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Differential activation of the plantar flexor muscles in balance control across different feet orientations on the ground

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ABSTRACT

The ankle plantar flexor muscles act synergistically to control quiet and dynamic body balance. Previous research has shown that the medial (MG) and lateral (LG) gastrocnemii, and soleus (SOL) are differentially activated as a function of motor task requirements. In the present investigation, we evaluated modulation of the plantar flexors' activation from feet orientation on the ground in an upright stance and the ensuing reactive response to a perturbation. A single group of young participants ($n = 24$) was evaluated in a task requiring initial stabilization of body balance against a backward pulling load (5% or 10% of body weight) attached to their trunk, and then the balance was suddenly perturbed, releasing the load. Four feet orientations were compared: parallel (0°), outward orientation at 15° and 30°, and the preferred orientation ($M = 10.5°$). Results revealed a higher activation magnitude of SOL compared to MG-LG when sustaining quiet balance against the 10% load. In the generation of reactive responses, MG was characterized by earlier, steeper, and proportionally higher activation than LG-SOL. Feet orientation at 30° led to higher muscular activation than the other orientations, while the activation relationship across muscles was unaffected by feet orientation. Our results support the conclusion of task-specific differential modulation of the plantar flexor muscles for balance control.

1. Introduction

The ankle plantar flexor muscles play an essential role in keeping a quiet stance and in generating fast and scaled responses to body balance perturbations. To play these stabilization and compensation roles in body balance control, the three heads of the triceps surae (plantar flexors), medial (MG) and lateral (LG) gastrocnemii, and soleus (SOL) act in synergy. These muscles have different characteristics potentially affecting their function in balance control. For example, both LG and MG have a higher proportion of fast-twitch fibers (Burkholder et al., 1994, Edgerton et al., 1975, Johnson et al., 1973), and lower muscle spindle density (Banks, 2006) than SOL. Additionally, LG has a greater fascicle length than MG, while MG has a larger fascicle pennation angle than LG (Kawakami et al., 1998). These structural differences among the plantar flexor muscles have been suggested to underlie their differential activation in motor tasks with distinct requirements (cf. Kamibayashi and Muro, 2006; Moritani et al., 1991a,b). Support for the notion of task-specific recruitment of the plantar flexor muscles has been provided by findings of higher activation of SOL than both the medial and lateral gastrocnemii in isometric plantar flexion (Crouzier et al., 2018; Hali et al., 2020), while MG displayed the highest activation, SOL intermediate, and LG the lowest activation during repetitive submaximal isometric contractions (Masood et al., 2014). Additionally, in the comparison of multiple tasks requiring isometric, isotonic, or isokinetic plantar flexion, and also in the performance of a squat jump task, MG has been found to contribute more to total muscle activation in isometric and isotonic tasks as compared to squat jump, with an inverted relationship for SOL (Ball and Scurr, 2015). Nardone et al. (1990) compared responses from the plantar flexor muscles to backward translation or upward tilt of the support base while standing for automatic postural responses to unanticipated perturbations. Their results showed that in the medium latency responses (~100 ms) MG showed the highest amplitude and frequency of occurrence of muscular responses, LG intermediate, and SOL the lowest. As a whole, these results support the perspective that the plantar flexor muscles are coordinated so that the different muscles can be independently controlled by the central

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nervous system to deal with specific task requirements (Windhorst et al., 1989). Selective muscle activation has been thought to be guided by its functional ability to perform a given motor task, like fiber type composition and mechanical advantage (Butler and Gandevia, 2008; Chanaud et al., 1991).

