Patterns of whole-body muscle activations following vertical perturbations during standing and walking

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Research

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Abstract

Background Falls commonly occur due to losses of balance associated with vertical body movements (e.g. reacting to uneven ground, street curbs). Research, however, has focused on horizontal perturbations, such as forward and backward translations of the standing surface. This study describes and compares muscle activation patterns following vertical and horizontal perturbations during standing and walking, and investigates the role of vision during the standing postural responses. Methods Fourteen healthy participants (ten males; 27±4 years-old) responded to downward, upward, forward, and backward perturbations while standing and walking in a virtual reality (VR) facility containing a moveable platform with an embedded treadmill; participants were also exposed to visual perturbations in which only the virtual scenery moves. We collected bilateral surface electromyography (EMG) signals from 8 muscles (tibialis anterior, rectus femoris, rectus abdominis, external oblique, gastrocnemius, biceps femoris, paraspinals, deltoids). Parameters included onset latency, duration of activation, and activation magnitude. Standing perturbations comprised dynamic-camera (congruent), static-camera (incongruent) and eyes-closed sensory conditions. ANOVAs were used to compare the effects of perturbation direction and sensory condition across muscles. Results Vertical perturbations induced longer onset latencies and durations of activation with lower activation magnitudes in comparison to horizontal perturbations. Downward perturbations while standing generated faster activation of rectus femoris and tibialis anterior, whereas biceps femoris and gastrocnemius were faster to respond to upward perturbations. Initial responses to downward and upward perturbations activated trunk/hip flexors and extensors, respectively. Eyes-closed conditions induced longer durations of activation and larger activation magnitudes, whereas static-camera conditions induced longer onset latencies. During walking, downward perturbations promptly activated contralateral trunk and deltoid muscles, and upward perturbations triggered early activation of trunk flexors. Visual perturbations elicited muscle activation in 67.7% of trials. Conclusion Our results demonstrate that vertical (vs. horizontal) perturbations generate unique balance-correcting muscle activations with prioritized control of trunk/hip configuration for postural control after vertical perturbations. Availability of visual input appears to affect response efficiency, and incongruent visual input can adversely affect response triggering. Our findings have clinical implications for the design of robotic exoskeletons (to ensure user safety in dynamic balance environments) and for perturbation-based balance and gait rehabilitation.

Introduction

Losses of balance associated with vertical maneuvers are common in daily life, such as when experiencing mis-steps on uneven ground or reacting to unexpected steps or street curbs [1-4]. Despite their commonality, the research on balance recovery mechanisms heavily focuses on horizontal perturbations [5-7]. The literature would benefit from a more mechanistic understanding of balance recovery in response to vertical perturbations in order to inform rehabilitation strategy or to support programming for assistive devices [8-11]. Therefore, in support of these goals, this study compares the muscle activation patterns induced by vertical versus horizontal perturbations and explores the role of vision in these responses.

Sudden, unexpected physical perturbations exerted over the human body can be a destabilizing force that compromises balance [6, 12]. For restoring balance after sudden physical perturbations, the central nervous system engages in rapid postural responses of contextually relevant muscle activation patterns [6, 7, 13-16]. These responses comprise complex patterns of muscle activation that progressively develop via supraspinal control [17] and are dependent on multisensory feedback [5, 15, 18]. Given the complex and context-dependent control of postural responses to extrinsic perturbations, it is important to understand the muscle response patterns to vertical perturbations.

After horizontal perturbations, assuming a full base of support, the strategy adopted by healthy adults often employs a distal-to-proximal, reciprocal muscle activation pattern; for example, anterior muscles such as the tibialis anterior, rectus femoris and rectus abdominis are primarily activated after anterior surface translations to correct an induced backward fall, and posterior muscles such as gastrocnemius, biceps femoris, and erector spinae are primarily activated after posterior surface translations to correct an induced forward fall [13-15, 19]. Fewer studies evaluated postural responses to vertical perturbations during standing [20-22] or walking [23-25]. The aforementioned studies, however, focused on stretch reflexes from leg muscles, not accounting for the coordinated, progressive, multi-segmental responses necessary to maintain functional balance [26]. The present study sought to elucidate leg-trunk-shoulder muscle activation patterns that characterize balance-correcting responses to vertical perturbations during standing and walking.

We hypothesized that muscle activation patterns in response to vertical perturbations will differ from those in response to horizontal perturbations, because vertical perturbations generate unique challenges to equilibrium [6, 13, 21, 27, 28] (for a detailed rationale of a priori predictions and hypotheses, see Supplementary File #1). We further hypothesized that the role of vision would differ for vertical versus horizontal perturbations due to the critical role of vision in maintaining equilibrium [29-31], and because visual perturbations can signal gravitational changes as well as positional changes [32, 33]. Specifically, since vertical visual scenes influence the apparent direction of gravity [33] and anteroposterior visual scenes act in advance of induced falls, we expect that visual conditions will modulate postural responses by adjusting the body against expected gravitational forces following vertical perturbations, and by activating muscles opposing a potential fall following horizontal perturbations. Last, because postural adjustments progressively adapt to environmental visual cues, and there is an attenuation of initial activity when visual cues are inconsistent with other sensory cues [34], we anticipate that incongruent (and absence of) vision will lead to longer latency, duration and increased magnitude of activation.

Methods

Participants. Fourteen young, healthy adults (mean age±SD: 27±4 y; BMI: 23.8±2.6 kg/m^2; 10 males, 4 females) participated in this study. None of the participants had sensory, motor or cognitive limitations that could potentially affect balance or gait. All participants were able to follow instructions and gave written informed consent before being enrolled in the study. The Institutional Review Board for Ethics in Human Studies at the Sheba Medical Center, Israel, approved the experimental protocol.

Apparatus. Experiments were conducted with a fully immersive virtual reality system (CAREN High End, Motek Medical, The Netherlands; Figure 1), containing a moveable platform with six degrees of freedom [35]. The platform included two force plates and contained an embedded treadmill that operated in self-paced mode, allowing participants to adjust treadmill speed to preferred walking speed [36]. An electromyography (EMG) system (ANT Neuro, Hengelo, The Netherlands) captured bipolar electrical activity of muscle activation with a sampling frequency of 1024 Hz bilaterally from the tibialis anterior, gastrocnemius lateralis, rectus femoris, biceps femoris, rectus abdominis, paraspinals, external oblique and medial deltoid (Figure 1C). A motion capture system (Vicon, Oxford, UK) concurrently tracked the three-dimensional coordinates of 41 passive-reflective markers affixed to the body of each participant with a sampling rate of 120 Hz and spatial accuracy of 1 mm.

Visual scenery. Standing and walking conditions incorporated two different visual sceneries (Figure 1 A-B). In standing conditions, we implemented a simulated room with objects such as paintings on the wall and plants on the floor. Objects provide depth cues and influence motion perception (e.g., via lines of depth perspective). In walking conditions, visual scenes simulated walking on an asphalt road in a park, with a brick wall ending at the horizon and greenery adjacent to the wall. Scenes were modeled in three dimensions with specialized software (Autodesk XSI). Textures were created and modified with Adobe Photoshop. Custom software (D-Flow, Motek Medical, The Netherlands) was used for programing, integration, and projection, as well as for displacing the platform and activating the treadmill in a synchronized manner with the EMG recording system. We placed a virtual camera in the virtual world, representing both the center of the lab and the center of the moveable platform. During the experimental walking conditions, the visual scene advanced in the sagittal plane (i.e., visual flow) at a speed synchronous with the speed of the treadmill – and the entire virtual world moved around the virtual camera. The visual scenes were projected on a 360° dome-shaped screen (six meters in diameter) by eight video projectors. Projector resolution was 1400x1050 pixels, and participant viewing distance was three meters.

Experimental procedures. A familiarization period for mastering the self-paced mode of the treadmill (10-15 min) ensued the calibration of EMG and motion capture systems. Participants were first exposed to visual perturbations (the virtual room moves a distance corresponding to a platform movement of 14 cm in 0.35 seconds while the participant is standing). Visual perturbations were downward, upward, forward and backward. Each perturbation direction repeated three times in random order, totaling 12 visual perturbations. The person was standing in the static virtual room and the first perturbation occurred after 45 seconds; subsequent perturbations occurred according to a random epoch of 5-10 seconds.

