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ORIGINAL ARTICLE

Aging effect on muscle synergies in stepping forth during a forward perturbation

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Abstract

Purpose We explored changes in muscle interactions during healthy aging as a window into neural control strategies of postural preparation to action/perturbation. In particular, we quantified the strength of multi-muscle synergies stabilizing the center of pressure (COP) displacement during the preparation for making a step associated with support surface translations.

Methods Young and elderly subjects were required to make a step in response to support surface perturbations. Surface muscle activity of 11 leg and trunk muscles was analyzed to identify sets of 4 muscle modes (M-modes). Linear combinations of M-modes and their relationship to changes in the COP displacement in the anterior–posterior direction were then determined. Uncontrolled manifold analysis was performed to determine variance components in the M-mode space and indices of M-mode synergy stabilizing COP displacement.

Results Prior to the step initiation, the older subjects showed strong synergies that stabilized COP displacement to forward perturbation of the support surface. However, the synergy indices were significantly lower than those of the young subjects during preparation for making a step. The timings of early postural adjustment (EPA) and anticipatory postural adjustment (APA) were consistently earlier in the young subjects as compared to the older subjects. For both groups, the timing of EPA did not change across tasks, while APA showed delayed timing in response to the support surface translations.

Conclusions We infer that changes in the indices of synergies with age may present challenges for the control of postural preparation to external perturbation in older adults. They may lead to excessive muscle co-contractions and low stability of COP displacement. The results reported here could have clinical relevance when identifying the risk of making a step, which has been linked to an increased risk of falls among the elderly.

Keywords Synergy · Anticipatory adjustments · Stepping · Perturbation · EMG

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Abbreviations

AP	Anterior-posterior
APAs	Anticipatory postural adjustments
ASAs	Anticipatory synergy adjustments
BF	Biceps femoris
COP	Center of pressure
EPAs	Early postural adjustments
ES	Erector spinae
GL	Lateral head of gastrocnemius
GM	Medial head of gastrocnemius
PCA	Principal component analysis
RA	Rectus abdominis
RF	Rectus femoris
SOL	Soleus
ST	Semitendinosus

TA   Tibialis anterior
UCM   Uncontrolled manifold
VL   Vastus lateralis
VM   Vastus medialis

Background

When a standing person makes a step, there are feed-forward adjustments in the activation levels of postural muscles starting several 100 ms prior to the takeoff of the leading foot. The purpose of these early adjustments has been assumed to allow unloading of the stepping leg and to create a moment of vertical force rotating the body about the ankle joints (Ito et al. 2003). Following a perturbation to standing balance, the ability to make a step requires controlling the relative motion between the body center of mass and its base of support, with large inertial forces that could potentially threaten stability (Wang et al. 2016). Because even a small error in motor performance during standing may result in catastrophic failure, making a step can become quite a demanding task and may pose great risk in aging adults.

With advanced age comes a decline in the neuromotor system (Iosa et al. 2014; Tsai et al. 2014). This decline can be manifested at different levels and in various functions, including reduction of muscle mass (Shumway-Cook and Woollacott 2000), altered muscle response organization (Tsai et al. 2014), more frequent co-activations of antagonist muscles (Shumway-Cook and Woollacott 2000; Papegaaij et al. 2014) and neuronal loss (Dinse 2006) in a number of structures within the central nervous system (CNS). All these changes can potentially contribute to impaired motor control, gait and balance in older adults, which can be seen across a variety of everyday tasks including less effective postural adjustments to external perturbations (Hicks et al. 2012; Kilby et al. 2014).

Our previous research has shown that the ability to use multi-muscle synergies was reduced in older people during preparations to making a step with obstacles (Wang et al. 2016). Although the ability to recover equilibrium in response to support surface translations is critical to avoiding falls, muscle synergies stabilizing the center of pressure (COP) have previously not been quantified among the elderly. Therefore, we focused on exploring the stability of muscle coordination in healthy older adults exposed to support surface perturbations induced in a sagittal plane. We investigated the organizations of leg and trunk muscles into groups (M-modes), as well as the trial-to-trial variance of M-mode involvement (M-mode synergies), to determine dynamic stability of the elderly throughout the perturbation process.

Recently, the framework of the uncontrolled manifold (UCM) approach has been used to analyze multi-muscle synergies for quantitative assessment (Latash 2010). Within this framework, the trial-to-trial variance of independent elemental variables (e.g., M-modes) is compared in two subspaces: variance within the UCM subspace (V_{UCM}) does not affect the performance variable of interest (e.g., COP trajectory), whereas variance in the subspace orthogonal to the UCM (V_{ORT}) leads to changes in that performance variable. If $V_{UCM} > V_{ORT}$, most variance reflects the use of a multi-element synergy to stabilize that performance variable (reviewed in Latash et al. 2007).

Previous studies of postural preparation to action/perturbation have shown anticipatory synergy adjustments (ASAs) during two stages of feed-forward postural adjustments: early postural adjustments (EPAs) are seen within a few 100 ms and anticipatory postural adjustments (APAs) occur 80–100 ms prior to the initiation of a voluntary action (Klous et al. 2011; Krishnan et al. 2012). During steady-state standing, postural muscles show high indices of co-variation stabilizing such variables as COP coordinates and the shear force magnitude (Robert et al. 2008; Wang and Asaka 2008; Klous et al. 2011; Krishnan et al. 2011, 2012). If a subject is required to produce a quick action from a steady state, the indices of co-variation drop are delayed until the action initiation (Wang et al. 2006). ASAs have been shown to shift towards the time of action initiation under the simple reaction time instruction (Wang et al. 2006) and are delayed and reduced in magnitude in the elderly (Wang et al. 2013, 2015a, b).