From the conceptualization of task-specific recruitment of the plantar flexor muscles, it is plausible that biomechanical constraints are considered by the central nervous system to modulate muscular activation in the generation of postural responses. Henry et al. (1998) provided preliminary support for this assumption by comparing muscular responses to different unpredictable directions of support base translations. They found that MG and SOL responded in a directionally specific manner, with higher activation magnitude generated in response to balance perturbations provoked by diagonal translations. More recently, Cohen et al. (2020) showed that the activation magnitude of MG and LG were modulated as a function of perturbation direction when keeping a unipedal stance, while SOL activation was unaffected by perturbation direction. Additionally, analysis of the principal contribution of both gastrocnemii to each perturbation direction indicated that MG and LG participate in body balance regulation not only in the anteroposterior but also in the mediolateral direction. Specifically, their results suggest that MG played a major role in producing inversion torques, while LG played a major role in producing eversion torques (see also Lee and Piazza, 2008; Vieira et al., 2013). Further investigation has evidenced that the feet spatial orientation on the ground affects balance regulation. Comparisons between distinct feet positioning on the ground during quiet stance have shown that augmented outward orientation stabilizes balance (Kirby et al., 1987; Uimonen et al., 1992), with higher balance stability achieved in the range of 15-45° from the midline (Mouzat et al., 2004). The effect of feet orientation on automatic postural responses was evaluated across feet positioning ranging from parallel to outward orientation at 30° regarding the midline when responding to different magnitudes of balance perturbations (Azzi et al., 2017). Results revealed that feet orientation at 30° led to the higher maximal angular displacement of the ankles than the other feet orientations. Given the task-specific activation of the plantar flexor muscles (e.g., Ball and Scurr, 2015), we pose the possibility that activation of the plantar flexors are modulated individually in response to stance perturbation as a function of feet orientation on the ground.

In the current investigation, we compared individual activation of the plantar flexor muscles to unanticipated stance perturbations across different feet orientations on the ground. The evaluation was made in three epochs: immediately before perturbation, and in the primary (0–150 ms) and secondary (150–300 ms) periods following stance perturbation. Considering the medial and lateral gastrocnemii's increased suitability for fast postural responses (Nardone et al., 1990), we also tested a possible differential modulation of the plantar flexor muscles as a function of perturbation magnitude. We hypothesized that SOL has a proportionally higher activation magnitude in keeping stance in the epoch preceding balance perturbation (H1), and that both MG and LG have a proportionally higher activation magnitude in reactive responses to stance perturbation (H2). Furthermore, from the evidence of the relevance of MG for inversion movements (Cohen et al., 2020), we also hypothesized proportionally higher activation of MG in comparison with LG and SOL as the feet are oriented outward (H3).

2. Method

2.1. Participants

Twenty-four healthy university students (12 males), age range 18–37 years ($M = 23.27$ years, $SD = 5.01$), participated in this study. Experimental procedures were carried out with the participants' written informed consent after approval by the local university ethics committee by the standards established in the Declaration of Helsinki.

2.2. Task and apparatus

The initial posture was keeping upright stance while resisting against a load pulling the participant's trunk backward (pre-perturbation). The load was attached to a harness around the participant's trunk, connected by an electromagnetic system through a steel cable (Fig. 1). At a variable time following a verbal prompt (2–4 s), the load was suddenly released through a custom-made soundless electronic device, inducing a fast forward body oscillation. The participant's task consisted of keeping a stable stance against the pulling load in the pre-perturbation epoch and then recovering a stable upright stance following the postural perturbation while maintaining both feet in place (for more details, see de Lima-Pardini et al., 2014). We measured activation of the muscles MG, LG, and SOL of the right leg (assuming symmetric activation between legs, cf. Vieira et al., 2014). Muscular activation was measured using wireless surface electrodes (Trigno^{TM} Wireless Sensors, Delsys inc., Boston, MA, model Trigno). Measurement of muscular activation was made in agreement with the SENIAM project recommendations (http://www.seniam.org/). A pulse of 5 V generated at the onset of the load release was used to synchronize signals across the EMG at the Vicon Nexus system.

