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Anticipatory Postural Adjustments and Spatial Organization of Motor Cortex – Evidence of Adaptive Compensations in Healthy Older Adults

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Author contributions:
JS and BF designed the study. JS performed data collection, processing and analyses. JS and BF interpreted the data. JS drafted the manuscript and BF provided critical review of the manuscript.

Running head:
APAs and M1 organization in older adults

ABSTRACT

During anticipated postural perturbations induced by limb movement, the central nervous system generates anticipatory postural adjustments (APAs) in the trunk and hip musculature to minimize disturbances to equilibrium. Age-related changes in functional organization of the nervous system may contribute to changes in APAs in healthy older adults. Here we examined if altered APAs of trunk/hip musculature in older adults are accompanied by changes in the representation of these muscles in motor cortex. 12 healthy older adults, 5 with a history of falls and 7 non-fallers, were compared to 13 young adults. APAs were assessed during a mediolateral arm raise task in standing. Temporal organization of postural adjustments was quantified as latency of APAs in the contralateral external oblique, lumbar paraspinals and gluteus medius relative to activation of thedeltoid. Spatial organization was quantified as extent of synergistic coactivation between muscles. Volume and location of the muscle representations in motor cortex were mapped using transcranial magnetic stimulation. We found that older adults demonstrated significantly delayed APAs in the gluteus medius muscle. Spatial organization of the three muscles in motor cortex differed between groups, with the older adults demonstrating more lateral external oblique representation than the other two muscles. Separate comparisons of the faller and non-faller subgroups with young adults indicated that non-fallers had the greatest delay in gluteus medius APAs and a reduced distance between the representational areas of the lumbar paraspinals and gluteus medius. This study indicates that altered spatial organization of motor cortex accompanies altered temporal organization of APA synergies in older adults.

KEYWORDS
Motor cortex; transcranial magnetic stimulation; torso; functional organization; aging; postural control

NEW AND NOTEWORTHY

Anticipatory postural adjustments (APAs) are a critical component of postural control. Here we demonstrate that in healthy older adults with and without a history of falls, delayed APAs in the hip musculature during mediolateral perturbations are accompanied by altered organization of trunk/hip muscle representation in motor cortex. The largest adaptations are evident in older adults with no history of falls.

1. INTRODUCTION

Falls are a significant cause of morbidity and mortality among older adults. Although falls have multiple causes, changes in postural control in older adults contribute significantly to fall risk (Rubenstein and Josephson 2006). It is becoming clear that adaptations in structure and function occur at every level of the postural control system in association with aging (Papegaaij et al. 2014a). In order to design effective exercise interventions to reduce the risk of falls, it is critical to understand how nervous system adaptations may contribute to age-related changes in postural control in healthy older adults.

Anticipatory postural adjustments (APAs) are an important component of postural control (Horak 2006). Anticipatory postural adjustments are synergies of feedforward muscle activation or inhibition that occur before a predictable perturbation. Disordered APAs may result in postural instability during self-initiated movements (Horak 2006; Kubicki et al. 2012). APA synergies can be characterized in terms of the timing of muscle activation or inhibition relative to the destabilizing event (temporal organization); in terms of the three-dimensional coordination of activity in multiple muscles (spatial organization); and in terms of the magnitude of muscle activation (amplitude scaling). The standing rapid arm flexion task is a simple paradigm that is often used to quantify these characteristics of APAs. Anticipatory postural control of the trunk and hip musculature during rapid arm raising in standing counteracts reactive forces from upper limb motion and helps to maintain the mass of the head and trunk within the base of support. During rapid arm flexion, APAs occur in the abdominals, paraspinals and hip extensors in healthy young adults (Hodges et al. 1999; Massé-Alarie et al. 2012). In older adults, APAs in the hip extensors are delayed relative to the onset of the agonist (deltoid) muscle compared to young adults (Rogers et al. 1992). In addition to this altered temporal organization, older adult have altered spatial organization of postural control with increased coactivation of lower limb muscles during standing and reaching (Nagai et al. 2011). It is not known if this coactivation is evident in the trunk and hip musculature during rapid arm raising.

Much of the research investigating APAs has utilized perturbations that are induced in the anterior-posterior direction, such as rapid arm flexion. However, postural control in the mediolateral plane is critical to maintaining dynamic stability (Rogers and Mille 2003), and disordered mediolateral postural control is associated with a history of falls (Maki et al. 1994). Research investigating externally-induced mediolateral postural perturbations has demonstrated synergistic APAs in the gluteus medius, external oblique, and paraspinal musculature in healthy young adults (Santos and Aruin 2008). Evidence from the same perturbations suggests that there is no change in the magnitude of trunk and hip APAs in older adults (Claudino et al. 2013). It is still unclear if the temporal and spatial organization of mediolateral APA synergies in the trunk and hip musculature are affected by aging.

Neural substrates of postural control are distributed throughout the central nervous system. The structure and function of these substrates is affected by heathy aging. In primary motor cortex, intracortical inhibition during standing is reduced in older adults compared with younger adults, and the extent of this reduction in inhibition is associated with worse postural performance (Papegaaij et al. 2014b). As the motor cortex contributes to preparation of postural adjustments (Tsao et al. 2008; Jacobs et al. 2009a; Chiou et al. 2016, 2018), age-related changes in motor cortex may also be associated with changes in APAs in older adults. In particular, excitability of cortical neural networks is modulated in response to use and with healthy aging. This has been demonstrated by changes in the topographic organization of muscle-specific corticospinal output evoked by transcranial magnetic stimulation (TMS)(Adkins et al. 2005; Plow et al. 2014; Masse-Alarie et al. 2017). TMS studies mapping motor cortical organization during voluntary motor tasks show that older adults demonstrate less distinct topographic representation of muscles, reduced representational volume (Coppi et al. 2014) and shifted representational area

(Bernard and Seidler 2012). Therefore, less differentiated and shifted representations of the postural musculature in M1 may underlie the impairments in APAs that are evident in older adults.

The primary purpose of this study was to compare temporal and spatial characteristics of anticipatory postural adjustments of the trunk and hip, and the motor cortical representation of trunk and hip musculature, in young adults and healthy older adults. A secondary purpose of this study was to explore if these variables differ in older adults with and without a history of falls. We hypothesized that latency of APAs would be delayed in older adults and that coactivation between muscles would be greater, and that this would be accompanied by reduced differentiation of the trunk and hip musculature motor cortical representation. We further hypothesized that these changes would be more evident in older adults with a history of falls than those with no fall history.

