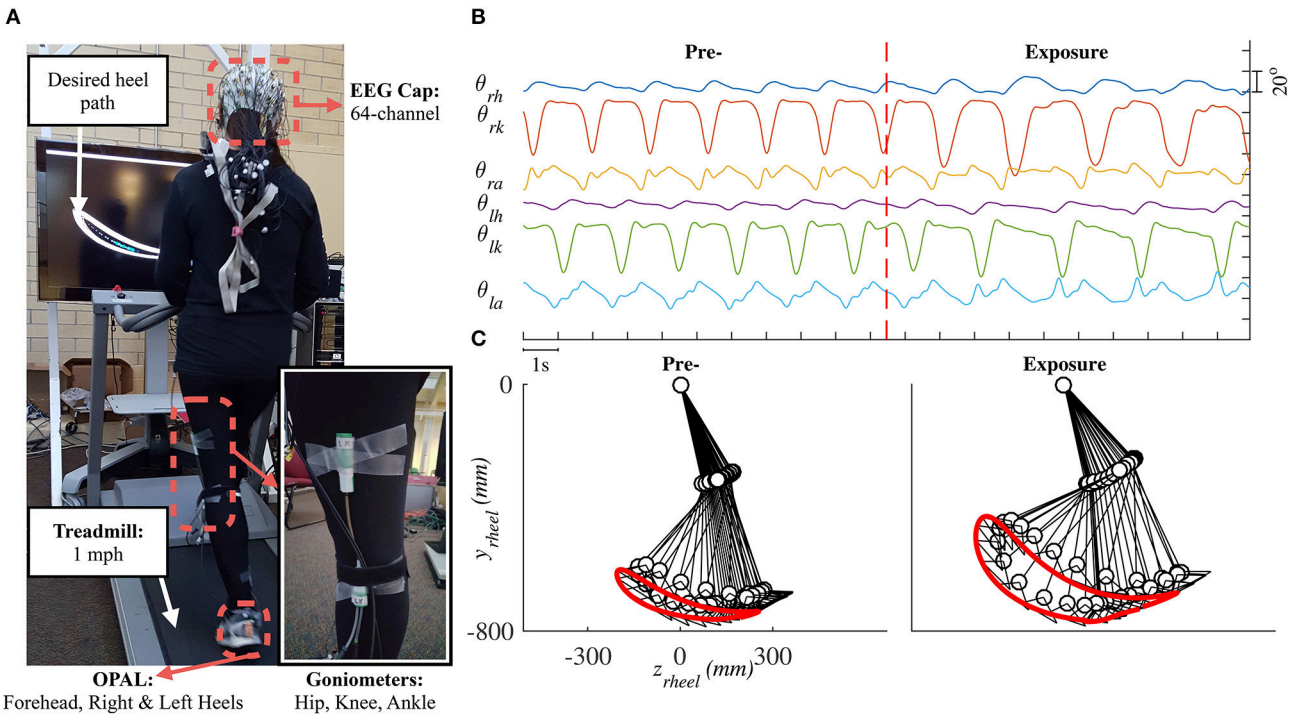

FIGURE 1 | (A) Experimental setup in this study. Each subject was instructed to walk on a treadmill while controlling a moving cursor to follow prescribed heel path profiles. Lower limb joint angles (θ_h, θ_k, θ_a) were recorded using six goniometers. **(B)** Example of joint angles in 20 s, vertical red line represents the time when the perturbation was introduced. **(C)** Illustration of the right leg in a full gait cycle during pre- and early-exposure.

derived as:

$$\nabla y_{heel} = \begin{bmatrix} \frac{\partial y_{heel}}{\partial \theta_h} \\ \frac{\partial y_{heel}}{\partial \theta_k} \\ \frac{\partial y_{heel}}{\partial \theta_a} \end{bmatrix} = \begin{bmatrix} l_1 \sin(\theta_h) + l_2 \sin(\theta_h + \theta_k) + l_3 \sin(\theta_h + \theta_k + \theta_a) \\ \quad + l_4 \cos(\theta_h + \theta_k + \theta_a) \\ l_2 \sin(\theta_h + \theta_k) + l_3 \sin(\theta_h + \theta_k + \theta_a) \\ \quad + l_4 \cos(\theta_h + \theta_k + \theta_a) \\ l_3 \sin(\theta_h + \theta_k + \theta_a) + l_4 \cos(\theta_h + \theta_k + \theta_a) \end{bmatrix} \quad (2)$$

Gait Segmentation and Temporal Gait Parameters

Kinematic data were segmented into gait cycles. Data from each trial were first divided into non-overlapping windows (window size of 10 s). Heel-strike and toe-off events for right and left legs were determined by using heel velocity profiles in the sagittal plane. Toe-off events in each window were defined by local maximum peaks of the heel velocity profile in the vertical direction (v_{yheel}) (Winter, 1992). The minimum distance between two consecutive peaks is 80% of signal period which was computed by using auto-correlation method. Subsequently, heel-strike was determined by the first local minimum peak of heel velocity profile in the horizontal direction (v_{zheel}) between two consecutive toe-offs. **Figure 3** illustrates the alignment of gait events with lower limb joint angles and heel velocity profiles. Definitions of temporal gait parameters are also depicted. *ST* is stance time period from heel-strike (*HS*) to toe-off (*TO*) for the same leg. Double support time *DS* in a walking gait cycle is the time when both feet are in contact with the floor. Right double support, DS_r, was defined as the time from left heel-strike to right toe-off, and vice versa for left double support, DS_l. Interlimb heel-strike duration (t) is defined as the time between the heel-strike of one leg to the subsequent heel-strike of the other.