In this study, we investigated the extent to which the coordination of postural muscles contributes to COP stabilization associated with support surface translation and how that coordination changes with aging. The main purpose of the current study was to examine the possible changes of M-modes, their effects on COP shifts, and multi-M-mode synergies in older adults. Based on previous studies of multi-muscle synergies in postural control (Wang et al. 2015a, b, 2016), we hypothesized that, compared with young adults, older adults would show age-related changes in the structure of M-modes.

Previous studies on young adults have shown that the synergy index (ΔV, the normalized difference between V_{UCM} and V_{ORT}) is typically high during steady-state standings (Wang and Asaka 2008; Klous et al. 2011; Krishnan et al. 2011, 2012). When a person is preparing for a quick action from a steady state, the synergy index drops prior to the action initiation. These ASAs represent an important reflection of controlled stability that allows combining stability during steady state and agility in transition to a quick action. Hence, our second hypothesis was that elderly adults would show a delayed and lower synergy index, which would decrease their ability to stabilize the COP shifts. This hypothesis has been motivated by reports of age-related decrements in the neuromotor system (Rogers

et al. 1992; Woollacott and Manchester 1993; Iosa et al. 2014; Tsai et al. 2014). If the hypotheses are supported, the results from this study could have clinical relevance in identifying step-making risks and increased risk of falls among the elderly.

Methods

Participants

Eight healthy young adults (four males and four females) and eight healthy older adults (four males and four females) without any known neurological or motor disorder volunteered to participate in the study. All participants were right-foot-dominant according to the preferred foot usage when kicking a ball, stepping up on a chair, and leaping off in the long jump (Nachshon et al. 1983). The mean age, height and mass were 24.4 ± 1.8 years, 166.9 ± 6.4 cm and 62.4 ± 9.1 kg for the young subjects and 61.9 ± 2.9 years, 164.9 ± 7.7 cm and 66.4 ± 6.4 kg for the older subjects. The methods used in the study were approved by the Institutional Review Board of Tianjin University of Sport. The experimental procedures were explained and all the subjects signed an informed consent form prior to data collection. Tianjin key lab of exercise physiology and sports medicine was the place of study performed.

Experimental setup and procedures

The postural perturbations consisted of 5-cm forward translations of the force plate on which the subject stood, with peak ramp velocities of 5 cm/s, and peak accelerations of 0.05 g. The subjects were instructed to stand with equally distributed weight with their arms hanging loosely by their sides. Sagittal plane balance was perturbed at random intervals by the movable platform in the forward direction.

The experimental condition was taking a step forward with the right leg in response to perturbations from an original posture of side-by-side quiet stance. The task goal was to step forward from a stationary position and subsequently both feet came to rest next to each other. In the initial position, subjects maintained a comfortable posture with their feet placed shoulder width apart while standing on the force plate installed on the movable platform. The initial stance was consistent across trials by having subjects stand within tracings of their foot outlines on the force plate. The subjects were instructed to look straight ahead throughout the trial, and react naturally to forward perturbation of the support surface under the subjects' feet. In the normal stepping task (ST_{NS}), the subjects were free to initiate the step following a 'get ready' cue. In the perturbation stepping task (ST_{PS}), they were instructed that, at any given time, the platform would suddenly translate forward. The subjects were asked to respond in a natural way to make a step with preferred spatial–temporal dynamics.

Before the start of data collection, 1–3 practice trials in each experimental condition were given to all subjects for familiarization with the task. The subjects were free to choose their preferred pace and distance when taking a step. Data were collected for 5 s per trial, including a 1–2 s quiet standing period prior to platform motion. A total of 20 trials for each condition were performed. Four blocks of normal stepping trials (ST_{NS}) were alternated with four blocks of perturbation stepping trials (ST_{PS}). Two different conditions were thus presented in blocks of five trials. To prevent fatigue, the subjects were allowed to rest at their request, and rested at least 5 min after 4 blocks (20 trials). For safety precautions, an assistant stood in reaching distance behind the subject to prevent a fall in each perturbation trial.

Data collection

Electromyographical (EMG) activity was recorded from eleven lower limb and trunk muscles of the subject's right side. After the skin was shaved and cleaned with alcohol, bipolar, pre-gelled Ag/AgCl surface electrodes were placed on the muscle bellies and were oriented in the direction of the muscle fibers. The surface EMGs (Noraxon Telemyo 2400T V2, Scottsdale, AZ, USA) were recorded from the tibialis anterior (TA), lateral head of gastrocnemius (GL), medial head of gastrocnemius (GM), soleus (SOL), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), biceps femoris (BF), semitendinosus (ST), rectus abdominis (RA), and erector spinae (ES). The electrodes were placed in pairs with the center-to-center distance of 25 mm; the ground electrode was placed over the epicondyle of the tibia. EMG signals were band-pass filtered at 10–500 Hz and sampled at 1500 Hz with a 16-bit resolution. Kinetic data were collected at 1500 Hz from a force platform (model 9281B, Kistler Instrumente AG, Winterthur, Switzerland) under the feet. A foot switch was attached under the heads of the metatarsal bones of right foot to measure the timing of toe off and thin socks were used to secure the sensor in place.

Data analysis

All signals were processed offline using MATLAB (The MathWorks, Natick, MA) version R2015b. Raw EMG signals were first rectified and low-pass filtered at 50-Hz (fourth-order zero-lag Butterworth filter). Signals from the force plate were low-pass filtered at 20 Hz. The 'time zero' (t_0) was defined by the toe off time using the signal from the foot switch. Then, all trials were aligned to t_0 and

integrals of EMGs were calculated. To do this, the data for further analysis were selected in the range from -1000 ms (before t_0) to t_0, out of which -1000 ms to -900 ms of the data in the ST_{NS} condition were taken for the baseline activity.