2. METHODS

2.1 Participants

The study was approved by the Institutional Review Body of the University of Southern California and all participants gave written informed consent before enrollment and data collection. Participants were recruited from the local community. Participants in the older adult group were over 65 years, community-dwelling, independent with activities of daily living and ambulation, able to stand upright without assistance for two minutes and able to follow verbal directions (Newton 2001). A history of falls was determined with a questionnaire (Claudino et al. 2013), with a fall defined as an unplanned contact with a support surface below knee level (Takahashi et al. 2006). Fallers were defined as those who had experienced at least one fall in the past year (Hass et al. 2004). Participants in the young adult group were between 18 and 30 years old (Isles et al. 2004). Exclusion factors in both groups were a history of disorders affecting balance,significant/persistent low back pain, vestibular disorders, and inability to abduct both arms to at least 90°. As per current TMS recommendations, participants were also excluded if they had metal, electrical or magnetic implants, a personal or family history of epilepsy, or other medical history/use of medications or substances that are known to lower seizure threshold (Rossi et al. 2011).

2.2 Experimental procedure

Balance and mobility were assessed in older adults with the Anticipatory Postural Adjustments section of the BESTest (Horak et al. 2009) and the Timed Up and Go test. Self-selected gait velocity in older adults was calculated from the average of two 10m walking trials.

2.2.1 Mediolateral anticipatory postural adjustments

Bipolar, disposable surface electromyography electrodes (inter-electrode distance 22mm, Myotronics-Noromed, Inc., Tukwila, USA) were placed on external oblique (EO), thoracic longissimus pars lumborum at the level of L1 (LL) and gluteus medius (GMED) in accordance with established guidelines (Hermens 2000). The electrodes were placed on the same side as the dominant limb. Additionally, electrodes were placed on the deltoid muscles. EMG data were transmitted and digitally sampled at 1500Hz using a wireless telemetry system (base gain 400; TeleMyo DTS Telemetry, Noraxon USA Inc, Scottsdale, USA).

Anticipatory postural adjustments were quantified during a rapid arm raise task (Figure 1a). A 2lb weight was placed on the wrist of the limb contralateral to the trunk/hip EMG instrumentation (i.e. left arm in an individual who identified their dominant limb as the right) (Horak et al. 1984). As APAs are direction-specific, the contralateral side was selected for the arm raise task as existing research and preliminary data suggested that this would maximize activity in two out of the three muscles under investigation (Santos and Aruin 2008). The weight was used since preliminary data indicated clearer and more consistent APAs in the trunk and hip musculature with external loading. Participants stood barefoot with their feet parallel and heels 10cm apart. In response to an auditory/visual cue, participants abducted the arm to 90° as rapidly as possible. Six trials were collected (Tsao et al. 2010a). The time taken to reach 90° of glenohumeral abduction was monitored utilizing a laser trigger system.

2.2.2 Motor cortical representation

Topographic organization of muscle representational areas in primary motor cortex were quantified with motor evoked potentials from single-pulse TMS. TMS procedures were conducted and are described here in accordance with current guidelines (Chipchase et al. 2012).

Motor evoked potentials (MEPs) were elicited using a single-pulse magnetic stimulator (MagStim 200[2,] Magstim Inc, NC) and a 110mm double cone coil (Magstim Inc, NC) (Lagan et al. 2008; Tsao et al. 2008; Fisher et al. 2013). Stimulation was applied on the hemisphere contralateral to the side of EMG instrumentation (i.e. on the left if the dominant limb was the right). The previously described surface EMG electrodes on the external oblique, thoraco-lumbar longissimus and gluteus medius were attached to a pre-amplifier (Motion Lab Systems, 15003 Hz, bandpass filter 1 - 1000 Hz, base gain 2000). MEPs were acquired and stored using Signal software (Signal v6, Cambridge Electronic Design Ltd, Cambridge UK). A lycra cap marked with a 1cm grid was placed over the participant's scalp and the location of the vertex determined. To ensure correct and consistent coil placement the Brainsight® Frameless stereotactic image guidance system was used (Rogue Research Inc, Montreal, Canada). Landmarks on each participant's head were co-registered with the Brainsight™ system using an infra-red marker tracking system. The position and orientation of the coil was then tracked relative to the position of these markers and to a 3-D reconstruction of a standard brain MRI.

Prior to the TMS data collection, the maximal voluntary isometric contraction (MVIC) for each muscle was determined. Manual resistance was provided to the participant against the lateral border of the dominant limb as they performed hip abduction in side lying (gluteus medius) and at the shoulders as they performed maximal trunk flexion/rotation in supine (external oblique). Due to the small representational area of the trunk and hip musculature, MEPs are not consistently elicited when the muscles are at rest, therefore motor thresholding and mapping was performed during a submaximal contraction for all three muscles (Lagan et al. 2008; Tsao et al. 2010a; Massé-Alarie et al. 2012)

Lumbar longissimus/gluteus medius - TMS mapping of the lumbar longissimus and gluteus medius were conducted during double-leg bridging in supine (Fisher et al. 2013). Consistent bridge height was ensured by having participants raise the pelvis up to the height of a reference marker placed at a 150% of the vertical distance of their anterior superior iliac spines to the table. Additional resistance to hip abduction was provided by a band placed around the distal thighs (Figure 1c). Each TMS stimulus was delivered as the participant maintained the correct test position and gluteus medius contraction at 20 % MVIC. A consistent level of muscle activation was ensured by providing real-time visual feedback of the root mean square averaged amplitude of the gluteus medius contraction relative to the 20% MVIC activation target. Feedback was provided for amplitude of gluteus medius EMG activity only, as pilot data indicated a consistent activation ratio of approximately 1.6: 1 for the longissimus and gluteus medius during a double-leg bridge at varying heights. Participants received a TMS pulse every 5-10 seconds and rested in supine between each stimulus. Commencing approximately 2 cm lateral to and anterior to the vertex (Tsao et al. 2008; Fisher et al. 2013), the optimal site of stimulation, or “hotspot” was determined by systematically stimulating a series of locations using the cap grid reference until the location that consistently produced an MEP was determined.

The active motor threshold at the gluteus medius hotspot was quantified as the stimulator intensity that produced at least 5 out of 10 MEPs with an amplitude of at least 100 μV. The motor cortical representation of gluteus medius and lumbar longissimus were mapped at 120% of the active motor threshold, by delivering stimuli at 24 locations spaced 1cm apart in a 6 by 4 grid encompassing the motor cortex (MNI x coordinates -1.04:-30.36; MNI y coordinates -42.34: 8.23; Figure 1d) (Mayka et al. 2006). Five stimuli were delivered at each location.(Masse-Alarie et al. 2017)

External oblique – TMS mapping of the external oblique was conducted during posterior pelvic tilting in supine. A consistent level of muscle activation at 20 % MVIC was ensured by providing visual feedback of the external oblique contraction intensity. TMS stimuli were delivered as the participant maintained a sub-maximal posterior pelvic tilt. Participants rested in the supine position for 5 -10 seconds between each stimulus. Determination of the hot-spot, active motor threshold and mapping was conducted as previously described.