Assessment of Subjects' Performance during Visual Kinematic Perturbations

In order to evaluate the performance of participants in adapting to the visual kinematic perturbations, we defined tracking error and response time as performance measurements. Tracking error for each gait cycle was defined as the difference between the moving cursor path and the prescribed heel path (average of gait templates across gait cycles). A value closed to zero would signify that the moving cursor which represents the subjects' heel position followed the prescribed heel path profile correctly. We first converted the desired heel path and the moving cursor's path into regions and placed them on an image of 1,000 × 1,000 pixels. The tracking error was then computed by subtracting the area inside the moving cursor to the area inside the desired heel path (in pixels). Positive tracking error was defined when the

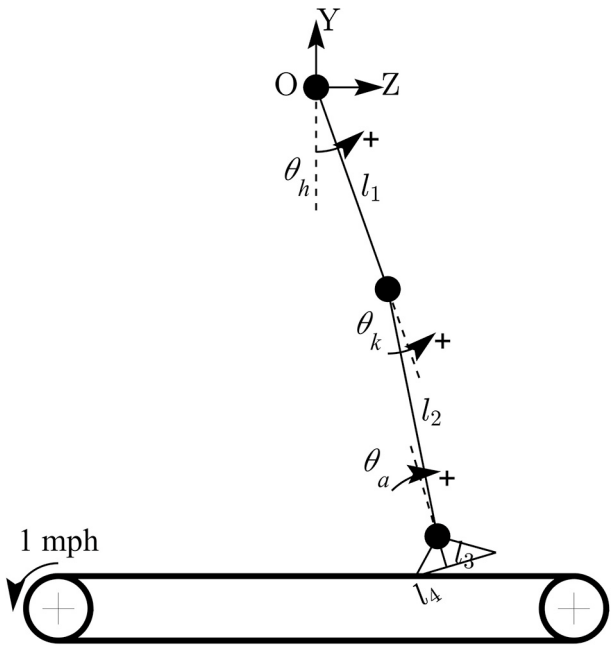

FIGURE 2 | Forward kinematic model of human walking in sagittal plane. Coordinate OZY was placed at hip position and hip joint position is assumed to be fixed. Hip joint angle was defined to increase during flexion, knee joint angle increased during extension, and ankle joint angle increased during plantar-flexion.

area of the moving cursor was larger than the area of the desired heel path and vice versa. **Figure 4** illustrates the computation of tracking error in one gait cycle.

We defined response time to measure how fast a subject responded to the visual perturbations. **Figure 5** illustrates the computation for the response time. First, the initial tracking error was computed as the average of tracking errors in the first 10 gait cycles before the subjects started responding to the perturbations, and the final tracking error was obtained by averaging tracking errors in the late exposure. We then applied cumulative sum (cusum) to track the deviations of each sample away from the initial tracking error. Cusum chart is especially useful in detecting if a signal has drifted beyond a pre-defined deviation above and below a target value. We identified the response time T_s by applying cusum with target value is the initial tracking error and the pre-defined deviation is the difference between the final and the initial tracking errors. The response time T_s was computed in the number of gait cycles.

Assessment of the Adaptations of Lower Limb Joint Angles across Subjects

To analyze the adaptation of lower limb joint angles under the presence of the visual perturbations, we computed the ratio between the range of movement (ROM) in late-exposure (Trial 4) and the ROM in normal walking (without visual feedback). The ROM ratios were computed for all joints (hip, knee, and ankle) of the right leg.

Assessment of Gait Symmetry during Visual Kinematic Perturbations

The changes of gait symmetry under constraint of visual kinematic perturbations were measured in both temporal and spatial domains. Previous studies on locomotion adaptation using split-belt treadmill have demonstrated that the motor system may generate temporal motor outputs to minimize the difference in double support times when the subjects were walking under perturbations (Reisman et al., 2005; Malone et al., 2012). These studies also suggested that the temporal motor outputs from motor system approach a desired value defined as the normalized stance time difference. In this study, the gait symmetry index in the temporal domain is defined as follows:

$$S_{temporal} = \frac{ST_l - ST_r}{t_r + t_l} \quad (3)$$

where t_r and t_l are right and left step times; ST_r and ST_l are stance times of right and left legs, respectively.

In the spatial domain, the differences between lower limb joint angles of the right and left legs were defined to characterize spatial asymmetry. The gait symmetry index in the spatial domain were defined as the difference between the range of motion (ROM) of the right and the left legs normalized by their sum:

$$S_{spatial} = \frac{ROM_{r\gamma} - ROM_{l\gamma}}{ROM_{r\gamma} + ROM_{l\gamma}} \quad (4)$$

where γ is the angle between the vertical line (to the ground) and the line that connects right hip (greater trochanter) and heel (the posterior aspect of the calcaneus) positions.

Gait symmetry indices in both temporal and spatial domains were normalized by subtracting the mean of these values in the period when the subjects walked without the visual feedback on the screen. Gait symmetry values closed to zero indicate that a subject's gait pattern was highly symmetrical.

Statistical Analysis

Statistical analyses were performed to analyze the changes of tracking errors, which had non-normal distributions, across different phases in the 4 training trials: pre-exposure, exposure (from trial 1 to trial 4), and post-exposure. Kruskal-Wallis non-parametric statistical tests with Tukey-Kramer correction for *post-hoc* multiple comparison was applied to assess the changes of tracking errors and response time across all trials. This model was also applied to test the adaptation of the spatial and temporal gait symmetry across all trials. To compare the adaptation of lower limb joint angles, which had normal distributions, under the presence of perturbations, we used a within subject, repeated-measures one-way ANOVA test.