Physical perturbations followed visual perturbations. Participants were exposed to 12 types of perturbations during standing and 12 types of perturbations during walking (Figure 1 A-B). Each type of perturbation was repeated three times, totaling 36 perturbations (i.e., 72 physical perturbations combined across standing and walking conditions). Both standing and walking perturbations were divided into three trial blocks. Each trial block included 12 perturbations taking place in random order (i.e. three blocks for standing and three blocks for walking). To minimize learning effects, before starting the research experiments, we randomized for all participants to start with either a standing or walking trial block. Trial blocks were then alternated between standing and walking until completing all six blocks. Within each single block, the type of perturbation was also randomized (out of 12 possibilities; see Figure 1).

Walking was performed in self-paced mode. Except in one occasion, however, due to technical constraints (for one participant) the treadmill was limited to a maximum walking speed of 1.4m/s. The dataset generated in this occasion was included in analysis because the imposed limit on walking speed did not affect this participant's balance performance. All trial blocks were completed in a single session and participants were offered a resting period in all intervals between trial blocks.

Standing perturbations (see Figure 1A**).** Perturbations were downward, upward, forward, and backward, each within three sensory conditions: static-camera, dynamic-camera, and eyes-closed. We used upward perturbations to balance participant expectations to downward perturbations (i.e. to avoid expecting downward perturbations in larger proportion), and horizontal perturbations for comparison due to the more-developed literature for horizontal perturbations. Perturbations were displacements of the moveable platform integrated into the VR system. The displacement was 12 cm, with a duration of one second for each direction. These parameters were chosen to facilitate feet-in-place responses rather than inducing stepping responses. Participants were asked to maintain an upright position with the feet within marked boundaries, defined by the initial positioning of their feet (i.e. stance width) when asked to stand comfortably. Perturbation intensity was selected to allow most participants to maintain balance without stepping [37]. In dynamic-camera conditions, the virtual room moved according to the physical displacement of the platform, whereas in static-camera conditions, the virtual room remained static, thus providing a sense of sensory conflict or incongruence. During eyes-closed conditions, a pre-recorded audio message asked the person to close the eyes, which was accompanied by the virtual environment being turned off; and then after the perturbation occurred, a pre-recorded audio message asked the person to open the eyes and the virtual environment was turned on. The experimenter periodically confirmed via direct observation that the participant was complying with the recorded audio commands. No 'ignoring' behavior was noted.

Walking perturbations (see Figure 1B and *Video 1* in *supplementary file #2***).** There were four perturbation directions: downward, upward, forward and backward. All perturbations were of sub-gravitational intensity (i.e. a platform displacement of 20 cm occurring in 300 ms). In addition, we included vertical perturbations (downward, upward) that approximated gravitational intensities (i.e. 20 cm in 202 ms). In this study, however, we focus on perturbations with sub-gravitational intensities for comparison of the four directions. Perturbations were displacements of the moveable platform occurring during either left- or right-foot contact of early stance [24, 25]. A real-time algorithm identified foot contact based on a combination of the vertical coordinates of heel markers and the pressure force on the platform. The first perturbation was triggered either after attaining steady-state velocity (SSV) or after one minute (without attaining SSV), and a random epoch (<10s) was added for triggering subsequent perturbations to reduce the predictability of the perturbations in both timing and direction, which limits a participant's ability to pre-plan responses or generate anticipatory responses. SSV was defined as walking at least 30 s with a 12 s consecutive period in which the coefficient of variance of walking speed was less than 2%, either after initiation of a trial block or since the previous perturbation occurred.

Analysis of EMG activity (Figure 2). EMG signals were filtered (finite impulse response band-pass of 20-400 Hz) and full-wave rectified. Calculated EMG parameters were onset latency, duration of activation, and activation magnitude. The calculation of EMG parameters was based on a three-second window: one second before (baseline) and two seconds after perturbation onset. EMG signals were then integrated and normalized within each window, i.e. normalized so that the integrated EMG value and the time for analysis had a final value of 1. The latter process is intended for the purpose of identifying burst onset and burst offset, and not for calculation of activation magnitude. Onset latency was defined as the period between perturbation onset time and the onset of EMG activity beyond baseline levels. The method for calculating onset latency has been previously described in detail [38]. In summary, onset latency represents the largest distance between the normalized, integrated EMG signal and a unitary line serving as reference. The algorithm focuses on identifying the early burst of EMG activity occurring after perturbations. When the rate of growth in the normalized, integrated EMG (for each three-second window of analysis) identifies an onset latency before perturbation time, there is an indication that the EMG activity did not increase after perturbation. We marked those cases as "no response". The same method was used to calculate the duration of activation. For this, the three-second window of the EMG signal was inverted in order to identify the initial (i.e. the last) part of the EMG burst. Duration of activation was defined as the period elapsing between the onset and the end of the EMG burst. We used numerical integration (i.e. trapezoidal method) on the identified period of EMG activation for the calculation of activation magnitude (i.e. over the filtered and rectified EMG signal, between "onset latency" and "activation end", see Figure 2). Because the evaluated burst period led to unequal durations, we calculated magnitude based on numerical integration for every single perturbation to obtain average magnitude during burst activity. In each type of perturbation, we averaged the values of the three repetitions for each participant, without including in the average those cases marked as "no response". No rescaling or normalization was employed to calculate activation magnitude due to the within-subject, intra-session nature of this study's analysis.

Analysis of extrapolated center of mass. In standing conditions, we computed 95% confidence ellipses for extrapolated center of mass (COM_x) [39, 40], both during baseline (i.e. six seconds before perturbation onset) and for 5 seconds after perturbation onset (period defined after an overall visual inspection of commonly occurring effects). COM_x is an extrapolation of the center of mass trajectory in the direction of its velocity, and the COMx position within the boundaries of the base of support works as stability condition [39, 40]. From each ellipse, we evaluated area, major and minor axis length, and orientation angle. Ellipse calculations followed previous methodologies [41].

Statistical analyses. The data are expressed as mean ± standard deviation unless otherwise stated. The Shapiro-Wilk calculation was used to test the hypothesis of normal distributions. For standing conditions, we computed a three-way analysis of variance (3 sensory conditions x 4 perturbation directions x 16 muscles) for two of the EMG parameters (onset latency, duration of activation). Due to the sensibility of the electrode position and the within-session nature of the experiment, for magnitude we applied a two-way analysis of variance per each muscle. For walking conditions, muscles were arranged as ipsilateral and contralateral muscles according to the side of stance-foot perturbation. We computed a three-way analysis of variance for onset latency and duration of activation (4 perturbation directions x 2 perturbation sides x muscle); for magnitude we computed a two-way analysis of variance for each muscle. For post hoc comparisons, we used the Fisher's least significant difference procedure. For comparison between baseline and after-perturbation values, we utilized two-tailed t-tests. The level of significance was set to 5% ($P<0.05$). Statistical procedures were implemented with a numerical computing environment (Matlab; The Mathworks, Natick, MA).

Results

Muscle activation in response to perturbations during standing (Figure 3)

Figure 3 illustrates the sequence and magnitude of muscle activations (color-coded) in response to physical perturbations during the standing conditions. The figure comprises data on EMG onset latency, duration and magnitude of each muscle activation seen during all standing experimental conditions. Complementing this figure is Table 1 (*Supplementary file #3*), which details the corresponding numeric values.

Description of muscle onset patterns of vertical perturbations

During standing conditions, downward perturbations led to a shorter onset latency of anterior muscles (earliest activation was observed at the rectus femoris; e.g. 0.66±0.32s, right-side muscle after eyes-closed conditions) when compared to posterior muscles (latest activation was observed at the paraspinals; e.g. 1.03±0.22s, right-side muscle after eyes-closed conditions). For instance, the pattern was observed in all comparisons between left and right paraspinals vs. all anterior muscles, with the only exception being left paraspinal vs. left rectus abdominis; the pattern was also evident in the comparisons between left biceps femoris vs. left tibialis anterior, left and right rectus femoris, right rectus abdominis, and left and right paraspinals; and for right biceps femoris vs. right rectus femoris ($P<0.05$ based on the computation of marginal means for each combination of muscle and perturbation direction, independent of the factor for sensory condition).

In contrast, upward perturbations triggered earlier onset latencies of posterior muscles, marked by earliest activation at the biceps femoris (e.g. 0.50±0.39s, left-side muscle following static-camera conditions) and latest activation at the rectus abdominis (e.g. 1.08±0.49s, right-side muscle following static-camera conditions). For instance, both (left and right) gastrocnemius and biceps femoris had an onset latency significantly earlier than the anterior muscles ($P<0.05$); only exceptions were left gastrocnemius vs. right tibialis anterior and right gastrocnemius vs. right tibialis anterior. Finally, the onset latency of lower-leg antagonist muscles (i.e. tibialis anterior and gastrocnemius) were not statistically different to each other following vertical perturbations, except that the left tibialis anterior was activated earlier than gastrocnemius after upward perturbations (P<0.05, Figure 3).