2.3 Data processing and analyses

2.3.1 Mediolateral anticipatory postural adjustments

To quantify performance of the rapid arm raise task, reaction time and movement time were calculated. Reaction time was defined as the duration from the cue to onset of deltoid muscle activity. Movement time was defined as the duration of time from onset of deltoid activity to the glenohumeral joint reaching 90° of abduction.

EMG data were processed in MATLAB® using custom-written code. After removal of the DC offset, the EMG signals were band-pass filtered between 40 and 400Hz. This high-pass threshold was set to minimize electrocardiogram (ECG) artifact in the EMG signal. Signals were then full-wave rectified. The latency of the onset of muscle activity for each individual was quantified using the integrated profile or iEMG method (Santello and McDonagh 1998; Allison 2003; Smith and Kulig 2016). Onset of activity in each muscle was quantified in ms relative to the onset of the deltoid muscle on the moving arm. Muscle activations were classified as anticipatory postural adjustments if they occurred from 100ms prior to deltoid onset to 50ms after deltoid onset (Figure 1b) (Massé-Alarie et al. 2012). For calculation of coactivation between pairs of muscles, the EMG data were additionally low-pass filtered at 12Hz to obtain a linear envelope and were amplitude normalized to the peak activation occurring in that muscle for that individual throughout the entire arm raise**.** A coactivation coefficient (CCI) was then calculated for each possible pair of muscles (LL/GMED; GMED/EO; LL/EO) in the same anticipatory postural adjustment time window utilizing equation i)

i) $\sum_{i=1}^{N}\left(\frac{EMG.low_i}{EMG.high_i}\right)(EMG.low_i + EMG.high_i)$

where *N* is the number of data points in the anticipatory window. For each instant in time, *EMG.high* and *EMG.low* are the amplitude of the signals from each muscle, with EMG.high being the muscle with the higher amplitude at that moment and EMG.low being the muscle with the lower amplitude (Nelson-Wong and Callaghan 2010). This index provides a sum of the normalized amplitude of activity for each muscle pair, weighted by the extent of coactivation.

2.3.2 Motor cortical representation

MEP data were processed in Signal software and MATLAB®. Peak-to-peak amplitude of each MEP was extracted from a window 5 to 45ms after the magnetic pulse. Average MEP amplitude was then calculated for each muscle at each grid location. This average amplitude for each location was then normalized to the peak MEP amplitude for that muscle across all grid locations (Tsao et al. 2011; Plow et al. 2014; Masse-Alarie et al. 2017). The center of each muscle representational area was determined by calculating the center of gravity (CoG). The

CoG is the amplitude-weighted center of each muscle representational area and is calculated with the following equations:

ii) $CoGx = \sum zixi / \sum zi$

iii) $CoGy = \sum ziyi / \sum zi$

where x_i and y_i are the medio-lateral and antero-posterior locations respectively and z_i is normalized amplitude (Wassermann et al. 1992; Uy et al. 2002). The CoG, determined using this methodology, is reliable in both young and older adults (Boroojerdi et al., 1999; Uy et al., 2002). Horizontal separation distance between the CoG for each possible pair of muscles was calculated with the Euclidian distance. The volume of the representational area for each muscle was calculated as the sum of the normalized amplitude of MEPs from all grid locations that produced an MEP. To check that the target activation of 20% MVIC had been maintained in gluteus medius and external oblique throughout the experiment, the mean amplitude of EMG activation in the 100ms window immediately prior to the delivery of each stimulus was also calculated.

2.4 Statistical approach

The normality and sphericity of data was assessed using standard procedures (version 24, IBM SPSS Statistics, Armonk, NY). Mann Whitney U tests were utilized to compare reaction time and movement time between groups and active motor threshold for both muscles. Independent t-tests were utilized to compare pre-stimulus activation of GMED and EO.

Separate mixed-model ANOVA with between subject factor (group; young adult and older adult) and within subject factor (muscle; lumbar longissimus, gluteus medius and external oblique) were conducted to compare the primary variables for anticipatory postural adjustments and motor cortical representation. Variables for APAs were muscle onset latency and coactivation coefficient between each muscle pair. Variables for motor cortical representation were CoG locations, CoG separation distance and volume of the representational area for the same three muscles. In the case of significant group by muscle interactions, paired post hoc comparisons of a) between groups for each muscle (independent t-tests) and b) within groups for each muscle (paired t-tests) were then made utilizing the Holm-Bonferroni correction for multiple comparisons within each cluster of tests. Estimates of effect sizes for comparisons that reached or approached significance were calculated with an unbiased Cohen's *d*, with correction for small sample size ($d_{unb,}$(Fritz et al. 2012)). 0.8 indicates a large effect size, .5 a medium effect size and .3 a small effect size

To examine the influence of falls history on all variables, exploratory comparisons between the subgroups of fallers and non-fallers within the older adult group, and between young adults and each subgroup were made with Mann Whitney U tests. Comparisons within subgroups for each muscle were made with the Wilcoxon Signed Ranks Test. Estimates of effect sizes for all non-parametric comparisons were calculated using Cohen's *r* with 0.5 indicating a large effect size, .3 a medium effect size and .1 a small effect size (Fritz et al. 2012).

3. RESULTS

3.1 Demographics and balance/mobility tests

Demographics of the young adult and older adult group are provided in Table 1. All of the older adult group participated in regular physical activity. The dominant limb was the right limb for all participants. Therefore, all participants were instrumented with EMG on the right side, utilized their left arm for the arm raising task, and had TMS applied to the left hemisphere. One male older adult with no history of falls did not complete the TMS data collection due to fatigue, and APA data for one female young adult were not recorded due to equipment failure.

Scores for the APA section of the BESTest, the TUG time, and self-selected gait speed for the older adults are shown in Table 1.

3.2 Mediolateral anticipatory postural adjustments

Reaction time and movement time were not significantly different between the young and older adult groups (Table 1, p = 0.740 and p = 0.288 respectively).

Muscle onset latency differed between groups, with a significant group by muscle interaction ($F_{(2,21)} = 4.681$, p = 0.014). GMED onset was significantly later in older adults than young adults (adjusted p = 0.039, unbiased Cohen's d (d_{unb}) = 1.07)(Figure 2a & b). Within the older adult group, but not the young adult group, there was a trend for GMED onset being significantly later than LL onset (adjusted p = 0.069, d_{unb} = 1.02).

