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Age-related changes in the behavior of the muscle-tendon unit of the gastrocnemius medialis during upright stance

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Baudry S, Lecoeuvre G, Duchateau J. Age-related changes in the behavior of the muscle-tendon unit of the gastrocnemius medialis during upright stance. J Appl Physiol 112: 296–304, 2012. First published October 27, 2011; doi:10.1152/japplphysiol.00913.2011.—Mechanical properties of the muscle-tendon unit change with aging, but it is not known how these modifications influence the control of lower leg muscles during upright stance. In this study, young and elderly adults stood upright on a force platform with and without vision while muscle architecture and myotendinous junction movements (expressed relative to the change in the moment on the x-axis of the force platform) were recorded by ultrasonography and muscle activity by electromyography. The results show that the maximal amplitude of the sway in the antero-posterior direction was greater in elderly adults (age effect, P < 0.05) and was accompanied by an increase in lower leg muscle activity compared with young adults. Moreover, the data highlight that fascicles shorten during forward sways and lengthen during backward sways but more so for young (−4 ± 3 and −4 ± 3 mm/Nm, respectively) than elderly adults (−0.7 ± 3 and 0.8 ± 3 mm/Nm, respectively; age × sway, P < 0.001). Concurrently, the pennation angle increased and decreased during forward and backward sways, respectively, with greater changes in young than elderly adults (age × sway, P < 0.001). In contrast, no significant differences were observed between age groups for tendon lengthening and shortening during sways. The results indicate that, compared with young, elderly adults increase the stiffness of the muscular portion of the muscle-tendon unit during upright stance that may compensate for the age-related decrease in tendon stiffness. These observations suggest a shift in the control strategy used to maintain balance.

MATERIALS AND METHODS

Subjects. Thirteen young adults aged from 23 to 36 yr (7 women) and 10 elderly adults aged from 68 to 83 yr (6 women) volunteered to participate in the study after informed consent was obtained. None of the subjects reported any neurological disorder. Participants reported to the laboratory for one session. Subjects were asked to refrain from intense exercise for 24 h before testing. The Ethics Committee of the Centre Hospitalier Universitaire Brugmann approved the protocol.

Experimental setup. Subjects were asked to maintain an upright stance on a force platform (OR6–6-2000; Advanced Mechanical Technology) that was surrounded by a wood frame covered by a soft mat. Subjects selected their initial foot position that was kept similar...
throughout the experiment by tracing the initial foot position on the force platform. Subjects stood with their arms by their sides, the knee fully extended and facing forward. A target was traced on a board positioned 1.5 m in front of the subjects at eye level. Signals from the force platform that were the force (N) on the x (frontal), y (sagittal), and z (vertical) plans and the moment (Nm) on the x, y, and z axes were sampled at 50 Hz and stored on a computer for subsequent analysis. Moreover, the moment on the x-axis of the platform (Mx) signals was A/D sampled at 50 Hz (Power 1401, 16-bit resolution; Cambridge Electronic Design, Cambridge, UK) to obtain a synchronized signal of the antero-posterior sway with the EMG signals and the ultrasonography videos.

To investigate the variations in MTU parameters (fascicle length, pennation angle, and displacement of the muscle-tendon junction) of the GM during upright stance, subjects were asked to keep quiet upright standing keeping the knees extended and avoiding trunk and arm movements. Two conditions of vision were investigated: eyes open (vision) and eyes closed (no vision). For each vision condition, subjects repeated three trials of 60 s in a counterbalanced order across the vision conditions. The whole sequence (6 trials of 60 s) was performed twice in a counterbalanced order to investigate 1) the muscle architecture parameters (fascicle length and pennation angle), and 2) the displacements of the myotendinous junction (MTJ).

Electromyographic recordings. Electromyographic (EMG) signals were recorded from soleus (SOL), GM and gastrocnemii lateralis (GL), and tibialis anterior (TA) muscles with surface electrodes (silver-silver chloride electrodes 8-mm diameter) placed in a bipolar configuration. To reduce the impedance at the skin-electrode interface, the skin was shaved when necessary and cleaned with a solution of alcohol, ether and acetone. The electrodes were filled with electrode gel and positioned longitudinally over each muscle belly. The reference electrodes were placed on the skin over the tibia. The EMG signals were amplified (×1,000) and band-pass filtered (10–1,000 Hz) before being A/D sampled at 2 KHz (Power 1401, 16-bit resolution; Cambridge Electronic Design) and stored on a computer. Voluntary contractions in the directions of ankle plantar flexion and dorsiflexion were used to determine the correct placement of the surface electrodes in a seated posture with the knee extended and the ankle flexed at 90°. In this posture, five young and five old adults performed maximal voluntary contractions with ankle plantar tarflexor and dorsiflexor muscles to record the corresponding EMG activity for SOL, GM, GL, and TA.