Muscle activation - Comparison of vertical and horizontal perturbations

Anterior and posterior muscles were the first to respond after forward and backward perturbations similar to downward and upward perturbations respectively (Figure 3). Unlike vertical perturbations, during which proximal leg muscles activated first, forward and backward perturbations elicited initial activation of the distal leg muscles (tibialis anterior and gastrocnemius).

Onset latencies were shorter during horizontal perturbations (fastest responses followed forward perturbations) in comparison to vertical perturbations (downward perturbations generated the most delayed responses); P<0.05, independent of the factors for muscle and sensory condition.

Duration of activation (similar to onset latency) was shorter following horizontal perturbations in comparison to vertical perturbations, with backward perturbations eliciting the longest durations; P<0.05, independent of the factors for muscle and sensory condition.

Magnitude of activation was usually larger for horizontal (forward and backward) perturbations when compared to vertical perturbations (downward and upward) (P<0.05). The pattern was observed for all muscles.

Muscle activation - Comparison of visual conditions during physical perturbations

Static-camera conditions led to longer onset latencies in comparison to both eyes-closed and dynamic-camera conditions (P<0.05).

The eyes-closed condition led to longer durations of activation in comparison to static-camera and dynamic-camera conditions (P<0.05).

Statistically different magnitudes were observed across the three sensory conditions (P<0.05). For instance, the eyes-closed condition elicited the largest magnitudes, which were significantly higher than in the dynamic-camera condition (P<0.05) that elicited the lowest activation magnitudes. This pattern was evident for all muscles, except for the right rectus femoris, right external oblique, and for both rectus abdominis muscles.

Extrapolated center of mass - Description and comparison after vertical and horizontal perturbations

Major ellipse angles were significantly larger (over 90 degrees) following both downward and upward perturbations, in comparison to both forward and backward perturbations (during which, angles were approximately 90 degrees) (Figure 4). Vertical perturbations generated larger minor ellipse angles (approximately 30 degrees) in comparison to horizontal perturbations (approximately zero degrees)

(P<0.05). Moreover, minor ellipse angles were greater in static-camera conditions in comparison to both dynamic-camera and eyes-closed conditions (P<0.05).

The area of the extrapolated center of mass was significantly larger following forward perturbations when compared to the remaining three perturbation directions (P<0.05). Similar results were found for the major and minor axes of the ellipses. Backward perturbations elicited larger areas and major (but not minor) axes than both vertical perturbations (P<0.05).

Extrapolated center of mass - Comparison of visual conditions and before vs. after perturbation

In the analysis of conditions *prior to perturbation onset*, we found that eyes-closed conditions generated larger major ellipse angles (near 90 degrees) in comparison to both static-camera and dynamic-camera conditions (P<0.05).

In the comparisons pre vs. post perturbation onset, we found that ellipse area, as well as major and minor axes increased after perturbation (P<0.05), which occurred for all combinations of sensory conditions and perturbation directions. However, major and minor axis angles only exhibited significant changes for both downward and upward perturbations and not for horizontal perturbations (P<0.05). For instance, major angles for dynamic- and static-camera conditions usually transitioned from ~60°-70° (before perturbation) to ~110-120° (after perturbation), while major axis angles during the eyes-closed condition commonly exhibited a transition from ~90° to ~30°.

Muscle activations in response to perturbations during walking (Figure 5)

Figure 5 illustrates the sequence and magnitude of muscle activations (color-coded) in response to physical perturbations during walking. The figure comprises data on EMG onset latency, duration, and magnitude of each muscle activation seen during walking. Complementing this figure is Table 2 (*Supplementary file #4*), which details the corresponding numeric values.

Description of muscle onset patterns of vertical perturbations

Following downward perturbations, the contralateral deltoid had an earlier response in comparison to the ipsilateral deltoid (0.38±0.33s vs. 0.55±0.36s, P<0.05), and the ipsilateral gastrocnemius had an earlier response in comparison to the respective contralateral muscle (0.50±0.32s vs. 0.95±0.52s, P<0.05). In addition, contralateral external oblique, paraspinal and deltoid muscles were the first to be activated; all of which had a latency significantly shorter than the ipsilateral tibialis anterior and rectus abdominis, and contralateral gastrocnemius (P<0.05).

Following upward perturbations, no differences between ipsilateral and contralateral muscles were found (P>0.05). The rectus femoris was first to respond on both sides (e.g. contralateral side: 0.34±0.16s), with a latency significantly shorter than that of the gastrocnemius bilaterally (e.g. contralateral side: 0.60±0.31s), as well as the ipsilateral external oblique and contralateral deltoid (P<0.05). After the activation of rectus femoris, the ipsilateral biceps femoris and the contralateral rectus abdominis activated, which exhibited earlier onset latencies than the gastrocnemius (P<0.05).

Downward perturbations led to a duration of activation in the contralateral gastrocnemius (0.53±0.29s) that was shorter when compared to all other muscles (P<0.05). In addition, the ipsilateral deltoid had a shorter activation when compared to the contralateral respective muscle (0.79±0.29s vs. 0.95±0.31s, P<0.05). The muscles with the longest durations of activation were the contralateral paraspinal, external oblique and deltoid.

After upward perturbations, the contralateral gastrocnemius had the shortest activation (0.67±0.25s) when compared to all other muscles (P<0.05, only exception was with ipsilateral external oblique: 0.77±0.28s). The longest durations were in the ipsilateral tibialis anterior, contralateral deltoid, and mainly, in both paraspinals; all of these muscles' durations of activation were significantly longer than those of the contralateral gastrocnemius and ipsilateral external oblique (P<0.05).

Muscle activation - Comparison of vertical and horizontal perturbations

Onset latency after downward perturbations was significantly longer (i.e. delayed) when compared to the three other perturbation directions (P<0.05).

Duration of activation after downward perturbations was shorter in comparison to both upward and forward perturbations (P<0.05), but not to backward perturbations.

Effects of visual only perturbations (Figures 6-7)

Responses to visual perturbations in each participant were evident (i.e., removing the "no response" cases, see Methods) from 118 to 143 trials (out of 192 trials: four types of perturbations, by 16 muscles, by 3 repetitions) for an average of 67.7%. For an example of a visual perturbation effect, see Figure 6.

Figure 7 illustrates the sequence and magnitude of muscle activations (color-coded) in response to visual perturbations. Complementing this figure is Table 3 (*Supplementary file #5*), which details the numeric values.

Forward visual perturbations led to the most delayed onset latencies when compared to the remaining three visual perturbation directions (P<0.05). No statistical effect on onset latency was found across muscles (Figure 7).

Longest duration of activation was observed in tibialis anterior, gastrocnemius and biceps femoris. In contrast, the left rectus abdominis presented with the shortest duration of activation (P<0.05). Backward visual perturbations led to the longest durations of activation, whereas forward visual perturbations led to the shortest durations of activation (P<0.05).

Within visual perturbations, different perturbation directions did not lead to significantly different magnitudes within each muscle (P>0.05).

Discussion

Summary of results

We show muscle activation patterns of leg, trunk and shoulder muscles that characterize balance-correcting responses following vertical perturbations (as compared to horizontal perturbations) during standing and walking, and in response to visual perturbations. We hypothesized that a coordinated activation of inter-segmental muscles would define postural control responses and that muscle response patterns would differ among vertical versus horizontal perturbations. The results largely support these hypotheses (Supplementary File #1 details how the results correspond to a priori predictions). Vertical perturbations usually led to early activation of rectus and biceps femoris, and to otherwise later onset latencies, longer durations of activation, and lower activation magnitudes in comparison to horizontal perturbations, which in contrast triggered an initial activation of tibialis anterior and gastrocnemius muscles (Figure 8).

Visual conditions modulated muscle activation patterns. Eyes-closed conditions led to longer durations of activation and larger activation magnitudes, whereas (sensory incongruent) static-camera conditions led to longer onset latencies. We show that mere visual perturbations can elicit muscle activation, although with a level of activation magnitude significantly lower when compared to physical perturbations.

Our results suggest that vertical perturbations promote differentiated balance-correction strategies oriented to prioritize trunk and hip configuration, and that the availability and manipulation of visual cues through VR can modulate inter-segmental muscle activation.