There was no difference between groups for coactivation index for any of the muscle pairs, with no main effect of group or group by muscle interaction. There was a significant main effect of muscle pairing ($F_{(2,21)}$ = 8.926, p = 0.001). Post hoc comparisons indicated that there was significantly greater coactivation between LL/GMED than between LL/EO (adjusted p = .009, d_{unb} = 0.44) (Figure 2c).

3.3 Motor cortical representation

Active motor thresholds, as a percentage of total stimulator output, were not significantly different between the young and older adult groups for either GMED or EO (p = 0.150 and p = 1.000 respectively). The % of MVIC of GMED and EO immediately prior to the delivery of the

TMS stimuli was also consistent between the young adult and older adult groups (p = 0.182 and 0.303 respectively).

Motor maps for each muscle in each group are shown in Figure 3. CoGx locations varied by group (group by muscle interaction $F_{(2,21)} = 4.360$, p = 0.019). Post hoc comparisons were not significant for any individual muscle. The two groups demonstrated different relative spatial organization of the three muscles. Within the young adults group, LL tended to be more lateral than GMED (adjusted p = 0 .162, $d_{unb} = 0.60$). Within the older adult group, EO was significantly more lateral than both LL and GMED (adjusted p = 0.015 and 0.028 respectively, $d_{unb} = 0.85$ and 0.79 respectively, Figure 4a). For COG y location there was a significant main effect of muscle $_{(2,21)} = 4.444$, p = 0.017). EO was significantly more posterior than LL (adjusted p = 0.045, $d_{unb} = 0.52$). There was no main effect of group, or group by muscle interaction (Figure 4b).

CoG separation distance did not differ between groups. There was a main effect of muscle pair, with LL/GMED separation distance tending toward being smaller than both LL/EO distance and GMED/EO distance (main effect $F_{(2,21)} = 5.059$, p = 0.020; post-hoc comparisons adjusted p = 0.096 in both cases, $d_{unb} = 0.70$ and 0.69 respectively).

Volume of motor cortical representational area did not differ between groups. There was a main effect of muscle ($F_{(2,21)} = 3.947$, p = 0.027). Volume was significantly larger in the GMED compared with LL (main effect adjusted p = 0.015, $d_{unb} = 0.73$).

3.4 Subgroup comparisons based on falls history

Five out of the twelve older adults reported at least one fall in the preceding year. There was no significant difference in age (p = 0.684) or weight (p = 0.361) between fallers and non-fallers. BESTest score and TUG performance were the same in fallers and non-fallers (p = 0.876 and

0.530 respectively). However, fallers had significantly slower gait velocity than non-fallers ($p = 0.016$, effect size $r = 0.49$). Performance of the rapid arm raise task was equivalent between the fallers and non-fallers, with no difference in reaction time or movement time between young adults and older adult fallers ($p = 0.959$ and 0.160 respectively) or young adults and non-fallers ($p = 0.682$ and 0.750).

The subgroup analyses comparing young adults with fallers and non-fallers separately showed that age-related changes in mediolateral APAs were most evident in the non-faller group. GMED was significantly later in non-fallers than young adults ($p = 0.022$, $r = 0.52$) but there was no difference in GMED latency between fallers and young adults ($p = 0.234$, Figure 5a). There was also a trend toward significantly less coactivation in the GMED/EO pairing in non-fallers compared with young adults ($p = 0.100$, $r = 0.39$) but no difference in coactivation for any muscle pairing between fallers and young adults ($p > 0.5$ for all comparisons).

Active motor threshold of GMED and EO did not differ between the subgroups ($p = 0.931$ and 0.662 respectively). Age-related changes in CoG location were most evident in the non-faller group. LL representation was significantly more medial in non-fallers than in young adults ($p = 0.017$, $r = 0.54$) but that there was no difference between the fallers and young adults for any muscle. In the non-fallers, the CoG location for EO was significantly more lateral than both LES and GMED ($p = 0.028$, $r = 0.90$ for both comparisons) but there was no significant difference between COG x locations for the three muscles in the faller group (Figure 5b). There was no significant difference in COG y locations for any muscle between fallers or non-fallers and young adults.

Subgroup analyses of separation distance also showed that age-related changes were most evident in the non-fallers. LL /GMED separation distance was significantly less in non-fallers than young adults ($p = .023$, $r = 0.52$) but that there was no difference between fallers and young adults (p = 0.246) (Figure 5c). The volume of GMED was significantly smaller in non-fallers than young adults (p = 0.017, *r* = 0.54) but that there was no difference between fallers and young adults.

4. DISCUSSION

This study compared the temporal and spatial organization of mediolateral APAs, and the functional representation of the trunk and hip musculature in motor cortex, in healthy young and older adults. For the first time, and in support of our original hypothesis, we found that latency of onset in GMED was delayed in older adults during mediolateral anticipatory postural adjustments. Older adults also demonstrated shifted representational areas for postural musculature in motor cortex. However, the separation distance between the center of gravity for individual muscle representational areas and the volume of each representational area did not differ between the young and older adult groups. The exploratory subgroup analyses indicated that, contrary to our hypotheses, the greatest age-related changes in latency of APAs, muscle coactivation, location of representational area, separation distance and volume of representational area were evident in the non-fallers rather than the fallers. These findings provide some preliminary evidence of potentially adaptive compensations in the non-faller subgroup.

In our cohort of healthy, active older adults, performance of the rapid arm raising task did not differ from the young adults in terms of reaction time or movement time. This finding is consistent with existing research indicating that simple (non-choice) reaction time is preserved in older adults (Rogers et al. 1992; Bleuse et al. 2006) and that the velocity of movement is also consistent under low-loading conditions (Bleuse et al. 2006). Despite this similarity in task performance, older adults demonstrated altered temporal organization of the APA synergy. In the young adult group, onset of activity in GMED was prior to that of the trunk muscles. This is consistent with findings from previous studies of anterior-posterior arm raising (Mank'kovskii et al. 1980; Horak et al. 1984). In contrast, GMED was activated last in the older adult group. To our knowledge, previous research examining mediolateral APAs in older adults has exclusively utilized predictable, externally induced perturbations rather than voluntary limb movement. This previous research demonstrated no difference in the magnitude of trunk and hip APAs in older adults with and without a history of falls compared with young adults but did not investigate onset timing or coactivation (Claudino et al. 2013). Taken together, these results support a hypothesis that the temporal organization of APAs and their amplitude scaling are separate constructs with distinct neural substrates and that they may be differently influenced by aging (Bleuse et al. 2006; Jacobs et al. 2009b; Huang and Brown 2013).