To identify the muscle onset for EMG data, we defined t_{EMG} as the instant in time when the average muscle activation across trials for each condition differed by more than ±2 standard deviations from the baseline activity for at least 25 ms continuously. Each muscle was assigned one t_{EMG} value that corresponded to either a burst or an inhibition.

Rectified EMG signals for each muscle for each subject were integrated over 10 ms intervals in a time window from -600 ms to t_0. These EMG integrals for each of 10 ms were corrected by subtracting the EMG integrals of the averaged 10 ms baseline activity (IEMG). ΔIEMG indices were further normalized (ΔIEMG$_N$) to the maximum integral magnitude across conditions. This method of normalization was used in earlier studies of muscle modes and synergies (Wang et al. 2005, 2014, 2015a, b).

Defining M-modes

For the ST_{NS} condition, we extracted groups of muscles (M-modes) from the IEMG$_N$ data matrix within the time window in relation to t_0 from -200 ms to t_0 using the principal component analysis (PCA). For each subject, the IEMG$_N$ data formed a matrix of 20 time intervals $\times$ 11 muscles $\times$ 20 trials = 4400 data points. The correlation matrix among the IEMG was subjected to principal component analysis with Varimax rotation, using procedures from SPSS (SPSS, Inc., Chicago, IL, USA). The factor analysis module with principal component extraction was employed.

For each subject, the obtained eigenvalues and principal components (PCs) were then considered. The first four PCs were selected for further analysis. This was determined by examining the scree plots and having at least two muscles significantly loaded per PC. We address these PCs as muscle modes (M-modes) and assume that the magnitudes of coefficients at the M-modes are manipulated by the controller to produce the COP shifts in the AP direction (COP$_{AP}$).

Defining the Jacobian

Since the support surface perturbations were induced in the sagittal plane, only the COP$_{AP}$ shifts were analyzed to explore covariation among the magnitudes of M-modes (ΔM) related to stabilization of the COP$_{AP}$ coordinate. Small changes in the magnitudes of ΔMs were related to the change in the COP$_{AP}$ shifts (ΔCOP$_{AP}$) through the Jacobian matrix (**J**). Multiple linear regression analysis over

the trials was used to define the **J** for each subject separately. The **J** was estimated as coefficients of multiple linear regression between ΔM and ΔCOP$_{AP}$.

Synergy analysis

For each trial of the ST_{NS} tasks, ΔIEMG$_N$ was computed and transformed into ΔMs by multiplying the loadings of the individual M-mode. The mean magnitudes of each ΔM for a selected time interval across a series of ST trials were computed. Since the model relating ΔMs to ΔCOP$_{AP}$ is linear, the mean values were subtracted from each computed value and the residuals were further analyzed.

The UCM represents different combinations of M-modes that keep the value of ΔCOP$_{AP}$ unchanged. The UCM was estimated as the null space of the corresponding **J** matrix. The null space is spanned by the basis vectors, ε_i. The vector of individual mean-free ΔMs was resolved into its projection onto the null space and the orthogonal subspace:

$$f_{UCM} = \sum_{i=1}^{n-d} \left(\underline{\varepsilon}_i^T \cdot (\Delta M) \right) \underline{\varepsilon}_i, \tag{1A}$$

$$f_{ORT} = (\Delta M) - f_{UCM}, \tag{1B}$$

where $n = 4$ and $d = 1$ are the total number of M modes and the number of degree of freedom describing the task; i.e., 1-dimensional COP$_{AP}$ shift.

Variance per degree of freedom within the UCM and orthogonal to the UCM across trials was computed as:

$$V_{UCM} = \sigma_{UCM}^2 = \sum_{i=1}^{N} \frac{f_{UCM}^2}{(n-d)N_{trials}}, \tag{2A}$$

$$V_{ORT} = \sigma_{ORT}^2 = \sum_{i=1}^{N} f_{ORT}^2 / (dN_{trials}). \tag{2B}$$

We computed an index of synergy (ΔV) reflecting the difference between the variance within the UCM and orthogonal to the UCM:

$$\Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}}, \tag{3}$$

where all variance indices are computed per degree of freedom; and V_{TOT} means the total variance. For further analyses, the ΔV values were transformed using a Fisher's z-transformation (ΔV_Z) adapted to the boundaries of ΔV:

$$\Delta V_Z = \frac{1}{2} \cdot \log \left[\frac{4 + \Delta V}{\left(1\frac{1}{3} - \Delta V \right)} \right]. \tag{4}$$

Anticipatory synergy adjustments (ASAs) were identified as a drop in the ΔV_Z time profile. The time of ASA initiation, t_{ASA}, was calculated for the z-transformed values of ΔV (ΔV_Z). The rate of change of ΔV_Z was computed from t_0 to -600 ms backwards; the time t_{ASA} was defined by two criteria: (1) when the magnitude of this rate was equal to zero ($d\Delta V_Z/dt = 0$), which was considered as the start of a drop; and (2) the drop had to be larger than 20% of the ΔV_Z magnitude at the time of $d\Delta V_Z/dt = 0$. All subjects showed 2 such anticipatory drops in the ΔV_Z time profiles before t_0. The outcomes of t_{ASA} were grouped into two time intervals with respect to t_0, $\{-600; -200\}$ ms (EPAs, early postural adjustments) and $\{-200; 0\}$ ms (APAs, anticipatory postural adjustments).

Statistical analysis

Descriptive statistics was used to compute the means and standard deviations for the outcome variables. The fractions of variance explained by the first four principal components were transformed into z-scores using standard Fisher's z-transformation. A paired t test was used for comparing the z-scores and the normalized peak COP_{AP} shifts between ST_{NS} and ST_{PS} conditions. To compare the indices of synergies (ΔV_Z) stabilizing the COP shift, a three-way analysis of variance was performed on ΔV_Z with group, condition, and time as factors. In the EPA and APA time intervals, to compare the initiation times of the synergy index (ΔV_Z), two-way analysis of variances were applied with group and condition as factors. For all statistical tests, a p value less than 0.05 was set as a measure of significance.