Comparison with the literature

Our observation that downward perturbations led to a predominantly initial activation of proximal muscles are consistent with findings showing that unexpected falls lead to landing-like muscular control [20]. This is in accordance with other studies suggesting that a flexed trunk reduces ground reaction forces while landing [42] and that an erect landing pattern represents injury risk [43]. The quasi-opposite patterns of muscle activation triggered by upward perturbations are compatible with another study [21], which showed that upward (compared to downward) perturbations lead to opposed changes in body height (e.g. flexion of ankles and knees) and vertical loading.

Furthermore, our results in respect to horizontal perturbations are largely consistent with previous results showing a dorsal-ventral pattern; i.e. a main activation of tibialis anterior, rectus femoris, and rectus abdominis ensuing anterior, forward surface translation, and opposing activation of gastrocnemius, biceps femoris, and paraspinals after posterior, backward translations [5-7, 13-15, 19]. Our findings that rectus abdominis, external oblique, and paraspinals had major balance-correcting roles support their function as prime movers for trunk stabilization during postural control tasks ensuing unexpected perturbations [6].

In addition, the quasi-opposite functional characteristics of initially-activated muscle groups responding to upward and downward perturbations are comparable to a previous study reporting that groups of muscles responding to unexpected lowered and level surfaces during walking were almost the exact opposite to each other [25]. Our finding of a leading contralateral deltoid activation following downward perturbations while walking seems consistent with the whole-body coordinated reaction theory [28] and supports the essential role of arm motion for perturbation recovery when the trunk moves downward [44, 45].

The abrupt abdominal depression caused by downward perturbations [46], combined with the characteristic locomotor body propulsion [47], might explain the distinct early activation of trunk extensors that followed downward perturbations during walking conditions (in comparison to the elicited early activation of trunk flexors in standing conditions). Presumably, while a trunk flexion (i.e. rectus abdominis, external oblique activation) is expected to counter body elongation following downward perturbations while standing, body inclination and locomotor propulsion are additional biomechanical constraints associated with walking, during which the activation of trunk extensors (i.e. paraspinals) is expected to counter the body shortening induced by body inclination/propulsion. Previous studies reporting trunk extension while walking on camouflaged drops [48] and paraspinals activation elucidated by unexpected foot-in-hole scenarios [24] support our findings. We hypothesize that similar postural strategies explain the distinctive early activation of (contralateral) trunk extensors/flexors during standing/walking conditions. In agreement with our results, a previous study found that the pattern of EMG activity during vertical, locomotor-like perturbations contrasted with the EMG pattern following vertical displacements during standing [21].

The relatively long onset latency after vertical perturbations (>600ms) while standing might be due to the perturbation intensity [49, 50]. While in walking conditions, perturbations were characterized by a 20cm displacement within 300 ms (~0.45 g), platform displacements during standing conditions were of 12 cm within one second; i.e., <0.2 g. In comparison, free fall studies found reflexes occurring 74.2 ms after fall initiation with a 160 ms fall duration [20]. EMG activity depends on the height and duration of the fall [20, 38, 51, 52]. Thus, generalizability within vertical perturbations may be limited across studies of different perturbation magnitudes.

Previous studies show that 80% of participants experience vection (i.e. self-motion sensation) when exposed to moving visual scenes [53]. We observed a response rate of 68% after visual perturbations. It may indicate that muscle activation requires an initial experience of vection (or environmental transition) to occur. Further studies can investigate the relation between vection and muscle activation. Several people may be insensitive to visual perturbations [54]. Our observed onset latencies ensuing visual perturbations are in agreement with the onset range of 0.5-2 seconds previously reported [53, 55]. At least three stages may explain longer onset latencies after visual perturbations: eliciting vection, realizing the conflict, and adjusting posture [34, 54]. We hypothesize that visual perturbations trigger certain awareness/prediction in preparation for an expected physical change that does not occur. More research is needed to elucidate whether visual perturbations alone have the ability to improve postural readiness and, if so, whether this occurs in anticipation of associated physical changes.

Limitations, strengths, future directions and implications

There are some limitations related to our study. The experimental paradigm required a definition of perturbation intensities. We introduced *slow* perturbation intensities to avoid stepping strategies (we also encouraged participants not to step during the standing experimental conditions). Nevertheless, as noted above, the muscle activation patterns observed in our experiments are similar to the ones previously reported in the literature, in particular following backwards and forward perturbations [6, 14, 15], which suggests that perturbation intensity in our study was sufficiently fast to induce the previously reported postural corrections.

Another limitation relates to the participant sampling and VR laboratory conditions. Our experiments exposed young, healthy participants to VR paradigms within a room-sized computer-assisted rehabilitation environment. These characteristics limit the extent to which our results may generalize to a broader population. Future research can investigate the feasibility of translating the described experimental paradigms for persons with sensory, motor and cognitive conditions in real-world scenarios.

A potential limitation was the method used for determining EMG onset, which within a three-second window normalizes the signal and determines the largest deviation from the integrated EMG. However, after visual comparison on our experimental data, this method was found to be more robust and to lead to fewer false onsets when compared to the conventional methods that determine EMG onset based on threshold (mean plus X standard deviations) [56].

Our study presents with some strengths. In particular, we introduce a comprehensive, full-body analysis of balance-correcting muscle responses following vertical perturbations. It enriches the literature because research had historically favoured horizontal perturbations and lower-limb muscles. In addition, the integrated, large-scale VR facility used for this study provides basis for further application in the growing adoption of digital tools of human-computer interaction, including the incorporation of VR for healthcare applications and clinical therapy.

Our findings may have translational benefits for balance and gait rehabilitation, such as for people at risk of falling, and for implementing perturbation-based treatments [9, 11]. Clinicians may incorporate the reported paradigm of unexpected perturbations within reactive postural control training programs. Rehabilitation treatments may initially focus on the response-leading muscles. For instance, the implementation of downward-perturbation training for activating deltoid muscles and increasing shoulder abduction might modulate the coordination of arm movements with trunk and leg motion to improve balance reactions during locomotion. In addition, gait treatments may expose patients to upward and downward perturbations for rehabilitation of trunk flexors and extensors, respectively. Else, standing upward-perturbation training may be used for stimulating hamstring activation. Given our observations that groups of muscles respond in unique sequence to different directions of perturbation, balance treatments can incorporate treatment approaches focused on specific groups of muscles, according to specific therapeutic goals. The differences in amplitude of activation across directions may also lend to progressive therapies in order to address a broader range of impairments across clinical populations while also enabling training of more diverse responses to more diverse perturbation characteristics. Furthermore, with the growing interest in the utilization of exoskeletal robotic devices designed to enable locomotion in, for example, persons suffering from paraplegia [57, 58], it is crucial to program these robots to respond to any unexpected physical perturbation in a manner ensuring user safety. Knowledge on natural muscle activation patterns in humans is imperative for such programming, as well as for programming robotic devices used for gait rehabilitation [8, 10].

Future directions from the present study relate to investigating the role of visual pathways in generating balance-correcting muscular responses. We observed that magnitude of muscle activation, for instance, was progressive: smallest after visual perturbations, followed by (physical perturbations) dynamic-camera, static-camera, and finally, eyes-closed conditions that usually led to largest magnitudes. Visual sensory cues have been suggested to be suitable for balance-control regulation [59, 60], and for locomotion modulation related to surface inclination changes [32]. Understanding the multisensory integration determining muscle activation patterns for postural control can have translational benefits for patients with sensory-integration dysfunctions, either to entrain compensations or to identify sources of sensory impairment.

This study also provides insights on how mere visual perturbations and the manipulation of visual cues during standing following physical perturbations may activate muscle response patterns and modulate postural control strategies. Such information can help for optimizing the design and planning of rehabilitation strategies using immersive VR tools in a safe and controlled environment. In terms of training intensity, for instance, we observed that horizontal physical perturbations triggered the most intense muscle responses, whereas visual perturbations elicited the lowest magnitudes of activation. Physical vertical perturbations, therefore, represent a medium-intense set of perturbations that will not necessarily be destabilizing, and can be incorporated during early stages of balance-reaction therapies and in research projects on falls risk. Our paradigm of visual perturbations can also be incorporated to determine levels of responsiveness towards VR visual stimuli.

Conclusion

We conclude that a coordinated activation of muscles across the body characterizes balance-correcting responses to vertical perturbations during standing and gait. Major trunk muscles such as paraspinals, rectus abdominis, and external oblique were among the first to activate during postural responses to vertical perturbations, which contrast the initial activation of distal leg muscles in response to horizontal perturbations. Further, the availability of visual cues supports more efficient responses, whereas visual conflict can affect the timely triggering of balance corrective responses.