During rapid mediolateral arm raising, reactive forces and moments caused by the motion of the arm result in trunk/pelvis flexion, trunk side bending and pelvis rotation toward the side of the moving limb (Hodges et al. 1999). APAs in the contralateral GMED, EO and LL resist these forces/moments. In particular, appropriate activation in GMED is critical to stabilize the trunk and pelvis (Santos and Aruin 2008) and to maintain dynamic mediolateral balance in standing (Granata et al. 2005). Therefore it is important to determine why postural GMED onset is delayed in older adults. Studies have demonstrated reduced peak torque and rate of torque development with aging in GMED (Rogers and Mille 2003). Underlying this is Type II fiber atrophy and fatty infiltration that is most evident in older adults with a history of falls (Sato et al. 2002; Inacio et al. 2014). Therefore, we speculate that delayed GMED APAs in the present study are reflective of a central nervous system strategy that possibly compensates for impaired GMED muscle composition by reducing the use of this muscle. However, it is also possible that delayed GMED APAs are purely a result of altered muscle fiber composition.

Interestingly, the present study did not demonstrate age-related increases in coactivation between the trunk and hip musculature during APAs. A majority of earlier work has demonstrated that older adults utilize greater muscle coactivation, but this has been reported between agonists and antagonists in the lower limb during static standing or walking rather than between synergists during APAs (Hortobágyi and Devita 2006; Hortobágyi et al. 2009; Nagai et al. 2011). Agonist/antagonist coactivation serves to stiffen joints in the presence of impaired postural control, and it is possible that this occurred in the present study in other lower limb muscles or between pairs of trunk and hip muscles that were not measured.

Altered temporal organization of APA synergies in the trunk and hip musculature in older adults was accompanied by shifts in the representational areas of these muscles in motor cortex. In young adults, the CoG for LL was more lateral than that of GMED. In contrast, in older adults, and particularly the non-fallers, the CoG for EO was more lateral than both LL and GMED. The spatial organization and excitability of representational areas for movement or muscles in motor cortex is highly plastic and is modulated by use or training (Remple et al. 2001; Perez et al. 2004; Adkins et al. 2005; Tennant et al. 2012). Therefore, reduced postural utilization of GMED in older adults may be accompanied by merging of the LL and GMED representational areas. These novel findings in older adults are similar to evidence of pain-related adaptations in trunk muscle APAs and reorganized trunk muscle cortical representation in individuals with low back pain (Tsao et al., 2008)**.** As the alteration in motor cortical representation was not accompanied by systematic changes in volume of representational areas or separation distance across our older adult group, it is unlikely that our findings are an artifact of the known reduced brain volume in older adults (Jäncke et al. 2015).

Dedifferentiation of the representational areas for the three muscles was not consistently evident in our older adult group. Existing evidence from voluntary motor tasks has suggested that older adults compensate for reduced gray and white matter volume by increased and diffuse activation of multiple motor areas and both hemispheres during movement (Seidler et al. 2010; Bernard and Seidler 2012). Ours is the first study to specifically examine if dedifferentiation of representational areas occurs between muscles within the motor cortex of a single hemisphere. The non-faller subgroup did have less spatial differentiation between the representational areas of LL and GMED. Therefore, our findings suggest that age-related dedifferentiation of representational areas is specific to individual muscles rather than a generalized characteristic of muscle representations in motor cortex. Greater overlap between individual muscle representational areas may facilitate task-specific synergistic activity in muscles that are frequently activated together (Masse-Alarie et al. 2017). In support of this, across both groups, the smaller separation distance between LES and GMED was accompanied by greater coactivation between those muscles during APAs. The subgroup analysis also showed that increased distance between EO and GMED was accompanied by decreased coactivation between those two muscles in the non-faller group.

As we did not follow these individuals over time, it is not possible to identify a causal or temporal relationship between adaptations in APAs, changes in motor cortical representational areas, and falls. However, our subgroup analyses suggest two possibilities. The first is that the significant adaptations evident in the non-faller group represent an adaptive response to altered GMED peripheral muscle characteristics. The adaptive response is evident as a lesser role for GMED in APAs and is accompanied by merging of the LL and GMED representational areas. The alternative interpretation is that the findings from the non-faller group are representative of normal age-related changes, and that the faller group had developed adaptations that make them more consistent with young adults as an attempt to improve postural control following a fall. However, since our faller group demonstrated impaired motor behavior, including decreased gait velocity, compared with the non-faller group, the latter explanation seems less likely.

There are some limitations to the present study. Although the sample size was small it was based on *a priori* power analysis. Further, our group comparisons are supported by a conservative approach to hypothesis testing and demonstrate large effect sizes. Challenges in recruiting male older adults who met the inclusion/exclusion criteria for TMS resulted in an unequal sex distribution. However, in the young adult group there were no differences between males and females for any of the variables, and we are not aware of any research indicating sex-related differences in APAs or motor cortical representations in older adults. Finally, the results of this study may not extrapolate to other postural motor behaviors as multiple task-dependent factors influence the temporal and spatial organization of APAs. These include the speed and direction of movement, self-paced versus external cuing, and whether the perturbation is induced by a voluntary movement or by an anticipated external perturbation (Horak et al. 1984; Santos and Aruin 2008).

This study demonstrates for the first time that motor cortical representation of trunk and hip musculature is altered in healthy older adults and that this is accompanied by disordered anticipatory postural adjustments. Understanding age-related changes in anticipatory postural adjustments, and the neural correlates of these changes will assist in optimizing interventions to maintain and improve balance in older adults.

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FIGURE LEGENDS

Figure 1. a) Experimental set up for standing rapid arm raise showing participant instrumented with surface EMG electrodes on deltoid, contralateral lumbar longissimus, gluteus medius and external oblique (not pictured). b) Window for anticipatory postural adjustments from 100ms before to 50ms after onset of deltoid. Task reaction time calculated as time from go signal to deltoid onset. Task movement time calculated as time from deltoid onset to 90 degrees shoulder abduction (end of trial). c) Experimental set up for TMS mapping of gluteus medius and lumbar longissimus. Participant is performing a double-leg bridge while applying an abduction force to the band placed around the distal thighs. d) 6 by 4 grid for mapping centered over motor cortex using stereotactic image guidance, with exemplar motor evoked potentials from 4 grid locations for the external oblique muscle.