2.3. Experimental design and procedures

Participants were tested in eight experimental conditions, given by the combination of feet orientation and load magnitude. Feet orientations were parallel (0°), outward orientation at 15° and 30° for each foot regarding the body midline, and the individual preferred feet orientation ($M = 10.5°$, $SD = 2.0$). The internal border of the feet was used to measure the angle of feet orientation, keeping the heels 5 cm apart across feet orientations. Feet orientations were outlined on the force plate with adhesive tape and monitored across trials. Two load magnitudes for balance perturbation were used: 5% (light) versus 10% (heavy) of participant's body weight. Arms were to be maintained crossed over the chest when responding to the load release while gazing at a 5-cm diameter spot, presented 2 m away, at eyes' height. After connecting the load to the harness, the participant assumed a stable body posture, with forward-leaning greater than that usually assumed in the normal upright posture, compensating for the load backward pulling. To achieve a consistent body posture across trials, a laser beam (projected from the top of a tripod) was aimed at the participant's right shoulder when a comfortable and stable posture was achieved when supporting the 10% body weight load. This initial posture was set in preliminary trials. Body leaning in the probing trials was referenced to positioning the shoulder marker at the laser beam, and it was the same for both the heavy and light loads. Appropriate body leaning and trunk-leg alignment were guided through verbal feedback over trials. Time of load release was unanticipated to participants, with perturbations applied randomly (through manual control) within a time window of 2–4 s after a verbal prompt. Skin under the EMG electrodes was shaved and cleaned with alcohol wipe. The EMG electrodes were attached to the skin using a double-sided adhesive skin interface.

Immediately before the probing trials, participants were provided with one familiarization trial for each experimental condition. For each condition, muscular responses were assessed using three consecutive trials, spaced by intervals of about 30 s. The sequence of loads by feet orientation on the ground was counterbalanced across participants. Intertrial intervals within a condition were 30-s long, while intervals between conditions endured 1 min. After half the trials, a 2-min. sitting rest interval was provided. Trials in which participants stepped following a perturbation were removed and immediately repeated.

2.4. Analysis

EMG signals were acquired at an effective signal gain of 909 V/V ± 5% with full dynamic signal range of ± 5 V, a bandwidth of 20–450 Hz, a

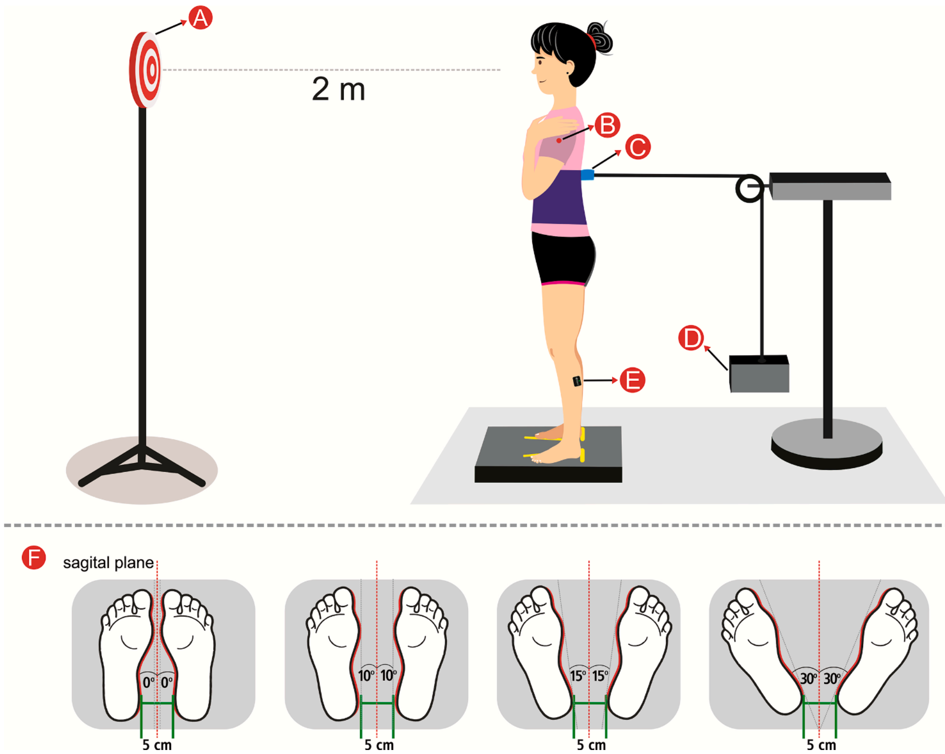

Fig. 1. Representation of the experimental setup in the period preceding balance perturbation, showing (a) visual target, (b) marker on the shoulder for initial posture alignment based on the laser beam (not represented), (c) harness connected to the steel cable, (d) pulling load (5% x 10% of body wright), (e) EMG electrodes, and (f) the tested feet orientations on the ground (10° correspond to the preferred feet orientation averaged across participants).