Abbreviations

BF - biceps femoris

BMI - Body Mass Index

COMx - Extrapolated center of mass

D - deltoid medial

EMG - Electromyography

EO - external oblique

GC - gastrocnemius lateralis

PS - paraspinal

RA - rectus abdominis

RF - rectus femoris

SSV - Steady-state velocity

TA - tibialis anterior

VR - Virtual Reality

Declarations

Ethics approval and consent to participate. All participants were able to follow instructions and gave written informed consent before being enrolled in the study. The Institutional Review Board for Ethics in Human Studies at the Sheba Medical Center, Israel, approved the experimental protocol.

Consent for publication. Not applicable.

Availability of data and materials. The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests. The authors declare that they have no competing interests.

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Authors' contributions. MP initiated and conceptualized the study, participated in study design and assumed overall supervision. DCP participated in the study design, led data collection, processed the experimental data and took the lead in writing the manuscript. JVJ participated in the study design, development of outcome measures, and contributed to the analysis and theoretical formalism. DCP, JJ, RI, GZ and MP iteratively revised the manuscript and contributed to the interpretation of the results. YB developed the virtual environments and participated in carrying out the experiments. All authors discussed the results and contributed to the final manuscript.

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Supplementary Material

Rationale and description of specific predictions/hypotheses about muscle activations

Tables 1, 2 and 3.

Video 1: https://drive.google.com/file/d/1kULJr0IeVQVFiR5ClfglritPSYsZddl2/view?usp=sharing

Figures

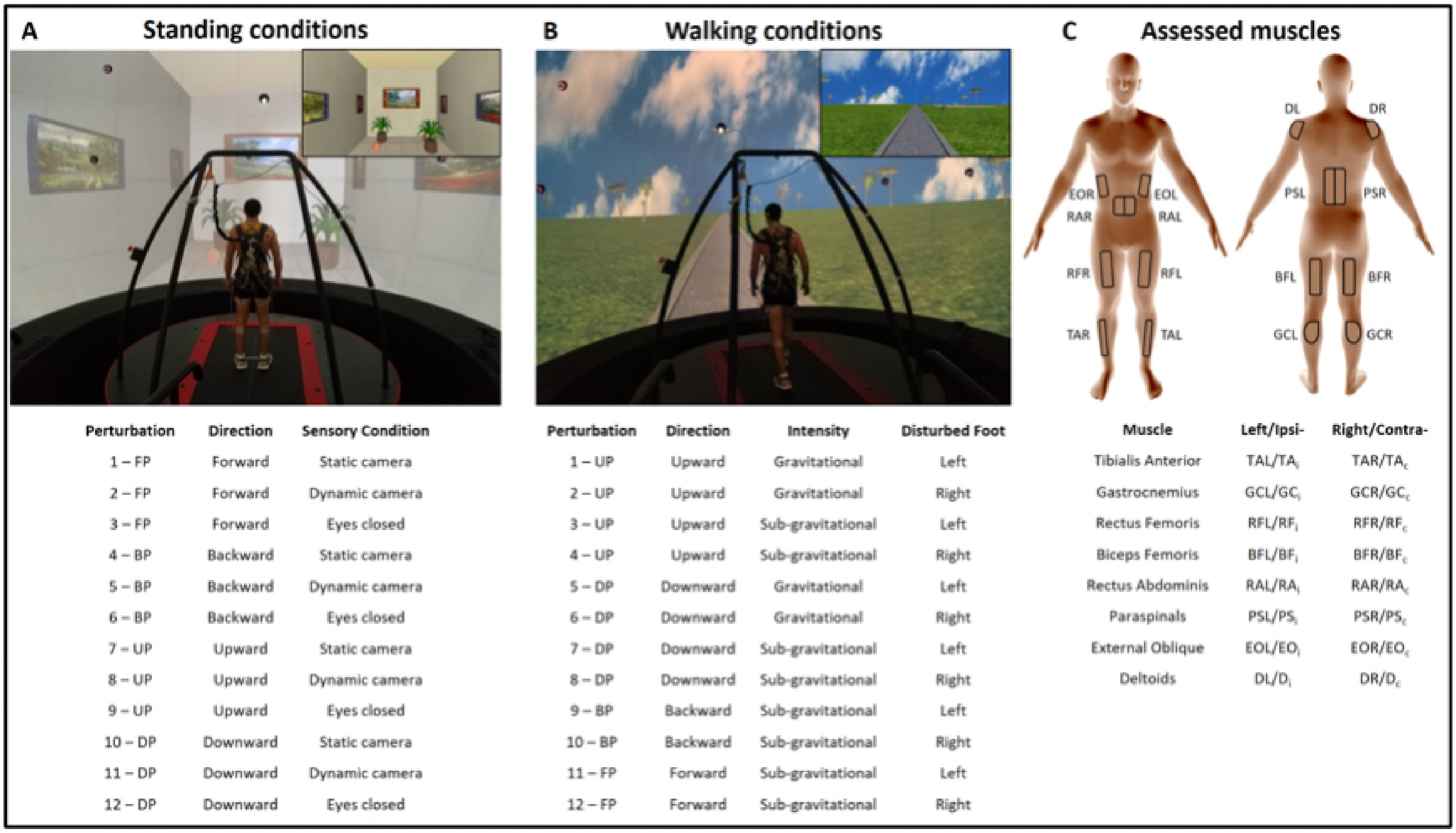

Figure 1

Apparatus and experimental conditions. (A) Virtual visual scenery of a simulated room used for both physical and visual perturbations while standing. Objects and walls in the virtual room provided depth cues that were manipulated in relation to the physical actions of the platform and participant. There were four perturbations directions (forward, backward, upward, and downward; FP, BP, UP, DP, respectively) and three sensory conditions: static-camera, dynamic-camera, and eyes closed. (B) Virtual visual scenery used during walking conditions projected a moving road on a large 360° dome-shaped screen. There were four perturbation directions, and perturbations occurred either during left or right foot contact. (C) Depiction of the 16 muscles assessed. Ipsilateral muscles (sub-index "i") refer to those recorded from the perturbed stance foot during walking conditions (contralateral denoted by sub-index "c"). The electrodes' positions were determined according to SENIAM guidelines. TA: tibialis anterior, GC: gastrocnemius lateralis, RF: rectus femoris, BF: biceps femoris, RA: rectus abdominis, PS: paraspinal, EO: external oblique, and D: deltoid medial.