Figure 2. a) Exemplar EMG data from a single trial for a young adult and older adult indicating onset of deltoid activation (red line). b) Group data for onset latency of contralateral lumbar longissimus (LL), gluteus medius (GMED) and external oblique (EO) relative to onset of deltoid activation (DELT). Negative values indicate onsets in postural muscles that occurred prior to onset in DELT. Note significant difference in GMED onset between young and older adults (*p = 0.039). c) Group data for the sum of the normalized amplitude of activity for each muscle pair, weighted by the extent of coactivation (coactivation index, CCI). Muscle pairs are lumbar longissimus/gluteus medius (LL/GMED), lumbar longissimus/external oblique (LL/EO), and gluteus medius/external oblique (GMED/EO). Note significant difference between CCI of LL/GMED and LL/EO (*p = 0.009).

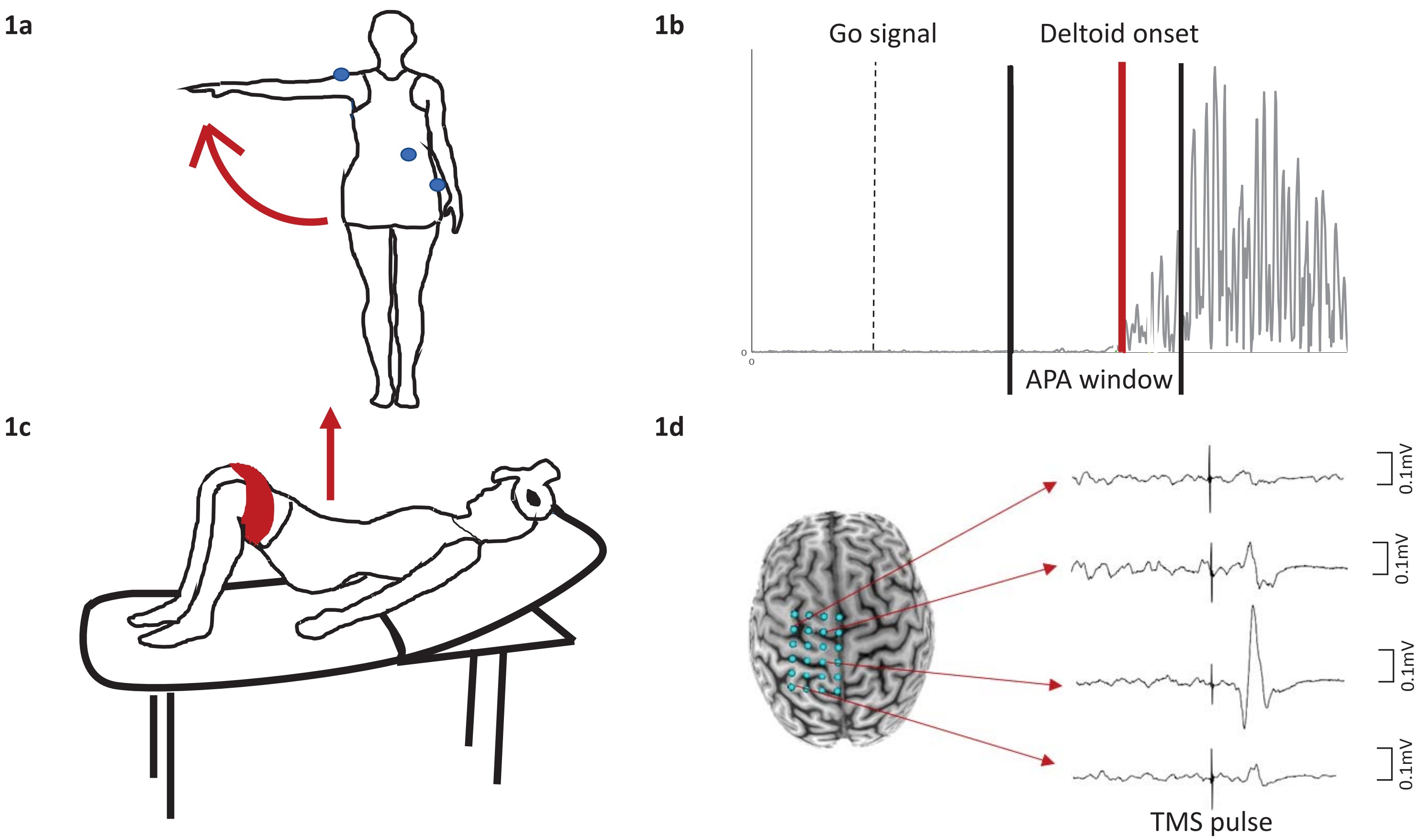
Figure 3. Averaged motor maps for the young adult group (top) and older adult group (bottom) showing location of the representational area for external oblique (EO), lumbar longissimus (LL) and gluteus medius (GMED) mapped on a 6 by 4cm grid. The colorbar indicates average normalized MEP amplitude. Average location of center of gravity for each group is superimposed in black on each map.