baseline noise < 0.75 μV (RMS), and a common mode rejection ratio (CMRR) > 80 dB. The EMG signal was sampled at 2000 Hz using a 16-bit analog/digital board. Analyses were made for the periods immediately before and following load release. Data were extracted and processed through MATLAB (Mathworks, Natick, MA) routines. Offline, the raw EMG signals were filtered using a fourth-order zero lag Butterworth filter with a 20 Hz high-pass and a 450 Hz low pass filtered to attenuate artefacts. The linear envelope of the EMG was estimated by rectification and low-pass filtering (anticausal Butterworth filter of order 4, cutoff frequency 10 Hz (Hermens and Freriks, 1999) during each task. Dependent variables were as follows: for reactive responses, (a) latency of muscular activation onset, having as a criterion the time of onset of sustained growing linear envelope of the EMG values two standard deviations above the average in the interval of 200 ms preceding load release; magnitude of muscular activation, determined by the root mean square (RMS) of the linear envelope of the EMG signal for three-time intervals: (b) 500 ms before load release, (c) initial 150 ms (primary response period) and (d) 150–300 ms (secondary response period) following muscular activation onset; and (e) rate of muscular activation, given by the increment of muscular activation over time based on the linear envelope of the EMG signal. To reduce interindividual variability of EMG data, activation magnitude values were normalized to the respective muscle EMG peak across all experimental conditions.

2.5. Statistical analysis

Analysis was performed on averages of the three trials for each experimental condition per participant. Data were analyzed through three-way 3 (muscle: MG × LG × SOL) × 2 (load: light × heavy) × 4 (orientation: parallel × preferred × 15° x 30°) ANOVAs with repeated measures on the last two factors. The significance level was set at 0.05, with post hoc comparisons made through the Newman-Keuls procedures. Effect sizes are given by partial eta-squared (η_p^2).

3. Results

For the heavy load, 15 trials were removed due to stepping, while in the light load no trials were removed. All participants performed three valid trials per experimental condition. In Fig. 2, we show single representative trials of (a) MG, (b) LG, and (c) SOL activation following load release (vertical dashed line), contrasting the extreme feet orientations (parallel [0°], red lines; 30°, black lines) for the light (dashed line) and heavy (solid line) loads.

3.1. Pre-perturbation epoch

Analysis of activation magnitude preceding perturbation indicated a significant muscle X load interaction, $F(2, 46) = 6.85$, $p < .01$, $\eta_p^2 = 0.23$ (Fig. 3A). Decomposition of the muscle by load interaction indicated that for the light load SOL (M = 0.023, SD = 0.016) and LG (M = 0.024, SD = 0.022) had higher values than MG (M = 0.012, SD = 0.011), with no significant difference between the former; for the heavy load, all between-muscle comparisons were significant, with the highest values for SOL (M = 0.034, SD = 0.028), followed by LG (M = 0.030, SD = 0.024), and the lowest values for MG (M = 0.015, SD = 0.013). Intra-muscle comparisons indicated that the heavy in comparison with the light load induced higher activation in all muscles.

3.2. Perturbed stance

Analysis of latency of muscular activation onset showed significant main effects of muscle, $F(2, 46) = 10.65$, $p < .01$, $\eta_p^2 = 0.32$, and load, $F(1, 23) = 156.07$, $p < .01$, $\eta_p^2 = 0.87$ (Fig. 3B). Post-hoc comparisons for the muscle effect indicated earlier activation onset in MG (M = 97.77 ms, SD = 37,32) than in LG (M = 106.39 ms, SD = 40.28) and SOL (M = 106.59 ms; SD = 39.58), with no significant difference between the latter. The effect of load was due to earlier activation onset for the heavy (M = 86.46 ms, SD = 33.01) than for the light (M = 120.62 ms, SD =