RESULTS

Subjects Adapted Their Gait in Response to Visual Kinematic Perturbations

We observed changes in both tracking errors and response time across training trials. **Figure 6A** shows the group means

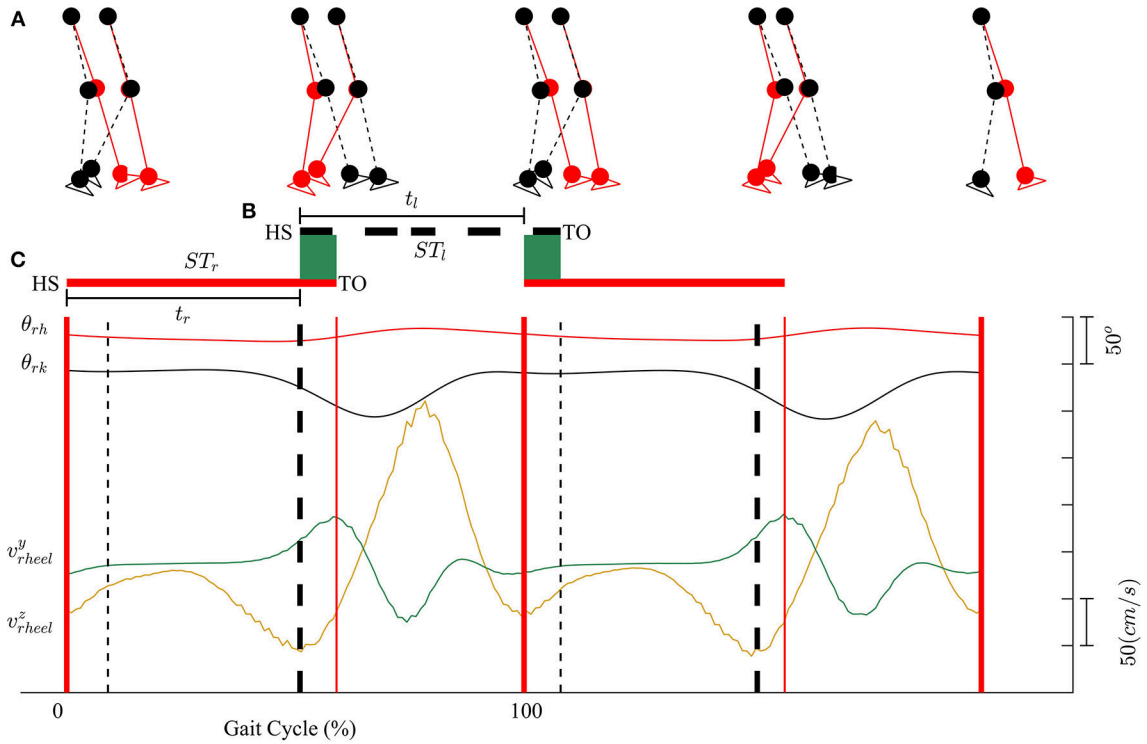

FIGURE 3 | (A) Diagram for human walking at different gait events, walking speed 1 mph. **(B)** Definitions of temporal parameters of human locomotion. HS, heel strike; TO, toe-off. Solid and dashed horizontal lines represent stance time period (*ST*) for the right (ST_r) and left (ST_l) legs, respectively. Shaded areas indicate double support periods when both feet are on the ground; DS_r and DS_l are the right and left double support periods, respectively. Step times (interlimb heel-strike durations) of the right and left legs (t_r and t_l) are defined as the time between consecutive heel-strikes. **(C)** θ_{rh}, and θ_{rk} are hip and knee joint angles of the right leg, respectively. v_{yheel}, and v_{zheel} are velocity profiles of heel in y and z directions. Thick solid and dashed vertical lines represent gait events for the right and left legs, respectively.

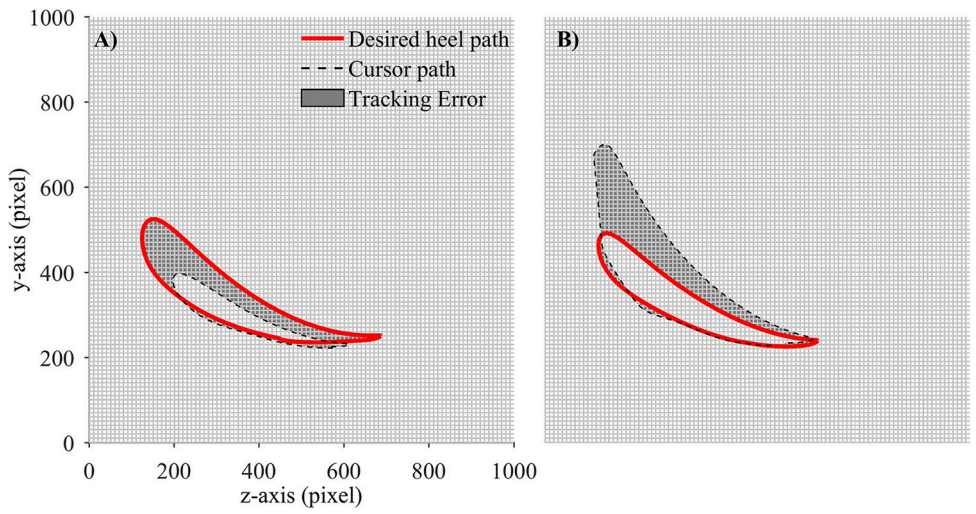

FIGURE 4 | Computation of tracking error in each gait cycle. Desired heel path (solid red line) and cursor path (dashed black line) were placed on a 1,000 × 1,000 pixel image. Tracking error was defined as the number of pixels in gray area. Each small square block in the grid contains 100 pixels. **(A)** Tracking error is negative and **(B)** Tracking error is positive.