Results

General EMG patterns

There were common features across the EMG patterns in both conditions and subject groups. Figure 1 shows the rectified EMGs averaged across trials for representative young and older subjects for selected muscles for the ST_{NS} and ST_{PS} conditions, respectively. Before the EMGs were averaged, the trials were aligned by the time (t_0) of toe off in the foot switch signal. These particular muscles were selected because they showed clear anticipatory postural adjustments across subjects. In the ST_{NS} condition, the stepping leg typically showed alternating bursts of activity in the ventral and dorsal muscles. In the ST_{PS} condition, there was a substantial increase in the level of activity in most muscles. The regularities in the patterns of activation of the leg and trunk muscles were consistently observed in the ST_{NS} and ST_{PS} conditions. Note that the muscle activity

of the elderly subjects was typically higher than that of the young subjects.

Figure 2 illustrates onsets of EMG activity averaged across subjects for the ST_{NS} and ST_{PS} conditions in the young and elderly groups. In the ST_{PS} condition, onsets of EMG activity were observed in both groups. However, anticipatory activity of the trunk and leg muscles in the young subjects occurred earlier as compared to the elderly subjects. Particularly, early EMG onsets were seen in the TA and RF muscles. The TA onset was -156.5 ± 45.1 ms in the older group and -118.6 ± 45.0 ms in the young group [$F_{(1,14)} = 11.447$, $p = 0.004$]. The RF onset was -186.9 ± 65.0 ms in the older group and -134.7 ± 51.2 ms in the young group [$F_{(1,14)} = 5.643$, $p = 0.032$]. Moreover, TA and ER muscles showed delayed onsets in the ST_{PS} condition as compared to the ST_{NS} condition ($p = 0.003$, $p < 0.001$, respectively).

In preparation for stepping, subjects shifted the COP in the AP direction backwards. This adjustment allowed unloading the stepping leg and creating a moment of the reactive force rotating the body forward about the ankle joints. In the ST_{NS} task, the amplitude of the peak COP_{AP} displacement normalized by foot length ($COP_{AP-NS} = -0.083 \pm 0.025$) was smaller for the young group than for the elderly group ($COP_{AP-PS} = -0.105 \pm 0.019$); the difference was statistically significant ($p < 0.05$). Note that the negative values correspond to backward displacements. In the ST_{PS} task, the amplitude of the peak COP_{AP} displacements normalized by foot length was $COP_{AP-NS} = -0.228 \pm 0.027$ and $COP_{AP-PS} = -0.202 \pm 0.028$ for the young and elderly groups, respectively. The difference was statistically significant ($p < 0.05$).

PCA and multiple regression analysis

On average, the first four principal components (PCs) accounted for about $62.3 \pm 2.8\%$ of the total variance in the muscle activation space in the young group and $62.2 \pm 4.2\%$ in the older group. Figure 3 illustrates the average amount of variance explained by each M-mode (M_1 through M_4) across subjects. For the data of the young subjects, the average amount of variance explained by the first four PCs was 21.4 ± 2.2, 16.7 ± 2.1, 13.0 ± 1.3 and $11.3 \pm 1.4\%$, respectively. For the data of the older subjects, the average amount of variance explained by the first four PCs was 20.9 ± 2.4, 16.2 ± 2.6, 13.5 ± 1.9 and $11.6 \pm 1.3\%$, respectively. z-scores for the fractions of variance explained were computed to assess differences between groups. A one-way ANOVA with the factor Group (young and older) run for each PC data separately showed no significant differences between groups.