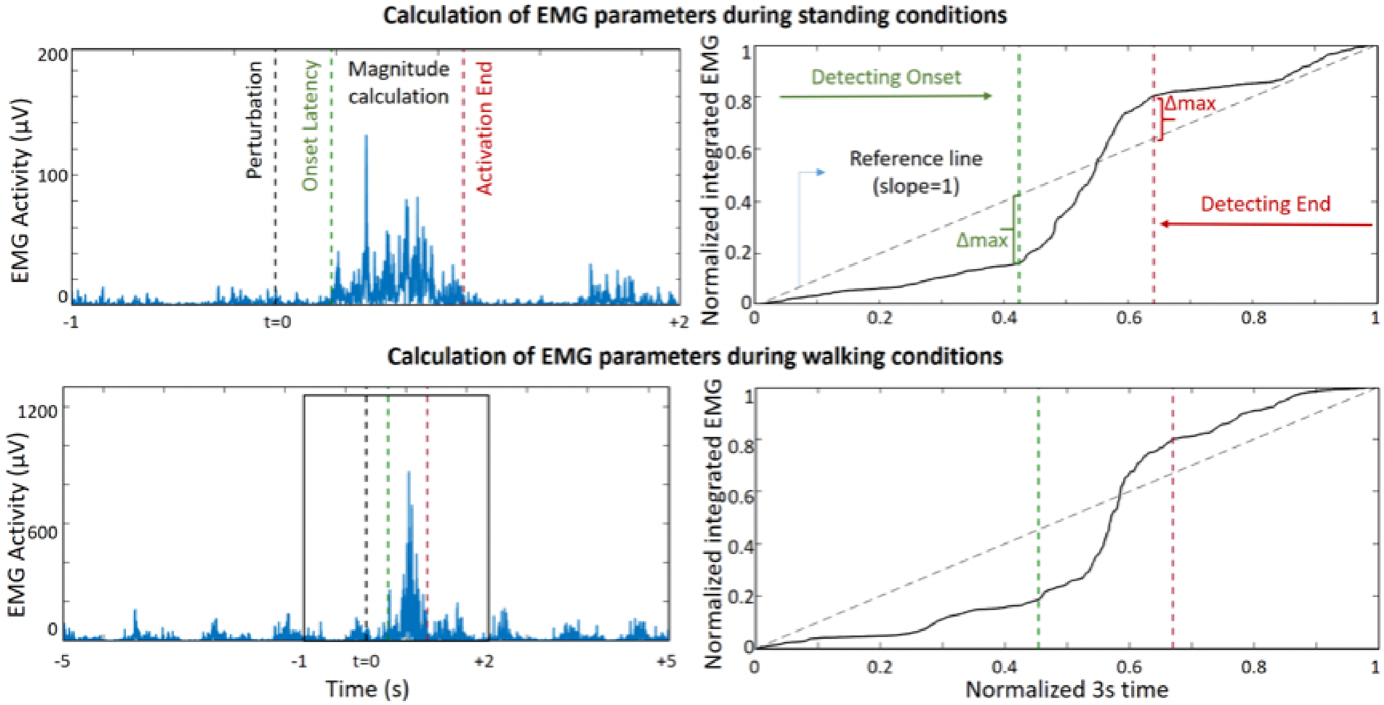

Figure 2

Calculation of electromyography (EMG) parameters during standing (upper plot) and walking (lower plot). The left column shows the filtered and rectified EMG activity with the calculated EMG parameters. The EMG signal is integrated and normalized in amplitude and time (right column) only for calculating “onset latency” and “activation end”. The detection of onset latency is defined as the maximum delta between a unitary, reference line (diagonal dashed line) and the integrated, normalized EMG signal. A similar approach, after inverting the signal, is used to identify the end of activation. Duration of activation is determined as the period between onset latency and the end of activation. For estimating activation magnitude, we calculated the area under the curve in the duration of activation period, on the filtered and rectified original EMG signal.

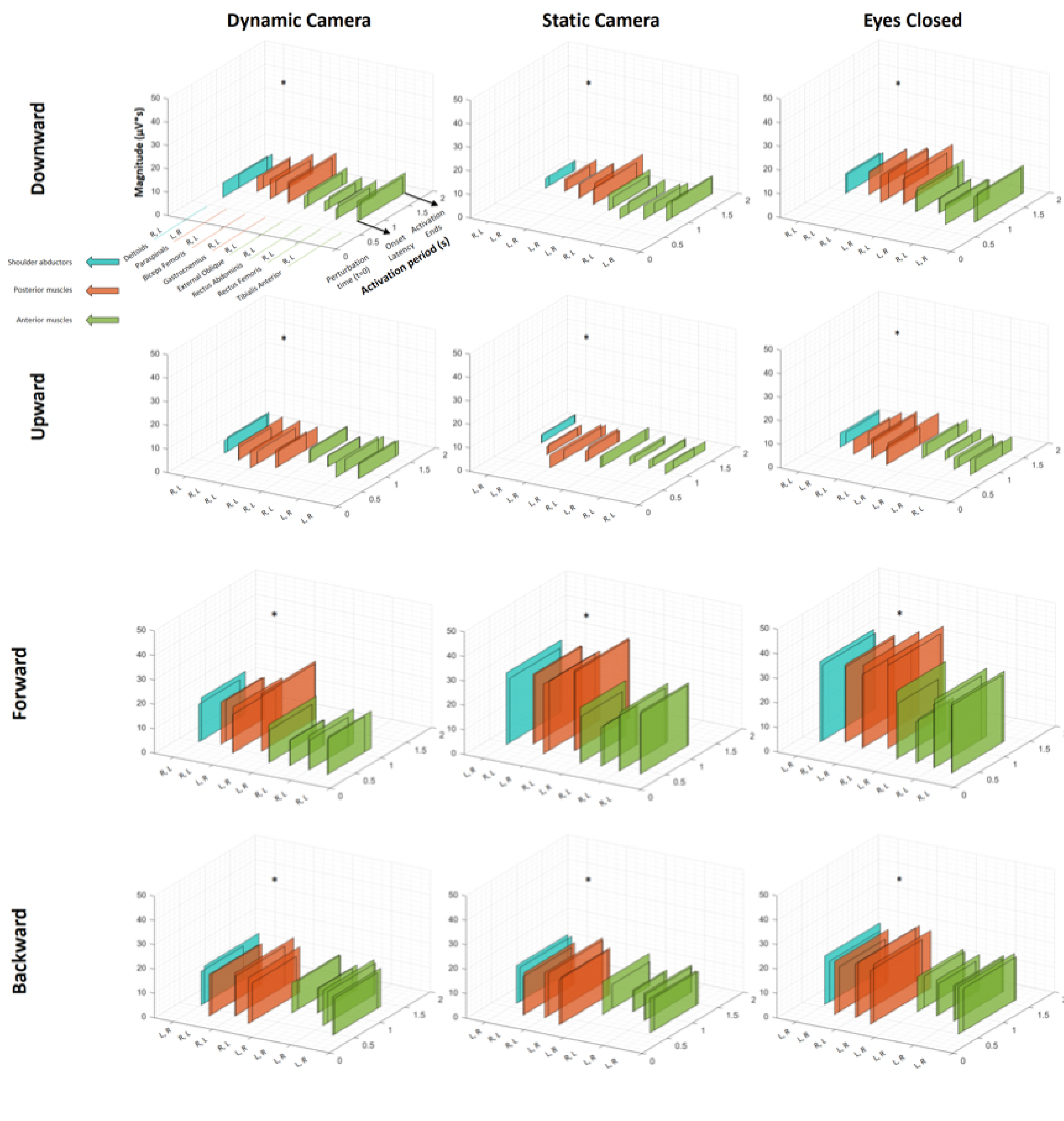

Figure 3

Patterns of muscle activation following perturbations while standing. Description of muscle activation patterns arranged by 3-D rectangles representing groups of shoulder abductors (blue), posterior muscles (orange) and anterior muscles (green). Figures show average values (from all participants) of onset latency and duration of activation (“Activation period” axis), and activation magnitude (vertical axis). In general, horizontal (forward, backward) perturbations (lower two rows) led to significantly larger activation magnitudes than vertical (downward, upward) perturbations (upper two rows). Anterior muscles were often activated before posterior muscles following both downward and forward perturbations, whereas posterior muscles were activated faster after backward and upward perturbations. Dynamic-camera conditions usually led to lower activation magnitudes when compared to static-camera and eyes-closed conditions. Table 1 (Supplementary materials) shows values of EMG parameters during standing conditions. The overlapping rectangles depict left (L) and right (R) body sides. The letters indicate the shorter and longer onset latency, respectively.