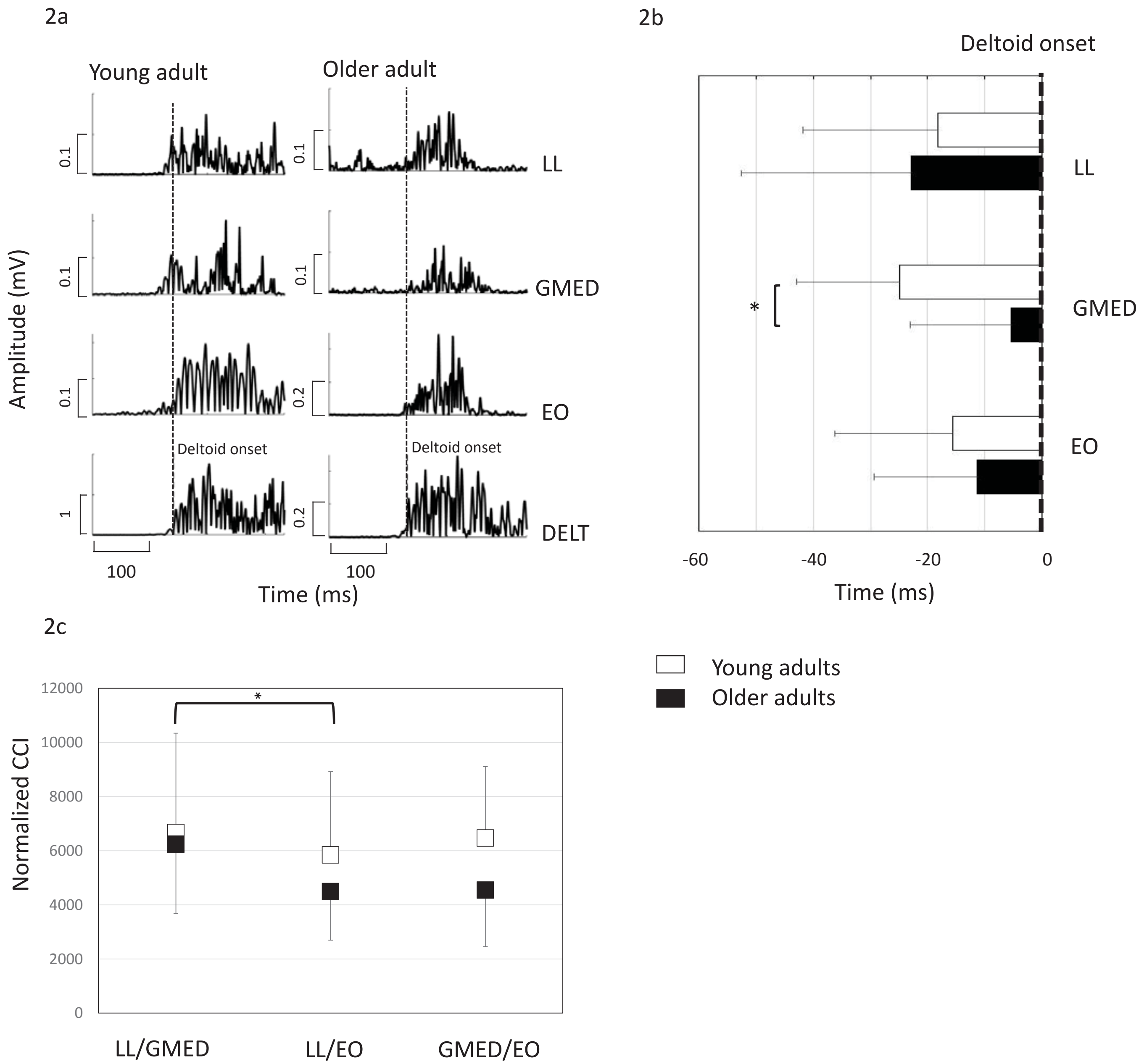
Figure 4. Location of center of gravity (CoG) for lumbar longissimus (LL), gluteus medius (GMED) and external oblique (EO) in the young adult group and the older adult group. a) CoG x location. Note that EO is significantly more lateral than LL and GMED in the older adult group (*p = 0.015 and 0.028 respectively). b) CoG y location. Note that EO is significantly more posterior than LL in both groups (*p = 0.045).

Figure 5. Subgroup comparisons based on falls history. a) Individual data for onset latency of contralateral gluteus medius (GMED) relative to onset of deltoid activation. GMED was significantly later in non-fallers than young adults (p = 0.022). b) Individual data for center of gravity x location (CoG x location) for lumbar longissimus (LL), gluteus medius (GMED) and external oblique (EO). LL representation was significantly more medial in non-fallers than in young adults (*p = 0.017). In the non-fallers, the CoG location for EO was significantly more lateral than both LL and GMED (*p = 0.028 for both comparisons).

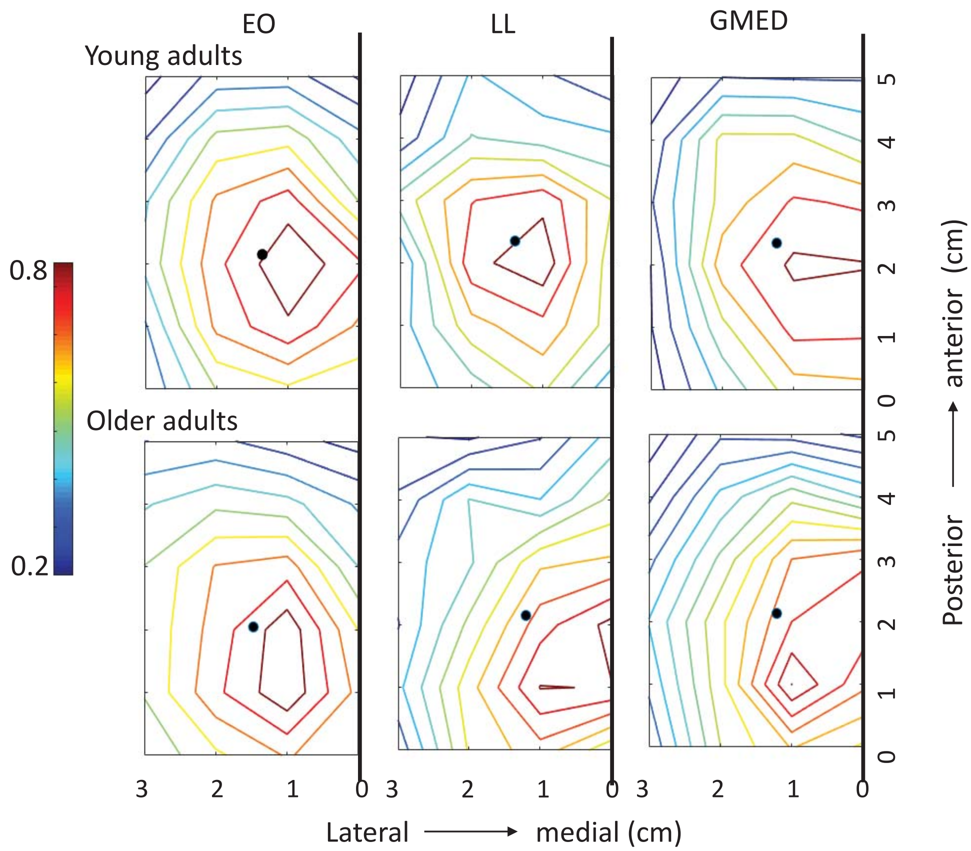
Table 1. Demographics and balance/mobility test performance for young adults (n = 13) and older adults (n = 12). Values are means ± standard deviation.