There was considerable variability across the subjects in the M-mode composition. Table 1 shows the loadings
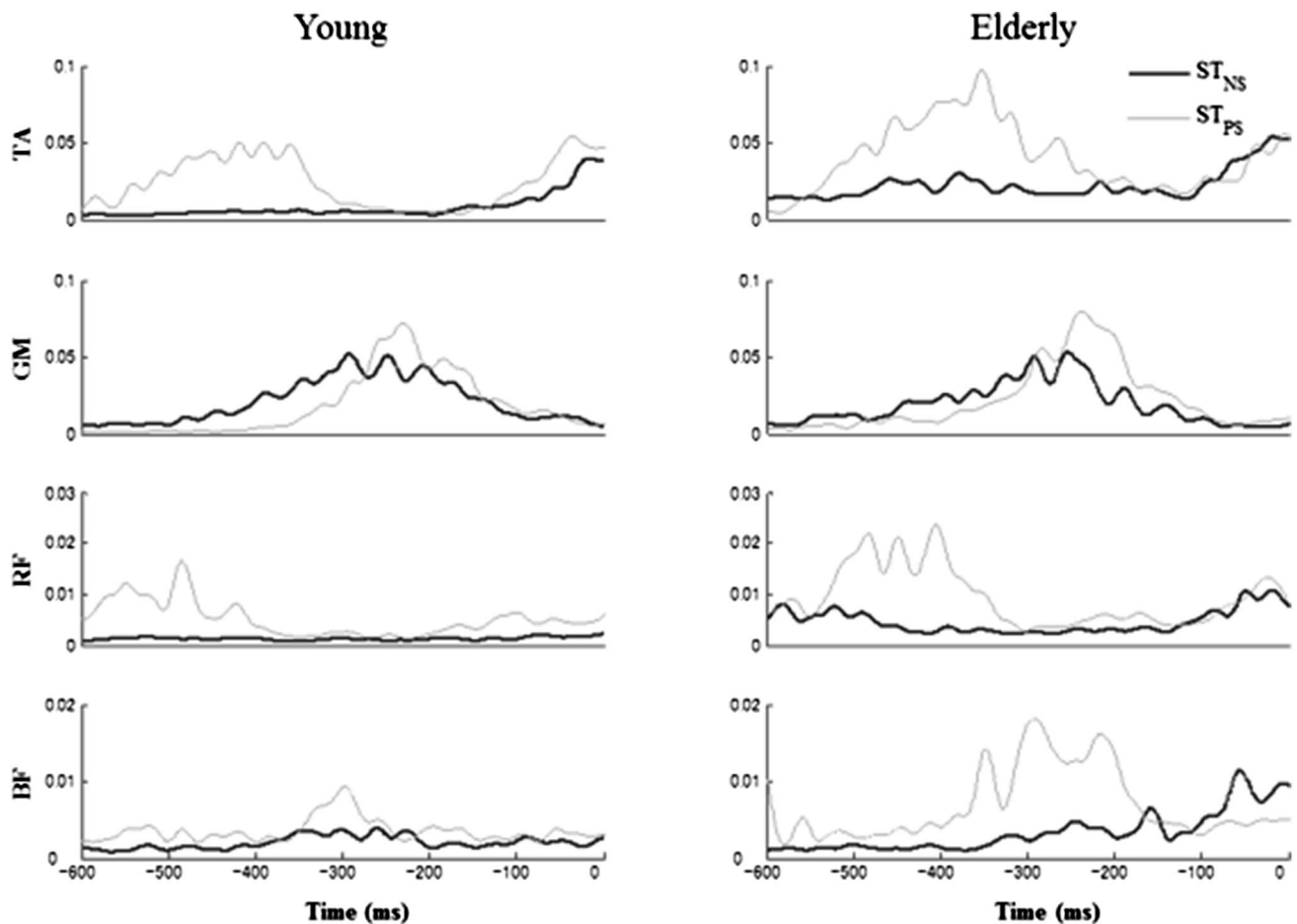
Fig. 1 Typical EMG patterns averaged across trials for representative young and older subjects for the ST_{NS} (*dark lines*) and ST_{PS} (*gray lines*) conditions, respectively. Time zero (t_0) corresponds to the alignment time, which is the time of toe off. The EMGs were recorded in muscles on the *right side* of the body. The EMG scales are in arbitrary units and time is in ms (*TA* tibialis anterior, *GM* medial head of gastrocnemius, *RF* rectus femoris, *BF* biceps femoris)

for all the muscles on the four factors for a representative young subject. Such typical M-modes did not show co-contraction M-modes. A co-contraction M-mode is defined as a pattern with significant loading coefficients on the same M-mode with the same sign for two muscles with opposing action at a particular joint (Asaka et al. 2008). Table 2 presents a representative result of the PCA of the older subject. The second M-mode depicted a co-contraction pattern between the RA (ventral) and the ES (dorsal) muscles.

For each subject, the number of times that reciprocal M-modes, co-contraction M-modes, and mixed M-modes were seen under the ST_{NS} condition was summed (Table 3). Wilcoxon's test showed that the number of times the co-contraction and mixed M-modes were seen in the older subjects was significantly larger than that of the young subjects ($p < 0.05$), while the number of times the reciprocal M-modes occurred in the older subjects was significantly smaller than the young subjects ($p < 0.05$).

Multiple regression analysis was performed to define the Jacobian mapping of small changes in the M-mode magnitudes onto COP_{AP} shifts. Results of multiple regression analysis were significant in most cases for each of the two groups. On average, the analysis accounted for 86.3 ± 3.6 and $84.3 \pm 4.4\%$ of variance in ΔCOP_{AP} in the young and older groups, respectively. There was no group difference in variations in the magnitudes of the four M-modes accounting for the total variance in ΔCOP_{AP} ($p > 0.05$).

Synergy analysis

The synergy index (ΔV) was computed as the normalized difference between V_{UCM} and V_{ORT}. Positive ΔV values indicated the existence of a multi-M-mode synergy in the M-mode space that stabilized the average COP_{AP} shift, while zero or negative ΔV meant no such synergy. For further analysis, ΔV data were log-transformed, resulting in the index ΔV_Z. To perform an across-subjects analysis
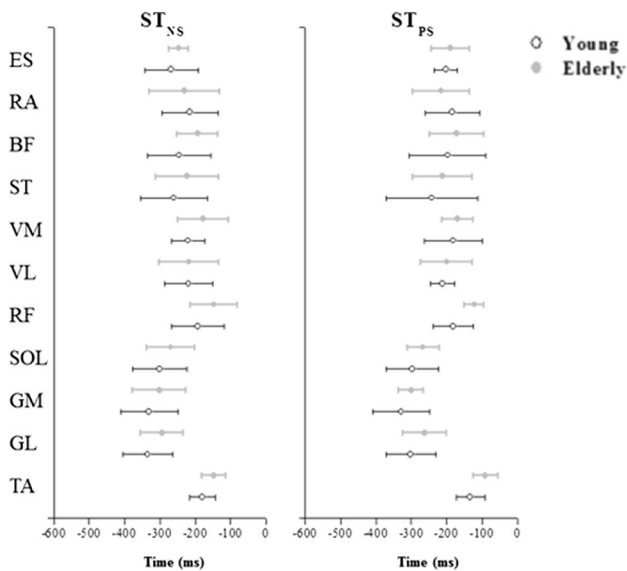
Fig. 2 Onsets of EMG activity averaged across subjects, plotted for the ST_{NS} and ST_{PS} conditions in the young and elderly groups. Onset of muscle activation is plotted in ms and the mean ± SD is shown (*TA* tibialis anterior, *SOL* soleus, *GL* lateral head of gastrocnemius, *GM* medial head of gastrocnemius, *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *BF* biceps femoris, *ST* semitendinosus, *RA* rectus abdominis, *ES* erector spinae)
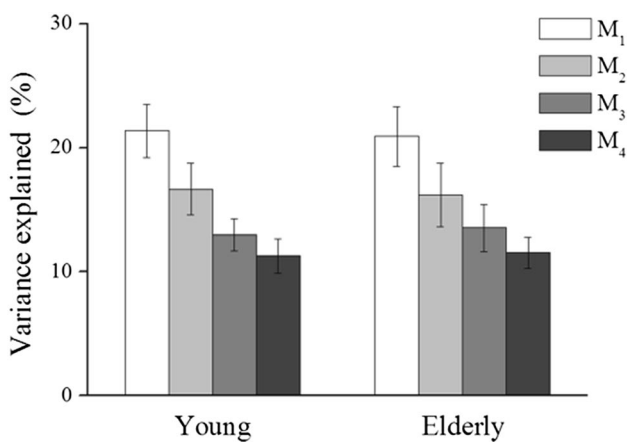