of tracking errors in different phase of training: pre-, exposure, and post-. During pre-exposure, subjects walked normally on treadmill and the moving cursor was closed to the prescribed heel path. When visual kinematic perturbations were introduced (lower limb joint angles were scaled down by 0.7), the moving cursor departed from the prescribed heel path and subjects

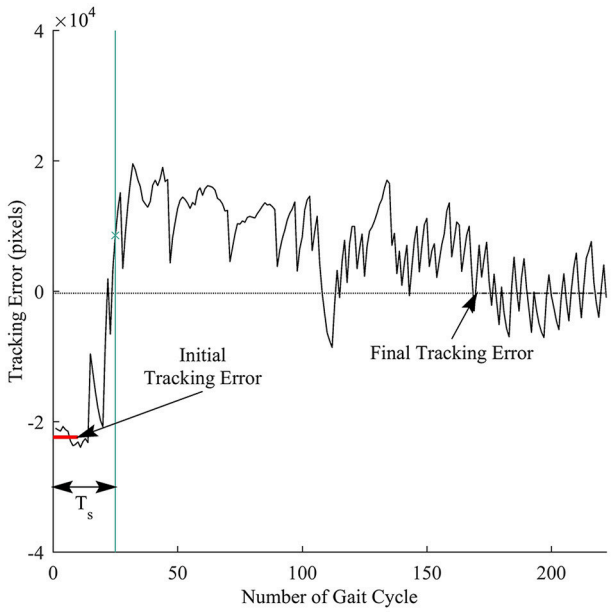

FIGURE 5 | Illustration of response time definition for each trial. Thick red line represents the initial tracking error (at the beginning of perturbation), and dashed line represents final tracking error (at late exposure). T_s is the response time computed in the number of gait cycles. Vertical green line is time when a subject responded to the visual perturbations.

started adapting their gait to the perturbation. The tracking errors in the early exposures gradually decreased across trials (from Trial 1 to Trial 4) as subjects were adapting to the visual perturbation. When subjects resolved the perturbation problem, the moving cursor were closed the prescribed heel path profiles again. In the post-exposure phase, the visual kinematic perturbation was removed. In this phase, the moving cursor departed from the prescribed heel path profiles again but in the opposite direction (positive tracking errors), reflecting after-effects of gait adaptation. By the end of this trial, the tracking errors returned to pre-exposure levels.

Figure 6B shows the results of statistical analysis for tracking errors. Significant increases in tracking errors [block means ($\times 10^4$ pixels): pre $= -0.47 \pm 1.21$; early exposure (the first 30 gait cycles in Trial 1) $= -2.07 \pm 1.25$, $P < 0.001$] were found immediately after the introduction of visual kinematic perturbations. As expected, the tracking errors gradually decreased with practice from Trial 1 to Trial 3 and reached a plateau in Trial 4 [block means for early-exposure ($\times 10^4$ pixels): Trial 1 $= -2.07 \pm 1.25$; Trial 2 $= -0.54 \pm 1.57$; Trial 3 $= -0.28 \pm 1.26$, and Trial 4 $= -0.29 \pm 0.97$]. There were significant after-effects for tracking errors in the early post-exposure phase (the first 1 min) when the visual perturbation was removed [group means ($\times 10^4$ pixels): pre $= -0.47 \pm 1.21$; early post $= 0.68 \pm 1.54$, $P < 0.001$]. **Figure 6C** shows the results of response time during exposure periods across 4 trials. When the visual perturbation was introduced in the first trial, the mean and one standard deviation of the response time across all subjects was 148.5 ± 69.1 gait cycles. These value substantially decreased in later trials except for Trial 4 (Trial 2: 56.2 ± 36.0; Trial 3: 19.3 ± 20.7; Trial 4: 35.7 ± 36.7). Although the response time in the trial 4 is higher than in the trial 3, the difference is non-significant (p-value > 0.05).

Strategies of Gait Adaptation Varied across Subjects

Figure 7 depicts the changes in lower limb joint angles during late-exposure (Trial 4) when subjects adapted to the visual kinematic perturbations. Results from *post-hoc* analysis show that subjects varied joint angles differently when adapting to the perturbation. For example, SG01 had more changes in ankle joint angles (Hip: 1.35 ± 0.14; Knee: 1.57 ± 0.10; Ankle: 3.11 ± 0.34, $P < 0.001$), while SG02 had more changes in knee joint angles (Hip: 1.09 ± 0.15; Knee: 1.61 ± 0.09; Ankle: 1.02 ± 0.06, $P < 0.001$). **Figure 7A** shows that different strategies of gait adaptation affect tracking errors in the late-exposure. Specifically, the tracking errors of subjects SG01: 12.61 ± 6.95, SG06: 11.06 ± 6.25, and SG08: 10.46 ± 2.80 were significantly higher than the other subjects: 8.67 ± 4.45 (these values are in $\times 10^3$ pixels). **Figure 7B** reveals that SG01, SG06, and SG08 adapted more on the ankle joint angles instead of the hip and knee joints. This gait adaptation strategy resulted in larger tracking errors because the changes in the ankle joint angles have lesser effect on the variations of heel position as compared to the changes in the hip and knee joint angles (Equation 2).