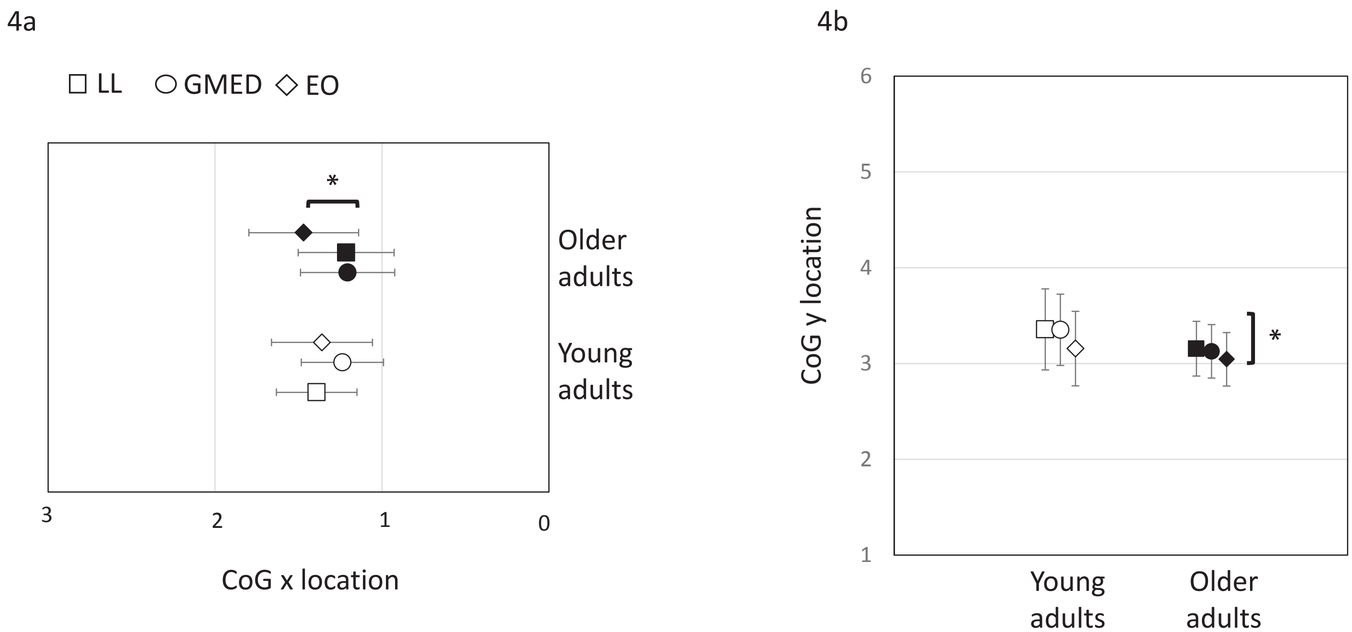
	Young adults	**Older adults**
Age (years)	25.75 (2.09)	72.42 (8.16)
Sex (number of females)	8	10
Mass (kg)	62.46 (9.82)	67.24 (11.75)
BESTest APA score (%)	-	80.56 (11.23)
Timed up and Go Test (s)	-	7.91 (1.56)
Self-selected gait velocity		1.27 (0.18)
Reaction time (s)	0.25 (0.04)	0.27 (0.06)
Movement time (s)	0.38 (0.06)	0.41 (0.09)


1a
1b
Go signal
Deltoid onset
0
0
APA window
1c
1d
0.1mV
0.1mV
0.1mV
0.1mV
TMS pulse

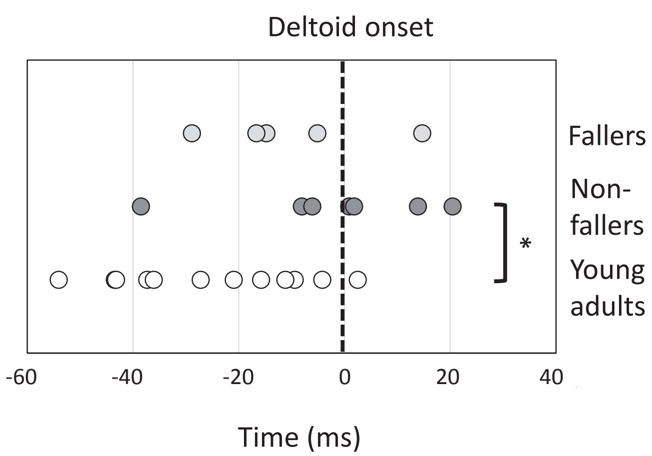


2a
Young adult
Older adult
Amplitude (mV)
0.1
0.1
0.1
0.1
0.1
0.2
1
0.2
LL
GMED
EO
DELT
Deltoid onset
Deltoid onset
100
100
Time (ms)
2b
Deltoid onset
LL
GMED
EO
*
-60
-40
-20
0
Time (ms)
Young adults
Older adults
2c
Normalized CCI
12000
10000
8000
6000
4000
2000
0
*
LL/GMED
LL/EO
GMED/EO


EO
LL
GMED
Young adults
Older adults
0.8
0.2
Posterior ⟶ anterior (cm)
Lateral ⟶ medial (cm)
3
2
1
0
5
4

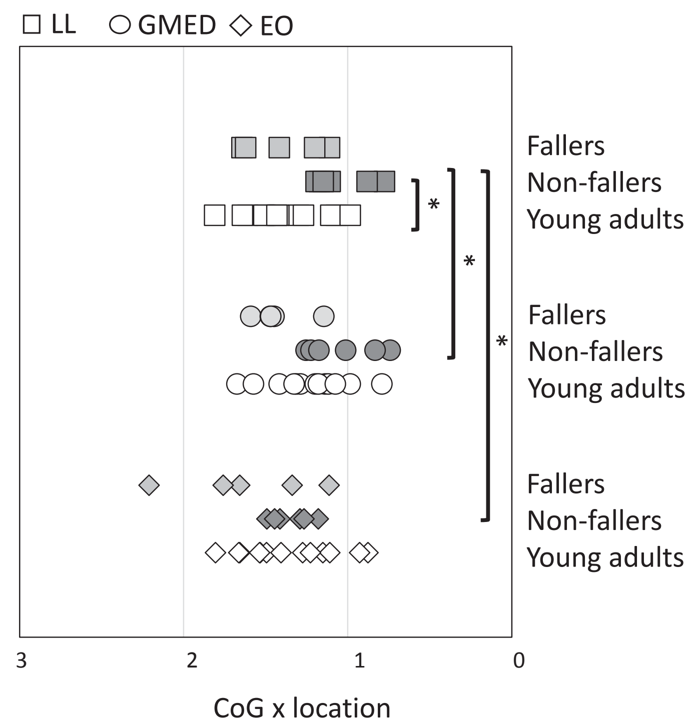

4a
LL
GMED
EO
*
Older adults
Young adults
3
2
1
0
CoG x location
4b
6
5
4
3
2
1
CoG y location
*
Young adults
Older adults

5a



Deltoid onset
Fallers
Non-
fallers
Young
adults
*
-60
-40
-20
0
20
40
Time (ms)

5b



LL
GMED
EO
Fallers
Non-fallers
Young adults
*
*
*
Fallers
Non-fallers
Young adults
Fallers
Non-fallers
Young adults
3
2
1
0
CoG x location