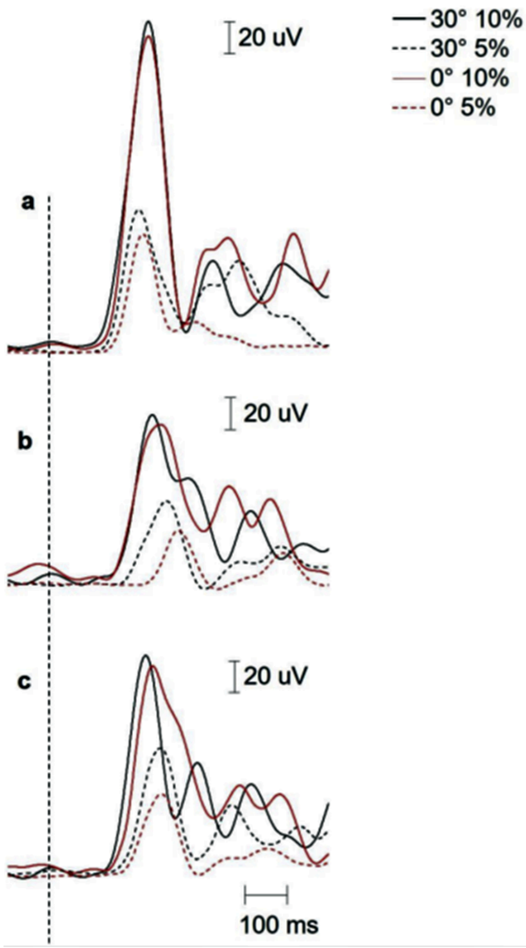

Fig. 2. Representative single trial EMG linear envelope signals of the (a) medial gastrocnemius (MG), (b) lateral gastrocnemius (LG) and (c) soleus (SOL) muscles following load release (vertical dashed line), contrasting the extreme feet orientations (parallel [0°, red lines] vs. 30° [black lines]) for the light (dashed line) and heavy (solid line) loads. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

37.59) load.

Results for activation magnitude in the primary reactive epoch (0–150 ms) indicated a significant main effect of orientation, $F(3, 69) = 6.00$, $p = < 0.01$, $\eta_p^2 = 0.21$, and a significant muscle X load interaction, $F(2, 46) = 10.65$, $p < .01$, $\eta_p^2 = 0.32$ (Fig. 3C). Post-hoc comparisons for the effect of orientation indicated that feet at 30° (M = 0.39, SD = 0.20) led to significantly higher values as compared to the other feet orientations. Decomposition of the muscle by load interaction indicated that for the light load MG (M = 0.35, SD = 0.14) had significantly higher values than LG (M = 0.23, SD = 0.12), and SOL (M = 0.21. SD = 0.13), with no significant difference between the latter; for the heavy load all comparisons led to significant differences, with the highest values for MG (M = 0.51, SD = 0.15), followed by LG (M = 0.48, SD = 0.18, and the lowest activation for SOL (M = 0.39, SD = 0.18). Intra-muscle comparisons indicated that the heavy load induced higher activation than the light load in all muscles.

Results for the secondary reactive epoch (150–300 ms) indicated a significant main effect of muscle, $F(2, 46) = 7.91$, $p < .01$, $\eta_p^2 = 0.26$, and a significant load X orientation interaction, $F(3, 69) = 9.68$, $p < .01$, $\eta_p^2 = 0.30$ (Fig. 3D). Post-hoc comparisons for the muscle effect indicated higher values for MG (M = 0.19, SD = 0.14) than for SOL (M = 0.13, SD = 0.12) and LG (M = 0.15, SD = 0.14), with no significant difference between the latter. Decomposition of the load by orientation interaction indicated that for the heavy load feet oriented at 30° led to higher muscular activation (M = 0.30, SD = 0.16) than for the other feet orientations; for the light load, no significant differences were found across feet orientations. The heavy in comparison with the light load led to higher activation in all feet orientations.

Results for muscular activation rate indicated significant main effects of muscle, $F(2, 46) = 22.42$, $p < .01$, $\eta_p^2 = 0.49$, and load, $F(1, 23) = 43.03$, $p < .01$, $\eta_p^2 = 0.65$ (Fig. 3E). Post-hoc comparisons for the muscle effect indicated higher values for MG (M = 1.67 μV/ms, SD = 1.12) than for LG (M = 0.98 μV/ms, SD = 0.63) and SOL (M = 0.96 μV/ms, SD = 0.69), with no significant difference between the latter. The effect of load was due to higher values for the heavy (M = 1.47 μV/ms, SD = 0.99) than for the light (M = 0.94 μV/ms, SD = 0.72) load.