Gait Symmetry in the Spatial and Temporal Domains during Visual Kinematic Perturbations

Figure 8 illustrates the changes of gait symmetry in the temporal domain to visual kinematic perturbations. Theoretically, the right and left double support limb periods are equal during normal walking conditions (pre-exposure). When visual kinematic perturbations were introduced and subjects started adapting their gait to the perturbation, the double support periods are different and the gait asymmetry in temporal domain increase. In the post-exposure phase, visual kinematic perturbations were removed and double support periods gradually return to symmetric step times.

We observed that $S_{spatial}$ and $S_{temporal}$ can characterize the adaptation of gait symmetry in the spatial and temporal domains, respectively. For example, results from **Figure 9** show that $S_{spatial}$ and $S_{temporal}$ significantly increased between the early (Trial 1) and late exposure phase (Trial 4), indicating the adaptation of motor outputs for gait symmetry ($S_{spatial}$ − Trial 1: 0.09 ± 0.09, Trial 4: 0.19 ± 0.06, $P < 0.001$; $S_{temporal}$ − Trial 1: 0.05 ± 0.07, Trial 4: 0.08 ± 0.08, $P < 0.001$). Moreover, there was significant difference between pre- and post-exposure ($S_{temporal}$ − Pre: 0.02 ± 0.07, Post-Exposure: 0.06 ± 0.09, $P < 0.001$), indicating that there were significant storages of new gait symmetry indices in the temporal domains.

Figure 9 also illustrates that the gait symmetry in the temporal domain is less sensitive to the visual kinematic perturbations and its after-effects are larger than those in the spatial domain. For example, when the perturbations were introduced, $S_{spatial}$

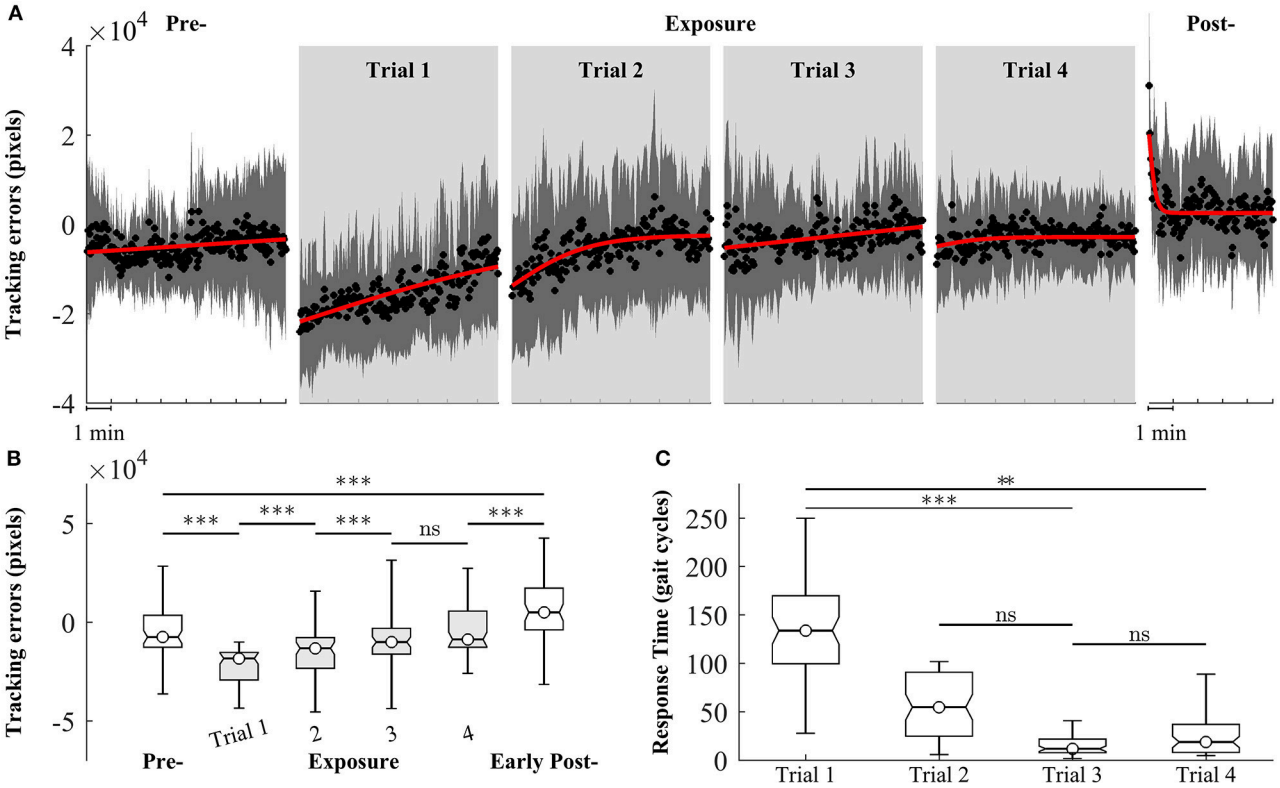

FIGURE 6 | Group averages of tracking errors across 4 trials of training, gray areas represent early exposure period. **(A)** Black circles represent mean of tracking errors across subjects, and shaded areas indicate one standard deviation. Solid lines are fitting curves using a sigmoidal model. **(B,C)** Statistical analysis of tracking errors and response time using multiple comparison test with Tukey-Kramer adjustment, respectively. $^{**}P < 0.01$ and $^{***}P < 0.001$. ns, non-significant.