Fig. 3 Total variance explained by the four M-modes across subjects. Mean values and standard deviations are shown for the percentages of the total variance accounted for by the first four principal components (PC) in the young and elderly groups

of M-mode synergies to stabilize the COP_{AP} shift prior to stepping, ΔV_Z indices were averaged over six 100-ms time intervals starting 600 ms prior to t_0 and ending up at t_0. The selection of these time windows was based on earlier studies which showed that M-mode synergies take time to emerge and develop prior to action initiation (Krishnan et al. 2011, 2012). The ΔV_Z values computed for the COP_{AP} shift as the performance variable became smaller

for the older subjects than for the young subjects, and the trend of ΔV_Z across time was similar for both groups. This finding was supported by a three-way Group × Condition × Time ANOVA. There was a significant effect of Group [$F_{(1,14)} = 6.858$, $p = 0.020$] with the young subjects ($\Delta V_Z = 1.11 \pm 0.48$) showing higher values than the older subjects ($\Delta V_Z = 0.91 \pm 0.50$). The main effect of Condition [$F_{(1,70)} = 6.015$, $p = 0.028$] confirmed that, for the older and young groups, ΔV_Z in the ST_{NS} condition had significant higher values than in the ST_{PS} condition. None of the time effects or interactions was significant. Overall, the results showed that strong M-mode synergies stabilized the average COP_{AP} shift in both subject groups.

The ΔV_Z time profiles computed for the ST_{NS} and ST_{PS} conditions in representative young and older subjects are shown in Fig. 4. In both groups and conditions, the ΔV_Z values remained positive during preparation for making a step associated with support surface translations. The two ΔV_Z profiles started with positive values and included a transient drop in ΔV_Z during the EPA time interval followed by another drop during the APA time interval. The timing of the drop varied across subjects such that averaged across subjects data did not show consistent behavior. For statistical analysis, we focused on the two drops in ΔV_Z computed using the criterion mentioned in the "Methods". The time of the ΔV_Z drop averaged across subjects for the EPA and APA time intervals are presented in Fig. 5. A two-way ANOVA on the timing indices for the EPA period with the factors Group and Condition showed a main effect of Group [$F_{(1,14)} = 5.028$, $p = 0.042$] without any other effects. There were significantly earlier timing indices in the younger group than in the older group. In contrast, for the APA time intervals, the time of ΔV_Z drop occurred earlier in the ST_{NS} condition than in the ST_{PS} condition. This finding was supported by a two-way Group × Condition ANOVA, which showed a significant effect of Condition [$F_{(1,14)} = 24.200$, $p < 0.001$] with the ST_{NS} condition showing significantly earlier timing indices than the ST_{PS} condition. The main effect of Group [$F_{(1,14)} = 5.715$, $p = 0.031$] confirmed that for both conditions, the time of ΔV_Z drop occurred significantly earlier in the younger group than in the older group.

Discussion

This study investigated the organization of multi-muscle postural control associated with support surface perturbations in both young and old subjects. We analyzed whether M-mode synergies stabilizing the COP_{AP} displacement during the preparation of making a step were influenced by age and support surface translation. The particular focus was an examination of the role of anticipatory synergy adjustments

Table 1 Representative loading coefficients for the PCA of the young subject

Muscle	M_1-mode	M_2-mode	M_3-mode	M_4-mode
TA	0.1469	−0.2758	−0.3002	**0.6473**
GL	**0.8196**	0.1653	0.2438	−0.0196
GM	**0.8967**	−0.1147	0.0703	0.0076
SOL	**0.6802**	0.1964	−0.0451	0.1108
RF	−0.0800	−0.1833	**0.8144**	0.0519
VL	0.5155	0.2301	**0.5535**	−0.1094
VM	0.4225	0.2528	**0.7136**	−0.0216
ST	0.2552	**0.7529**	−0.0391	0.1604
BF	0.4561	**0.6348**	0.4249	−0.1155
RA	0.1636	−0.0293	−0.1911	**0.8093**
ES	−0.0727	**0.8227**	−0.0012	0.0616

Loading magnitudes over 0.5 are shown in bold (significant loadings)

TA tibialis anterior, *SOL* soleus, *GL* lateral head of gastrocnemius, *GM* medial head of gastrocnemius, *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *BF* biceps femoris, *ST* semitendinosus, *RA* rectus abdominis, *ES* erector spinae