4. Discussion

In the present investigation, we evaluated differential activation across the muscles MG, LG, and SOL in distinct epochs of responses to sudden stance perturbations leading to fast forward body sway. We evaluated the extent to which activation of these plantar flexor muscles is modulated as a function of perturbation load magnitude and feet orientation on the ground. Corroborating the hypothesis that SOL has a proportionally higher activation magnitude across the plantar flexors in the pre-perturbation epoch (H1), our results showed higher activation magnitude of SOL in comparison with MG and LG in the period preceding perturbation onset when sustaining stance against the heavy pulling load across feet orientations (Fig. 3A). Conversely, MG activation showed the lowest proportional activation across the three muscles in all foot orientations in both the light and heavy loads. LG was shown to have an intermediate activation pattern regarding SOL and MG, with higher values than MG in all feet orientation by load conditions and equivalent values to SOL for the light load (cf. Héroux et al., 2014, for reduced LG activation in standing). These findings support the interpretation that SOL is more strongly activated in the control of quiet upright stance than both MG and LG. These results are consistent with previous findings showing that in isometric plantarflexion SOL displays higher activation than LG and MG (Crouzier et al., 2018; Hali et al., 2020). In this regard, higher SOL activation in quiet stance in the condition of heavy load can be thought to support the assumption that this muscle is particularly relevant in maintaining stances requiring continuous contractions of the plantar flexors to stabilize body balance. Previous studies have shown that SOL is continuously activated while maintaining a quiet stance, while both gastrocnemii muscles are featured by having a predominantly intermittent activation (Héroux et al., 2014; Mochizuki et al., 2006; Vieira et al., 2012). Higher magnitude of SOL activation in the maintenance of upright stance is thought to be associated with its greater proportion of slow-twitch fibers (Burkholder et al., 1994; Edgerton et al., 1975; Johnson et al., 1973), and higher muscle spindle density (Banks, 2006) in comparison with both the MG and LG muscles, favoring its participation in the regulation of balance stability over long time intervals. From this perspective, we conjecture that with the increased demand of muscular activation in the condition of heavy load, the central nervous system recruits SOL to a greater extent than the other plantar flexor muscles due to its structural composition.

4.1. Shift of muscle activation contribution between quiet stance and reactive responses

Following stance perturbation, results revealed a clear shift in the proportional activation across the three plantar flexors. In the primary reactive period, we found that MG was featured by the earliest activation onset (Fig. 3B), the highest proportional activation magnitude (Fig. 3C-D), and the highest activation rate (Fig. 3E) across the plantar flexor muscles. These results showed, then, a rapid shift of the activation relationship among the plantar flexor muscles, with MG changing from having the lowest proportional activation in the preceding balance