increased from -0.002 ± 0.07 (Pre-) to 0.12 ± 0.14 (Exposure, trial 1) while $S_{temporal}$ increased from 0.02 ± 0.07 to 0.05 ± 0.07. When the perturbations were removed, $S_{spatial}$ decreased from 0.18 ± 0.08 (Exposure, trial 4) to 0.006 ± 0.09 (Post-) while $S_{temporal}$ decreased from 0.08 ± 0.08 to 0.06 ± 0.09. Moreover, gait symmetry index in the spatial domain approached a new-steady state faster than in the temporal domain. For example, $S_{spatial}$ reached a new steady state on Trial 2 ($S_{spatial}$ was not significantly different from Trial 2 to Trial 4) while $S_{temporal}$ reached a new steady-state on Trial 4. The perturbation resulted in a stronger after-effect in the temporal domain as compared to the spatial domain. The temporal gait symmetry was significantly different between the pre- and post-exposure phase ($P < 0.001$) and it lasted for more than 5 min. However, there is no significant difference in the spatial gait symmetry index between pre- and post-exposure phase. When the perturbation was removed, the spatial gait symmetry index returned to the pre-exposure condition in <1 min.

DISCUSSION

This study investigated gait adaptation of healthy individual in the presences of visual kinematic perturbation (i.e., a gain change) of gait during treadmill walking across several trials. The visual kinematic perturbations, which caused a mismatch between actual and prescribed heel path trajectories displayed on a screen, were introduced to investigate visual-motor adaptation of human locomotion. We observed that, with practice, the subjects could reduce the errors induced by the visual kinematic perturbations and showed faster response time in later trials (Trial 1 to Trial 3). Thus, by late exposure, subjects have found a solution for the visual kinematic perturbations problem and acquired, at least partially, the internal model of the visuomotor transformation. Moreover, the strategies of gait adaptation varied across subjects and affected steady-state tracking errors in late-exposure. Our results also showed that the temporal gait symmetry in the post-exposure phase was significantly different from the pre-exposure phase. This after-effect suggested that there were significant storages of new temporal gait symmetry index.

Introduction of the kinematic gait perturbation showed an initial rise of tracking errors in early-exposure, the reduction of tracking errors in exposure, and the after-effect in post-exposure (**Figure 6**). The presence of after-effects is an indication that motor adaptation has occurred (Shadmehr and Mussa-Ivaldi, 1994; Kagerer et al., 1997; Buch et al., 2003; Krakauer et al., 2005; Scheidt et al., 2005; Choi and Bastian, 2007; Reisman et al., 2009; Kim et al., 2010). Although the experimental setup in this study is simple, the results reflect the decreases of tracking errors

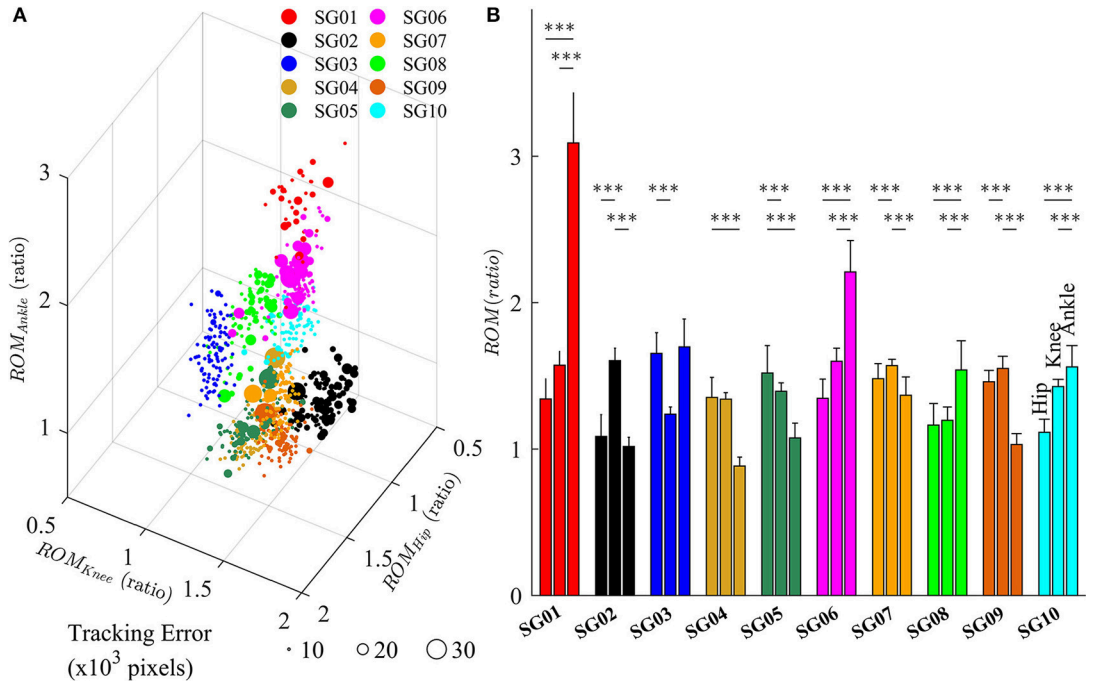

FIGURE 7 | (A) Variations of lower limb joint angles (hip, knee, and ankle) in the right leg for 10 subjects in late-exposure (Trial 4). The size of the symbols represents the tracking error. **(B)** ROM ratio is the proportion of range of motion in late-exposure compared to pre-exposure. *Post-hoc* analyses using multiple comparison with Tukey-Kramer adjustment. ***$P < 0.001$.