Table 2 Representative loading coefficients for the PCA of the elderly subject

Muscle	M_1-mode	M_2-mode	M_3-mode	M_4-mode
TA	0.1489	0.2656	**0.5158**	−0.1898
GL	**0.8574**	−0.0123	−0.0504	−0.1803
GM	**0.8181**	−0.0341	−0.0048	0.2257
SOL	**0.8045**	−0.0523	0.1322	0.1360
RF	−0.1075	−0.1287	**0.7550**	0.0401
VL	−0.0204	0.0127	**0.5494**	−0.3198
VM	0.1487	−0.0169	**0.5130**	0.2631
ST	−0.1752	−0.1409	0.3032	**0.5472**
BF	0.0148	−0.0490	0.0724	**0.8754**
RA	−0.1057	**0.8770**	0.0027	0.0166
ES	−0.0002	**0.8872**	−0.0198	0.0272

Loading magnitudes over 0.5 are shown in bold (significant loadings)

orthogonality of the components (Sabatini 2002; Tresch et al. 2006; Ting 2007). In those studies, synergies were associated with such muscle groupings. Our approach is different, viewing such groupings only as a set of elemental variables, which is the first step in identifying synergies. PCA defines orthogonal M-modes, which is preferred for computational reasons, because such M-mode sets correspond to equal amounts of variance in all directions in the M-mode space when in the absence of an organizing (synergetic) action. Using non-orthogonal sets of variables may be able to account for more variance in the original data at the first step of analysis (M-mode identification). However, it complicates interpretation of the second step (the UCM analysis) since differences in the amounts of variance in different subspaces may be due to the non-orthogonal axes rather than to a control strategy.

Within the UCM framework, M-modes represent combinations of muscle activations that reduce the number of degrees of freedom manipulated by the CNS. It has been suggested that the CNS has the ability to combine M-modes in different ways as the situation warrants to achieve performance stability (Latash et al. 2007). In most studies of whole-body actions, a few (3–5) M-modes have been identified: two of them united leg and trunk muscles crossing several joints on the ventral ("push-forward" M-mode) and dorsal ("push-back" M-mode) surfaces of the body. In more challenging conditions and in older people, agonist–antagonist muscle pairs entered the same M-mode with the same signs of the loading coefficients, which is a "co-contraction" M-mode (Krishnamoorthy et al. 2003; Asaka et al. 2008; Robert et al. 2008; Klous et al. 2010, 2011; Wang et al. 2013, 2015a, b). The reciprocal M-modes may effectively move the body forward or backwards, while the co-contractions M-modes may improve performance by stiffening the joints to resist perturbations.

The findings showed that the older subjects had more co-contraction M-modes than the younger subjects. There were only a few cases of co-contraction M-modes in the younger subjects despite the fact that the older subjects showed that similar variances were accounted for by four M-modes, which were similar to the younger subjects. It has been shown that there is a predominance of muscle co-contraction patterns in postural tasks in persons with an impaired postural control due to aging (Hatzitaki et al. 2005). Further, previous research on voluntary body sway has shown a more common occurrence of co-contraction M-modes in older people (Wang et al. 2015a, b). Therefore, more co-contraction M-modes among the elderly subjects found here reflect the generally observed co-contraction patterns with aging. This finding may be related to the preference for co-contraction motor patterns in the elderly, which replace the more typical reciprocal patterns that require accurately timed production of muscle

(ASAs) in the regulation of feed-forward postural control. Initiating a step with the constraints imposed by support surface perturbation involves multi-muscle postural control for balance stabilization, which must effectively manipulate the COP displacement to accelerate the entire body's center of mass forward. The mechanisms of balance maintenance while making a step with preferred spatial–temporal dynamics provide insight into the neural control of older adults in anticipation of a perturbation or an action.

We used PCA as the means of defining independent (orthogonal) elemental variables; i.e., M-modes. In other studies, other matrix factorization methods have been used to identify muscle groupings that do not require

Table 3 The number of occurrences of different M-modes

M-modes pattern	Group	
	Young	Elderly
Reciprocal M-modes		
Push-back	16	11
Push-forward	9	7
Co-contraction M-modes		
Hip	4	5
Knee	0	5
Ankle	0	0
Mixed M-modes		
Mix1	0	0
Mix2	2	1
Mix3	0	0
Mix4	0	0
Mix5	0	0
Singular	1	3

Data across all subjects are presented

Mix1: the combination of "co-contraction at the hip" and "push-back" M-mode

Mix2: the combination of "co-contraction at the hip" and "push-forward" M-mode

Mix3: the combination of "co-contraction at the ankle" and "push-back" M-mode

Mix4: the combination of "co-contraction at the ankle" and "push-forward" M-mode

Mix5: the combination of "co-contraction at the knee" and "push-back" M-mode

Singular: only one muscle loaded significantly on one of the first three PCs

forces (Benjuya et al. 2004). However, more co-contraction M-modes could be also a reflection of increased caution among the elderly to securely perform the task.

In previous studies, M-mode compositions and the corresponding Jacobian matrices were defined over different tasks (body sway and shoulder flexion) and over different time intervals within the shoulder flexion task (Klous et al. 2011; Krishnan et al. 2011). Despite major differences in the M-mode compositions, when different sets of M-modes were used to analyze the whole data set, striking consistency in both magnitudes and time profiles of the synergy indices was observed. Therefore, in this study, the M-mode composition and the Jacobian matrix were defined with respect to the APA time interval within the ST_{NS} condition, but were later applied to the whole time of data analysis in both conditions.