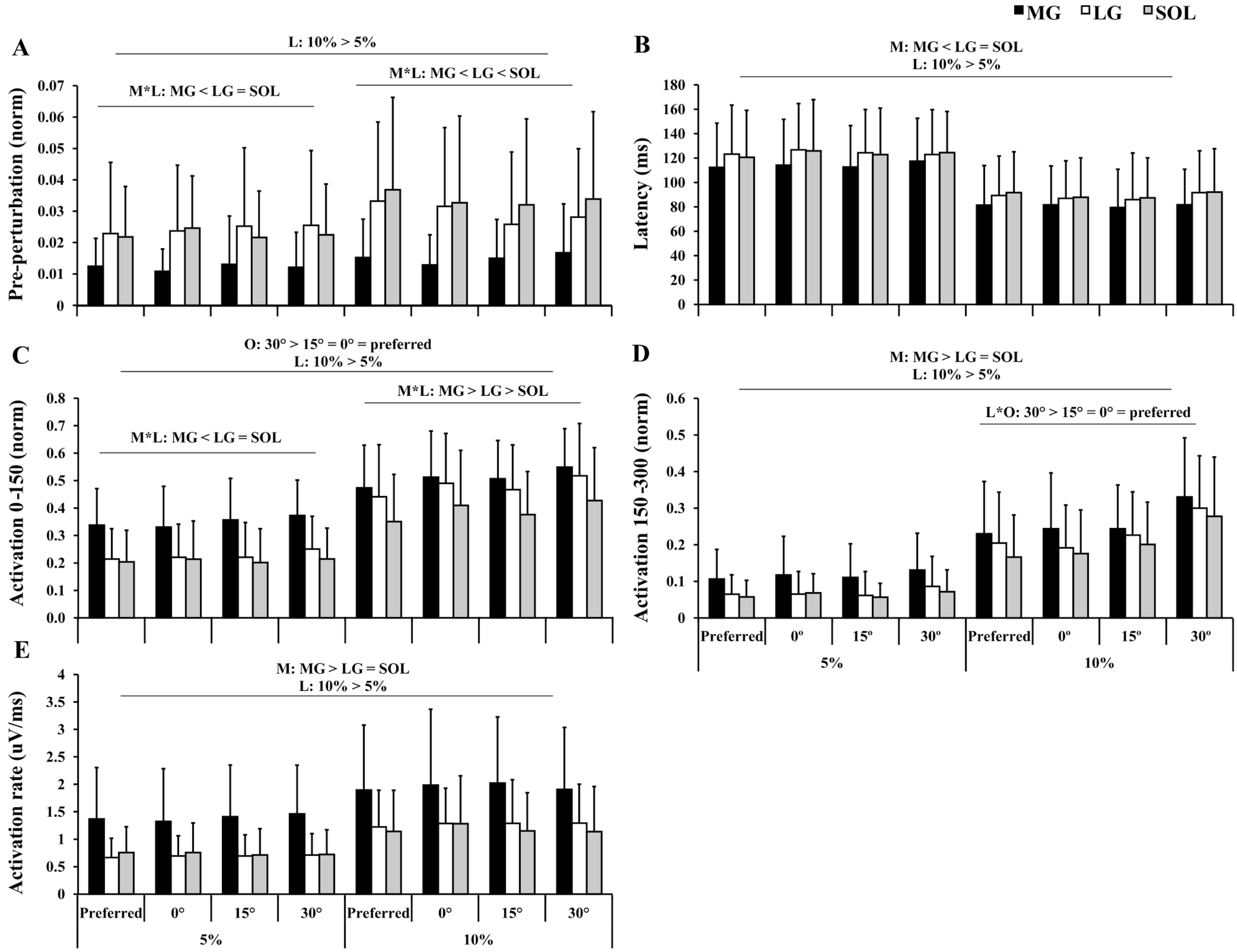

Fig. 3. Averages (standard deviation in vertical bars) of (A) pre-perturbation activation magnitude, (B) latency of muscular activation onset, and activation magnitude in the (C) primary (0–150 ms) and (D) secondary (150–300 ms) periods following perturbation onset, and (E) rate of muscular activation. Statistically significant effects are represented as it follows: M: main effect of muscle; L: main effect of load; O: main effect of orientation; M*L muscle × load interaction; O*L: orientation × load interaction.

stabilizing epoch to rapidly assuming the most prominent role in the automatic postural responses for balance recovery. This finding is consistent with a previous observation that in stance perturbations, either through backward translation or rotation leading to ankle dorsiflexion, MG had the highest activation magnitude in medium latency responses across the three plantar flexors (Nardone et al., 1990). Additionally, previous evaluation of hopping in both maximum height and high-frequency movements showed stronger and earlier activation of MG in comparison to SOL in the pre-contact and also in the eccentric movement phases (Moritani et al., 1991b). Our results brought additional light to this matter by showing that in automatic postural responses MG was not only activated more strongly and earlier, but it was also activated at a higher rate than LG and SOL. These properties have been shown to be functional to produce reactive postural responses for balance recovery (cf. Park et al., 2003; Teixeira et al., 2020; Welch and Ting, 2009). This differentiated MG activation in reactive postural responses may be related to its higher proportion of fast-twitch motor units, leading to larger ankle torques at faster rates of torque development than SOL (cf. Garnett et al., 1979). A faster rate of muscular activation in MG in comparison with LG-SOL suggests differential increased motor unit firing rates (Pollock et al., 2015) and/or increased rate of motor unit recruitment (Garland et al., 2009) in the generation of reactive responses in both the primary and secondary periods. We suggest that the shorter latency, steeper and higher activation of MG compared to LG-SOL is functional to generate a fast and a scaled response, preventing large magnitudes of body sway, potentially leading to critical balance instability.