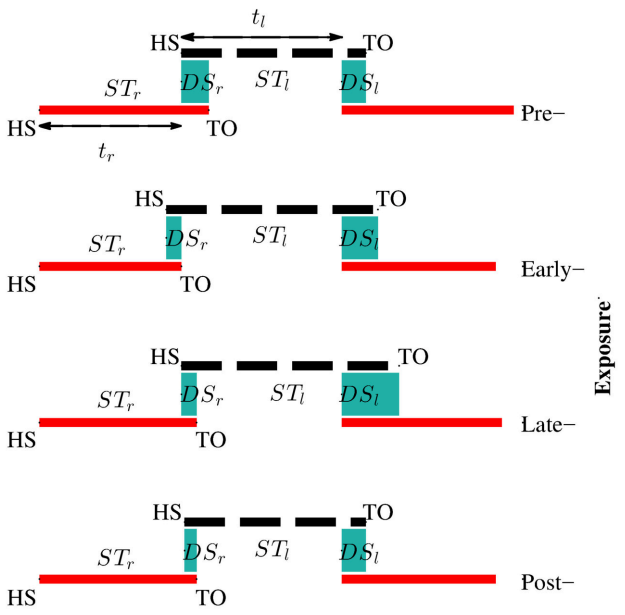

FIGURE 8 | Adaptation of temporal parameters during visual kinematic perturbations for subject SG04. The solid red line and dashed black line represent stance periods of the right and left leg, respectively. Double support periods are represented by the shaded sea green area. During the pre-exposure phase, the subject walked normally and the right and left double support times were equal. Temporal asymmetry increased in the exposure phases and sustained in post-exposure.

across trials and the after-effects that characterize the motor adaptation process. We hypothesize that the training method used in this study could be a feasible intervention to potentially improve asymmetries in post-stroke gait rehabilitation. Previous studies have shown that after-effects of locomotor or visuomotor adaptation improve task performance in individuals post-stroke (Rossetti et al., 1998; Patton et al., 2006). Moreover, Reisman et al. demonstrated that the improvements of task performance following split-belt treadmill adaptation could transfer to real world tasks such as overground walking (Reisman et al., 2009).

Gait asymmetry is an important gait characteristic that may have a role in guiding the clinician's treatment decisions (Patterson et al., 2008, 2010). Gait asymmetry may be associated with negative effects on human locomotion such as decreases in gait efficiency, balance control, and gait speed (Jorgensen et al., 2000). For example, asymmetric step length results in decreased walking speed, and both decreased propulsive force and increased severity of the paretic limb (Bowden et al., 2006; Balasubramanian et al., 2007; Jonkers et al., 2009). Asymmetric double support time is related to decreased gait speed (Olney et al., 1994). Asymmetric walking gait patterns are commonly found in individuals post-stroke. However, some individuals post-stroke have asymmetry in only one domain. For example, they only have either step length asymmetry (spatial) or double support time asymmetry (temporal). Therefore, it could be more efficient to target therapeutic rehabilitation to only the domain (spatial or temporal) of gait symmetry in which the post-stroke persons experience difficulty. Separate control of the