Based on the UCM hypothesis, muscle synergies were defined as neural organizations that ensure stability of the COP coordinate produced by a redundant set of M-modes to maintain and restore balance when perturbed. There
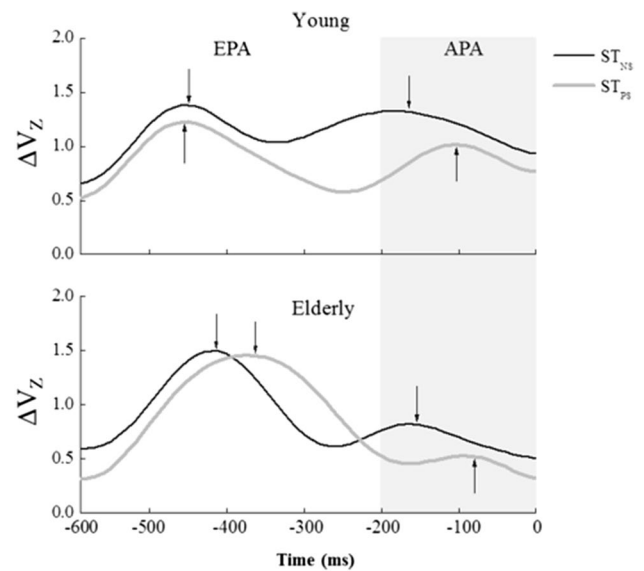

Fig. 4 Time profiles of the ΔV_Z index for representative young and elderly subjects in the ST_{NS} (*dark line*) and ST_{PS} (*gray line*) conditions. The two ΔV_Z profiles started with positive values and included a transient drop in ΔV_Z during the EPA time interval followed by another drop during the APA time interval (*gray-shaded area*). The *arrows* represent drops of anticipatory synergy adjustment (ASA). Time zero (t_0) corresponds to the alignment time, which is the time of toe off
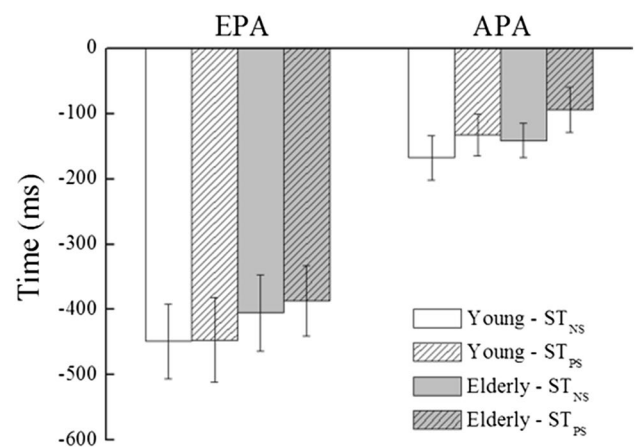

Fig. 5 Timing indices for the early postural adjustment (EPA) and anticipatory postural adjustment (APA) averaged across the subjects are shown for different conditions for the young and elderly groups

were similarities and differences in the M-mode synergies in the young and older subjects. Both groups were able to demonstrate M-mode co-variation stabilizing the magnitude of the COP_{AP} shift. Both groups showed higher synergy indices for the ST_{NS} condition than for the ST_{PS} condition. The main difference between groups was in the significantly lower values of the synergy indices for the COP_{AP} shift. Earlier studies documented lower synergy

indices in older subjects during step initiation that involved the obstacle-negotiation and reaction time task settings (Wang et al. 2006, 2015a, b). These observations implied that aging is associated with weakening of postural muscle synergies in response to support surface translations. This may be a reflection of a general trend of a shift from more complex, synergic control to more element-based control, possibly related to the progressive death of neurons at different levels of the neural axis (Eisen et al. 1996).

EPAs and APAs have been known for a long time (Belen'kii et al. 1967; Elble et al. 1994) and are viewed as reflections of feed-forward processes at the stage of planning a movement (Bertucco et al. 2013). However, APAs have frequently been used to describe adjustment seen prior to an expected perturbation that might or might not be time-linked to a voluntary action (Massion 1992). Recent studies have documented that EPAs and APAs are two separate phenomena of postural preparation with different purposes and variable timing (Klous et al. 2011; Krishnan et al. 2011, 2012). In particular, EPAs do not show consistent changes in their timing across different conditions of a task, while the timing of APAs changes. Our current study provides further support for these two postural adjustments. Our study is unique in documenting two stages of anticipatory changes in indices of multi-muscle synergies in older persons during preparation to making a step associated with support surface translation. Until now, such synergic adjustments (ASAs) have only been reported in healthy young subjects in standing postures (Klous et al. 2011; Krishnan et al. 2011, 2012) and they have been assumed to reflect purposeful destabilization of the COP coordinate in preparation to its quick change. We believe that our study is the first observation of age effects on EPAs and APAs in preparation for a step during support surface translation.

We observed two clearly different ASAs time intervals in preparation for making a step: EPAs started 400–500 ms prior to the stepping foot liftoff followed by APAs, 100 ms or so prior to the liftoff. Indeed, EPAs and APAs were seen in each of the subjects and the sequence was preserved with changes in stepping tasks (ST_{NS}, ST_{PS}). The timing of EPAs did not change across tasks, while APAs showed delayed timing in response to support surface translations. The findings were observed in both young and older groups. The timings of EPAs and APAs were consistently earlier in young subjects as compared to older subjects. These findings may have received contributions from major changes in the neuro-muscular system associated with aging. In particular, older adults show progressive loss of muscle coordination between posture and intended actions. Since the main purpose of a synergy is to stabilize a value of a performance variable, trying to change this variable in the presence of a synergy may be expected to meet resistance

of the synergy opposing the change. Hence, if a controller plans to produce a change in the COP coordinate, turning the synergy that is stabilizing the COP displacement off seems like a sensible strategy.

Conclusions

Prior to the step initiation, older subjects showed strong synergies that stabilized COP displacement to forward perturbation of the support surface. However, the synergy indices were significantly lower and delayed as compared to the young subjects during preparation for making a step. We infer that changes in the indices of synergies with age may present challenges for the control of postural preparation to external perturbation in older adults. They may lead to excessive muscle co-contractions and low stability of the COP displacement. The results reported here could have clinical relevance to identify the risk of making a step, which has been linked to an increased risk of falls among the elderly.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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