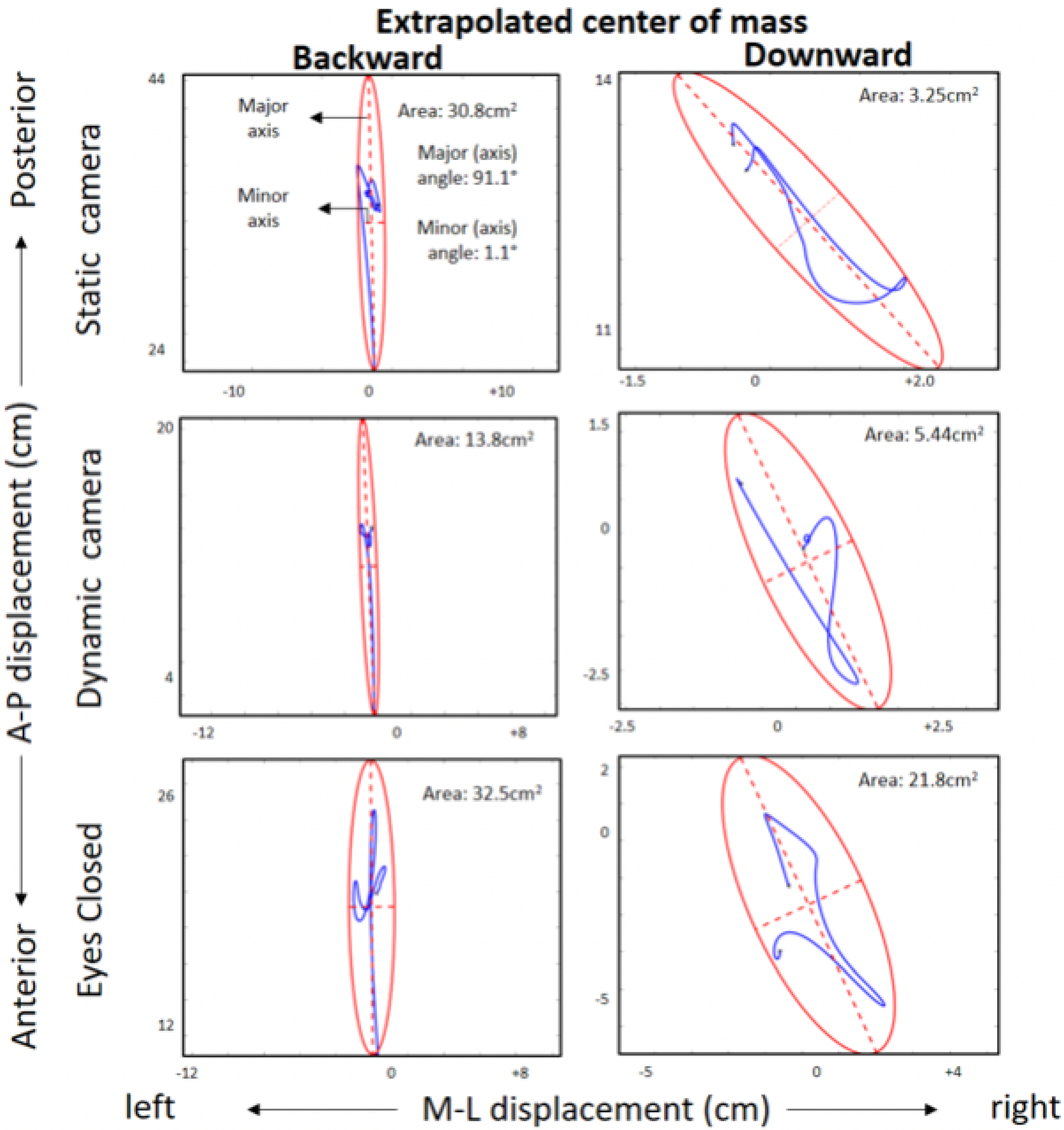

Figure 4

Ellipse fits for extrapolated center of mass (COMx) from two representative participants after downward and backward perturbations. Blue lines identify COMx antero-posterior (A-P) and medio-lateral (M-L) displacements. 95% confidence ellipses appear in red. Characteristic minor and major axes are shown as dotted lines. Ellipse features following forward perturbations were similar to those after backward perturbations. Minor and major axis angles were near 0° and 90° respectively, suggesting a dominant anterior-posterior postural reaction. Average COMx area for all 14 participants following upward perturbations were of 7.3cm2, 7.5 cm2 and 8.6cm2, respectively for static, dynamic and eyes-closed conditions. However, axis angles deviated from 0° and 90° during vertical perturbations (see text).

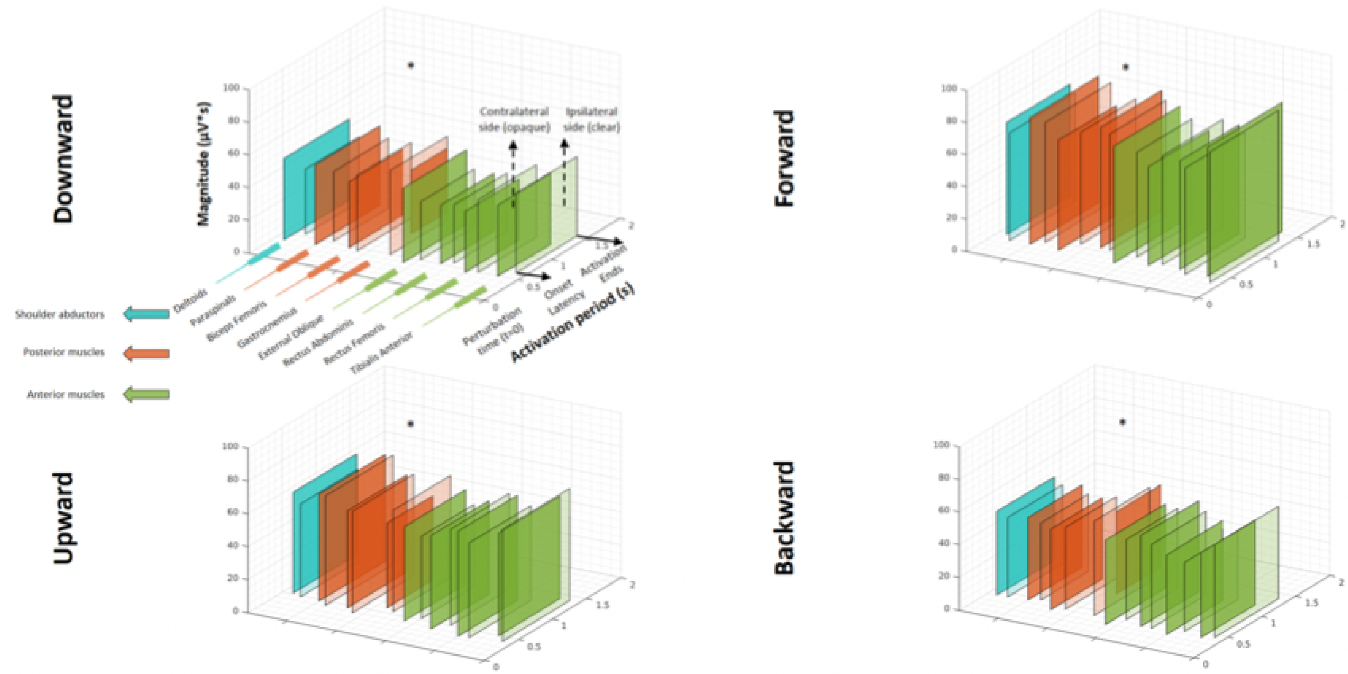

Figure 5

Patterns of muscle activation following perturbations while walking. Description of muscle activation patterns arranged by 3-D rectangles, representing groups of shoulder abductors (blue), posterior muscles (orange) and anterior muscles (green). Clear and opaque rectangles indicate, respectively, muscles in the ipsilateral or contralateral side of perturbation (e.g. side of early foot contact during perturbation). Average values shown from all participants for onset latency and duration of activation (“Activation period” axis), and for activation magnitude (vertical axis). In general, forward perturbations led to the largest activation magnitudes and downward perturbations to the lowest activation magnitudes. Trunk and hip muscles responded earliest, particularly on the contralateral side. Early activation of the contralateral deltoid was observed after downward perturbations. Table 2 (Supplementary materials) details the values of EMG parameters during walking conditions.

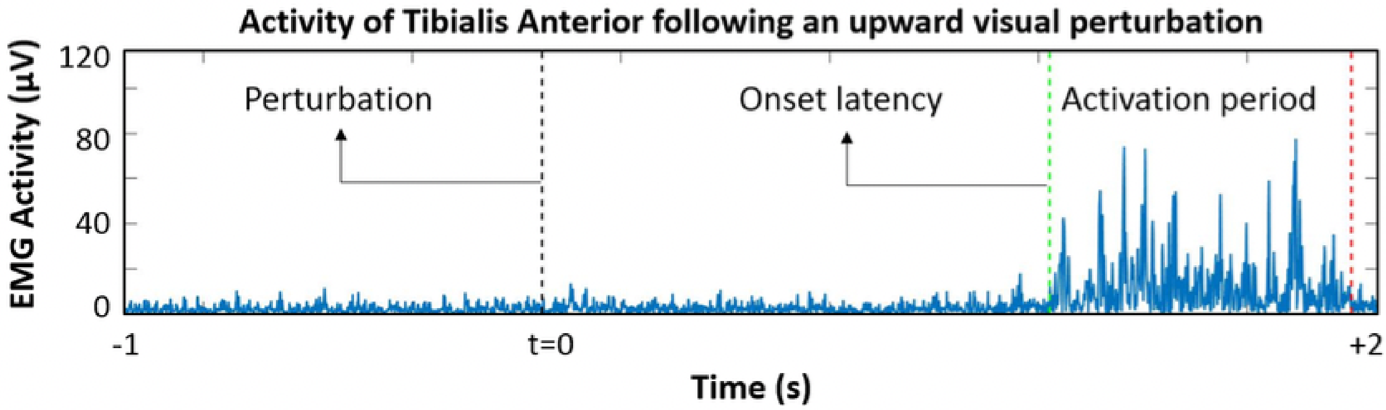

Figure 6

Electromyography (EMG) activity driven by visual perturbations. Filtered and rectified EMG activity of left tibialis anterior following an upward visual perturbation while standing. The figure shows a time window from one second before to two seconds after visual perturbation. Onset latency was 1.2 s, duration of activation was 723 ms, and magnitude of activation was 3.85 μV*s. Visual perturbations led to longer onset latencies and smaller magnitudes of activation when compared to physical perturbations while standing.