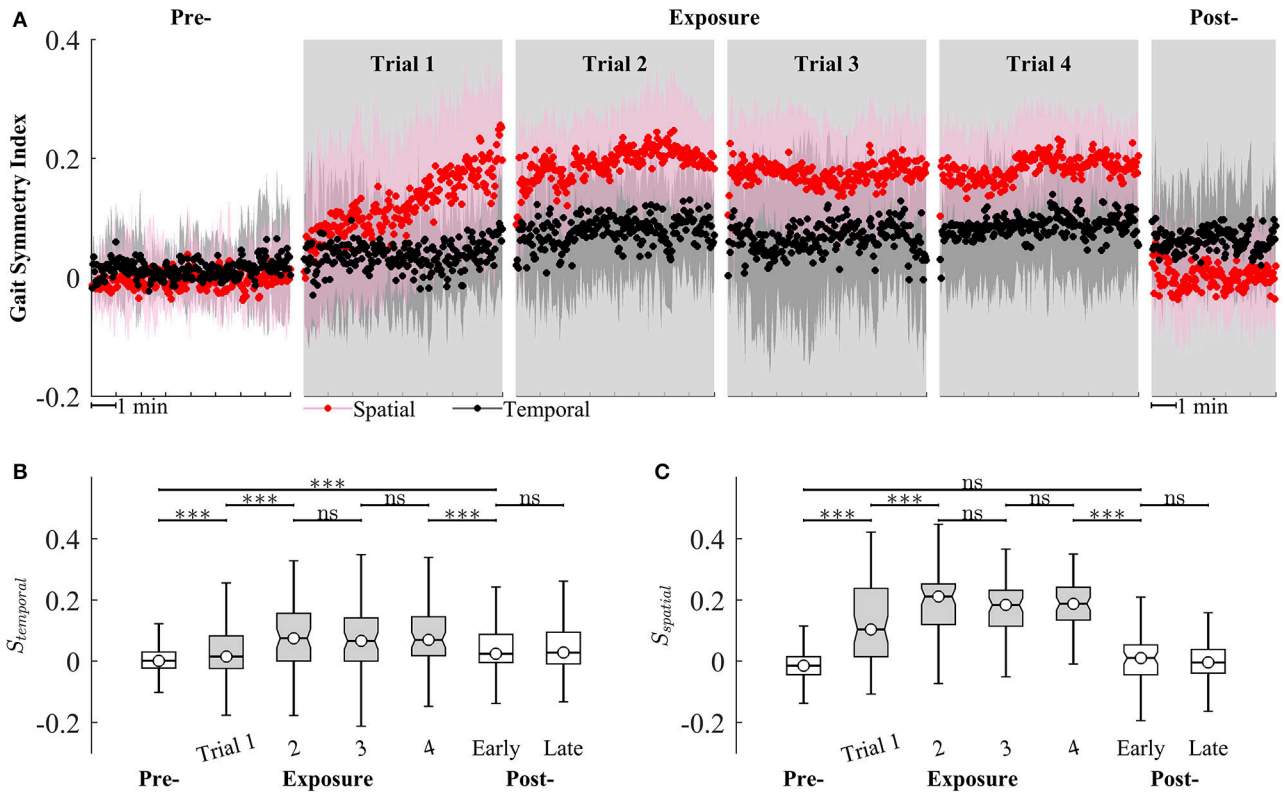

FIGURE 9 | (A) Group averages of gait symmetry indices across 4 trials of training. Black and red circles represent mean values of temporal and spatial gait symmetry indices, respectively. Shaded areas indicate one standard deviation. **(B,C)** Statistical analysis for gait symmetry index in the temporal ($S_{temporal}$), and spatial ($S_{spatial}$) domain using multiple comparison with Tukey-Kramer adjustment. ***$P < 0.001$, *ns*, non-significant. Box plots in gray represent exposure period.

temporal and spatial control of human locomotion has been demonstrated in studies of locomotor adaptation to split-belt treadmill training (Reisman et al., 2009; Malone et al., 2012). However, interventions that target only one domain of gait asymmetry have not been fully developed. In this study, multi-trial locomotor training using visual kinematic perturbations was implemented and the subjects adapted to the perturbations by modifying their gait patterns. Once adapted, the subjects could not retrieve their normal gait pattern immediately when the perturbations were removed. Instead, they had to "de-adapt" their gait patterns back to original state. This after-effect was a strong clue that motor adaptation has occurred and a new representation of visuomotor mapping has been learned. Results in **Figure 9** show the after-effects of gait symmetry indices in the temporal domains in early post-exposure phase, indicating that there were significant storages of new temporal gait symmetry index. However, after-effects were not observed for the spatial gait symmetry index. These findings have implications for a possible intervention to improve gait symmetry in the temporal domain for individuals post-stroke and the setup in this study could be beneficial to gait rehabilitation.

Our results suggest differential temporal and spatial symmetry effects to the kinematic perturbations. For example, we observed after-effects of the temporal gait symmetry index after the presence of kinematic perturbations, indicating its adaptation. However, the after-effect or adaptation of the spatial gait symmetry was missing. These results support previous findings suggesting that the adaptation of spatial and temporal gait symmetry is dissociable (Malone et al., 2012). The tracking task in this study was mainly spatial because the subjects followed the desired heel path without considering the time to reach a specific point. Interestingly, the adaptation occurred nevertheless in the temporal gait symmetry. This could have the implication that the subjects unconsciously adapted temporal gait symmetry under the visual kinematic perturbations. This findings are aligned with previous studies suggesting that subjects may not be able to consciously prevent adapting temporal motor output under split-belt conditions (Malone et al., 2012), and that temporal gait symmetry is harder to influence with conscious efforts (Malone and Bastian, 2010). Additionally, our findings support the hypothesis that the temporal control of human gait is more automatic and depends more heavily on subcortical circuits. Vasudevan et al. (2011) also showed that temporal adaptation was found to be fully developed earlier than spatial adaptation (by 3 year old and until adolescence, respectively).

The feasibility of this intervention to improve gait asymmetry might also be extended to target only specific joints that may be affected more than others. Our results demonstrated that

subjects use multiple solutions, i.e., multiple ways for subjects to alter their joint movements, to adapt to the visual kinematic perturbations (**Figure 7**). For example, while the subject SG01 preferred to adapt the ankle joint angles, the subject SG02 favored to adapt the knee joint angles instead. **Figure 7** illustrates that different strategies of gait adaptation affect tracking errors in late-exposure. Moreover, **Figure 7B** reveals that subjects who adapted more on the ankle joint angle instead of the hip and knee joints (SG01, SG06, and SG08) showed larger steady-state tracking errors in the late-exposure phase. This gait adaptation strategy resulted in higher tracking errors because the changes in the ankle joint angles have lesser effect on the variations of the heel positions as compared to the changes in the hip and knee joint angles (Equation 2). Overall, these findings are supported by the motor equivalence problem (Bernstein, 1967), which characterizes the kinematic redundancy of motor control systems: in this case, using three degrees of freedom (hip, knee, and ankle joints) to control the heel position in a two-dimensional space. Therefore, even though there are multiple solutions (due to redundant degrees of freedom) to accomplish a motor task, we can indirectly influence the motor system to favor one solution by controlling the rules that generate visual kinematic perturbations (i.e., using different scaling factors for each joint angle), which can allow for personalized gait therapy based on the current state of the patient.

Findings of this study are currently limited to healthy individuals. Future investigations should consider implementing the framework of visual kinematic perturbations for gait rehabilitation in individuals post-stroke. In this regard, the motor task is expected to be more challenging for persons post-stroke. The number of trials required to achieve significant performance improvement may also increase. It will also be important to examine the changes in the representations of gait at cortical level during the visual kinematic perturbations. The understanding of neural mechanisms of human gait adaptation is important for designing an effective training paradigm of gait rehabilitation in a top-down approach. Noninvasive electroencephalography (EEG) studies could be designed to investigate the underlying patterns of neural activity during the visual kinematic perturbations.

AUTHOR CONTRIBUTIONS

TPL contributed to task design, developing software for data collection, acquisition of the data, interpretation for the work, and manuscript draft. YH contributed to developing software for data collection, acquisition of the data, and literature review. SN, KN, and JG contributed to experimental design, data acquisition, and revising the draft. SB contributed in developing software for data collection and manuscript review. JC conceived the experiment, edited the manuscript and approved the final version of the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2017.00320/full#supplementary-material

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