Similar weaker and slower responses of LG and SOL across feet orientations and loads, with both muscles showing delayed, reduced gain rate and weaker activation than MG, refuted our hypothesis that both MG and LG have a proportionally higher activation magnitude in reactive responses to stance perturbation than SOL (H2). Given the structural similarity of LG and MG, this result is inconsistent with the notion that the plantar flexor muscles are selectively activated only based on their structural characteristics related to response requirements (cf. Cohen et al., 2020; Vieira et al., 2013). Similar inconsistency of muscular activation to task requirements has been found previously in the comparison of different tasks, with greater participation of SOL (predominance of slow-twitch fibers) in a dynamic squat jump task. In contrast, MG (predominance of fast-twitch fibers) contributed more in tasks requiring isometric contraction (Ball and Scurr, 2015). While our results do not allow for an explanation of the observed similarity between the activation patterns of LG and SOL, they seem to indicate that factors other than histologic or anatomic features guide the task-specific modulation of plantar flexors' activation.

4.2. Effect of feet orientation

One of the main issues leading to the current investigation was understanding the extent to which the biomechanical constraint represented by feet orientation on the ground differentially affects the activation of the three plantar flexors in response to stance perturbations. Because MG has been demonstrated to play a major role in ankle inversion movements (Vieira et al., 2013) and to have its activation modulated as a function of perturbation direction (Cohen et al., 2020; Henry et al., 1998), we hypothesized a proportionally higher activation of MG in comparison with LG and SOL as the feet are oriented outward (H3). Contrary to this expectation, our results revealed that the three plantar flexors were sensitive to feet orientation, with overall higher muscular activation magnitude in the first reactive epoch after perturbation when the feet were oriented at 30° in comparison with the other feet orientation after perturbation (Fig. 3C). In the secondary reactive epoch (Fig. 3D), increased overall muscular activation was found in the condition of feet oriented at 30° in comparison with all the others in responses to the heavy but not to the light load. These results showed the sensitivity of the postural control system to a condition imposing increased balance perturbation because of the large outward feet orientation (cf. Azzi et al., 2017). Although MG is in a mechanically advantageous position to produce greater torques at the ankles to oppose forward body sway following stance perturbation with the feet oriented outward (cf. Cohen et al., 2020), our results showed that the magnitude of muscular activation was increased equivalently in the three plantar flexor muscles in the most outward feet orientation. These results refuted our hypothesis of higher proportional activation of MG as the feet are oriented outward on the ground. The unchanged relationship between MG and LG-SOL diverges from previous results showing the specificity of MG and LG to the direction of stance perturbation (Cohen et al., 2020; Henry et al., 1998). This unchanged relationship across feet orientations and perturbation magnitude may be due to the sharp prevalence of MG even in the less challenging perturbations, like in the condition of light load with the feet oriented in parallel. We interpret this finding as indicating that the preferential recruitment of MG in the whole set of experimental conditions likely serves to generate the required torque at the ankles with a short delay (Hali et al., 2020). These results suggest that activation of the three muscles of the triceps surae are modulated similarly as a function of feet orientation on the ground.

5. Conclusions and limitations

As main conclusions, our results suggest a distinction of activation patterns between SOL and MG in body balance control. For balance stabilization against a posterior pulling load, SOL was found to have a proportionally higher activation to load magnitude than both MG and LG. In the ensuing reactive response to balance perturbation, MG was found to have earlier, steeper and proportionally higher activation than both LG and SOL. The three plantar flexor muscles were sensitive to load, producing increased, steeper and earlier activation in response to the heavy than the light load. Feet oriented at 30° led to increased muscular activation than in the other feet orientations in response to balance perturbation in an equivalent way across the three plantar flexor muscles.

As the main limitation, our reference for normalization of muscular activation was of submaximal rather than maximal magnitude in the performance of the experimental task. Although in some individual cases participants were unable to keep the feet in place, apparently reaching their maximum muscular activation magnitude for the experimental task, in other cases higher perturbation magnitudes could have been applied by using heavier loads than the 10% body weight to achieve individual maximum muscular responses for balance recovery. Considering that all analyses were based on intra-individual comparisons, this limitation can be thought to have only minor implications for the conclusions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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