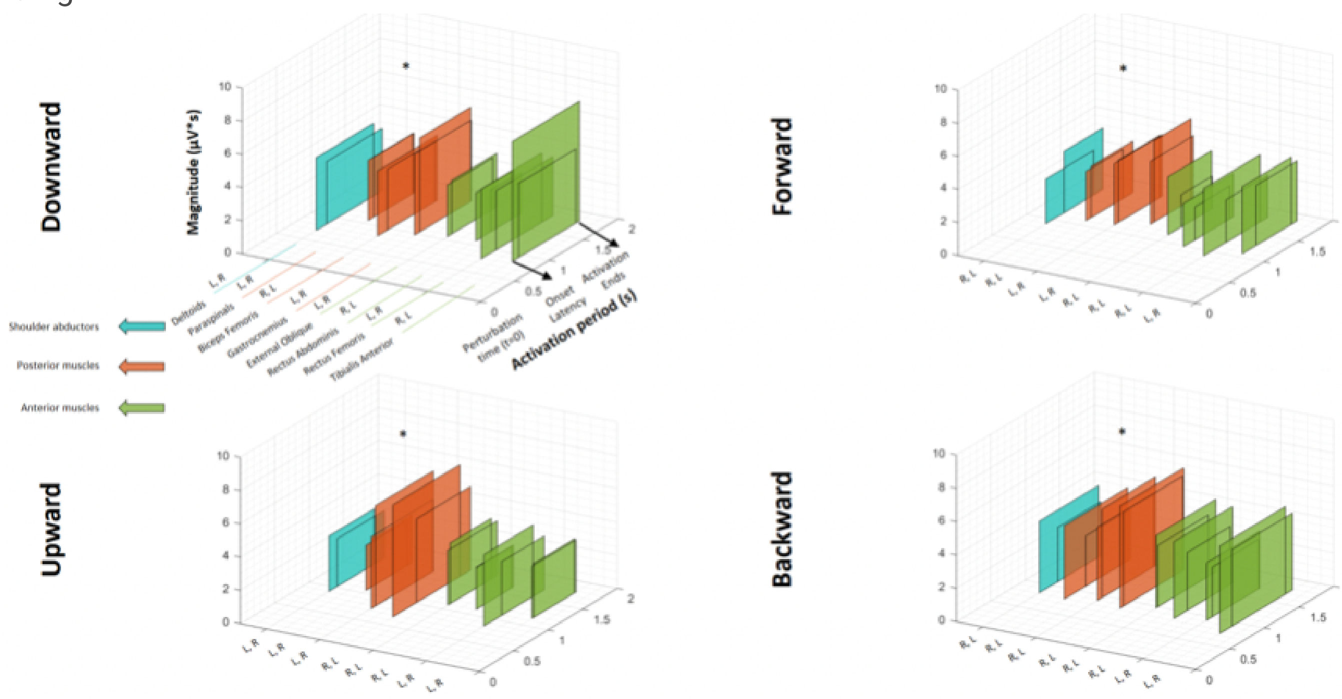

Figure 7

Patterns of muscle activation following visual perturbations. Description of muscle activation patterns arranged by 3-D rectangles representing groups of shoulder abductors (blue), posterior muscles (orange) and anterior muscles (green). Figures show average values (from all participants) of onset latency and duration of activation ("Activation period" axis), and activation magnitude (vertical axis). In general, horizontal (forward, backward) perturbations led to significantly larger activation magnitudes than vertical (downward, upward) perturbations. Forward visual perturbations led to the most delayed onset latencies and shortest durations of activation. In contrast, backward visual perturbations led to the longest durations of activation. Table 3 (Supplementary materials) details the values of EMG parameters triggered by visual perturbations. The overlapping rectangles depict left (L) and right (R) body sides. The letters indicate the shorter and longer onset latency, respectively.

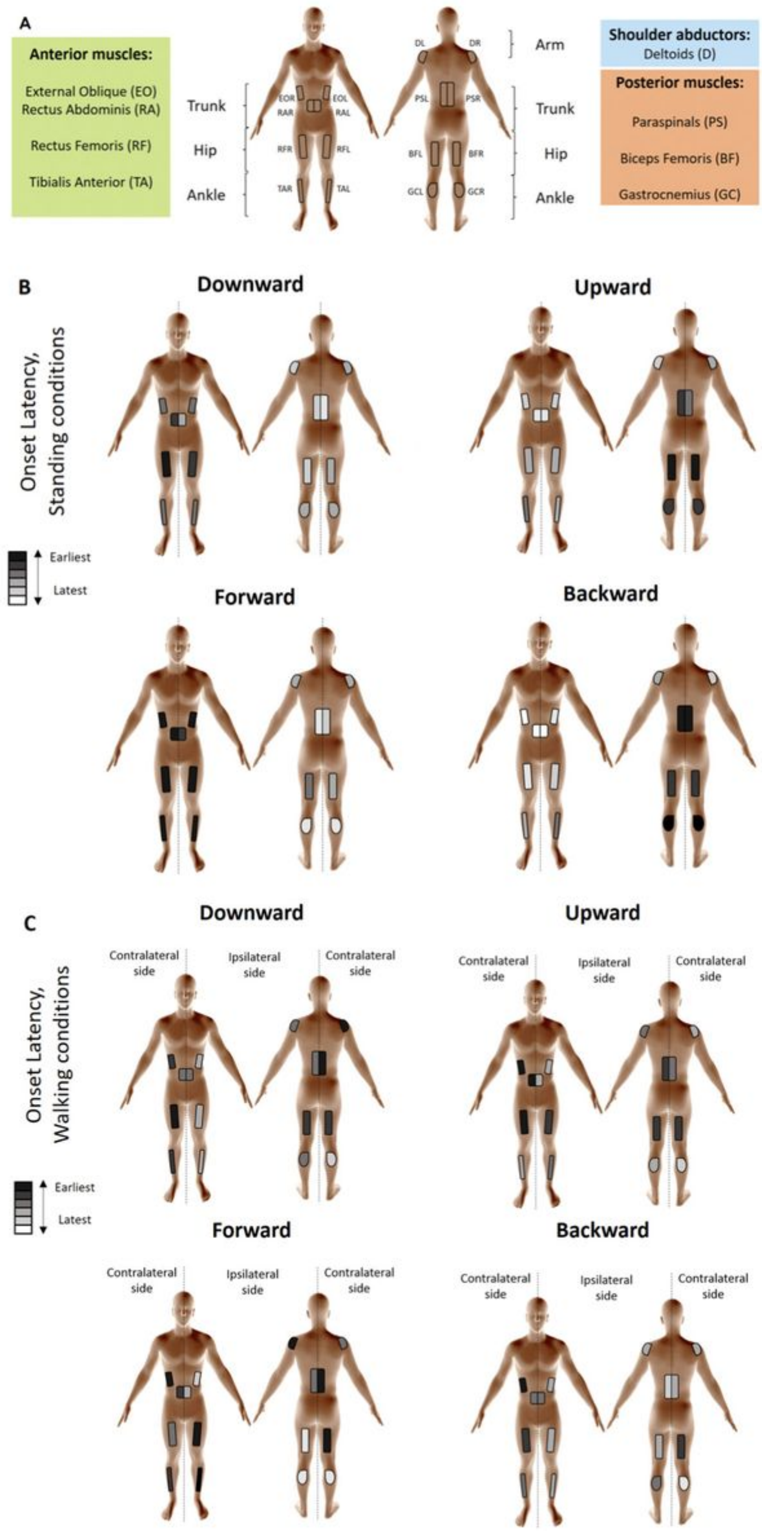

Figure 8

Schematic representation of muscle activation patterns. A) Assessed muscles grouped by anterior muscles (TA: tibialis anterior; RF: rectus femoris; RA: rectus abdominis; and EO: external oblique), posterior muscles (GC: gastrocnemius lateralis; BF: biceps femoris; and PS: paraspinals) and shoulder abductors (D: deltoid medial). L or R at the end of abbreviation refer to left/right side (e.g. TAL: tibialis anterior left). The figures show patterns of electromyography activation arranged from earlier to later onset latencies within horizontal and vertical perturbations following B) standing perturbations (combining all three sensory conditions) and C) walking perturbations (combining both left and right perturbations). A color-code identifies those muscles responding earlier (darker) or later (whiter) in each perturbation direction.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Video1.mp4
- Table3.EMGparametersaftervisualperturbations.pdf
- File1Descriptionsofpredictionsv1END.docx
- Table2.EMGparametersduringwalkingconditions..pdf
- Table1.EMGparametersduringstandingconditions..pdf