Ultrasonographic recordings. The architectural changes of the GM muscle during upright stance were investigated by ultrasonography. Longitudinal images were obtained using real-time B-mode ultrasonographic apparatus (DP-6900Vet; Shenzhen Mindray Bio-Medical Electronics) with a 6-cm width linear-array probe (7.5-MHz; 7SL60EA, Shenzhen Mindray Bio-Medical Electronics) positioned at ~30% of the distance between the popliteal crease and the center of medial malleolus, over the midbelly of the muscle. Once at least one muscle fascicle was clearly identified (between 1 and 3 muscles fascicles have been analyzed for each subject), the position of the probe was firmly held in place using a custom-made resin sheath strapped to the skin. The restraint ensured a constant orientation and pressure of the probe on the skin. The probe was moved downward to obtain images of the MTJ of the gastrocnemius medialis defined as the convergence of the deep and superficial aponeuroses (27). A metallic marker was placed between the skin and the ultrasound probe to verify that the probe did not move during the recordings (13, 14, 20). The probe was coated with a water-soluble transmission gel to provide acoustic contact. Images were acquired on a personal computer at a sampling rate of 25 Hz (Power 1401, 16-bit resolution; Cambridge Electronic Design) and analyzed offline. On average, two fascicles have been tracked successfully for each subject.

Ankle angle recordings. During the balance task, video recordings of the lower limb of the subjects on the sagittal plane were performed. Adhesive markers were fastened on the skin over the fibula head, lateral malleolus, and metatarsophalangeal joint of the fifth toe. The range of motion for the ankle angle corresponding to the maximal variation in Mx was measured for each subject by means of a public domain image program (Image J; National Institutes of Health).

Data analysis. The displacement of the center of pressure (CoP) was computed offline by means of the Octave software (GNU General Public License). Command lines were written specifically to compute platform signals into CoP parameters. First, force platform signals were low-pass filtered (cut-off frequency: 10 Hz) by means of a butterworth fourth-order filter. From the filtered data, the following parameters were computed for a 20-s epoch within each trial after stabilization of the subjects on the force platform:

\[ A-P_{\text{max}} = \text{max}(\text{CoP}_i - \text{CoP}(\text{mean})) \]

\[ A-P_{\text{SD}} = \text{SD}(\text{CoP}_i - \text{CoP}(\text{mean})) \]

CoP path length that represents the distance of the CoP during the trial:

\[ \sum_{i=1}^{n} \sqrt{[\text{CoP}_x(i) - \text{CoP}_x(i - 1)]^2 + [\text{CoP}_y(i) - \text{CoP}_y(i - 1)]^2} \]

In these equations, CoPy and CoPx represent the coordinate of the CoP on the antero-posterior and the medio-lateral axis, respectively. The mean of the three trials were averaged for each subject and vision condition.

The EMG and ultrasound data were analyzed during antero-posterior sways defined as following: 1) during the 20-s epoch used to compute CoP parameters, the mean ± SD of the moment on the x-axis of the platform were calculated from the Mx signal recorded by the data acquisition system (Power 1401, 16-bit resolution; Cambridge Electronic Design); and 2) the sways taken into account for analysis were determined by changes in the moment on the x-axis of the platform that was >1 SD from the mean value (Fig. 1A).

Two muscle architectural parameters were measured from each MG ultrasound videos: muscle fascicle length (Lf) and pennation angle (p). Lf was defined as a clearly visible fiber bundle lying between the two aponeuroses (superficial and deep), and p was defined as the angle formed by the fascicle tracked and the deep aponeurosis (Fig. 1B). The two parameters were measured by using a public domain image program (Image J; National Institutes of Health).

Lm was measured along the marked fiber bundle from the superficial to the deep aponeurosis (see Refs. 1, 18). When the end of the fascicle extended off the acquired ultrasound image and the superficial and deep aponeuroses were parallel, Lm was estimated by trigonometry [total Lm = Lf1 (measured fascicle length) + Lf2 (estimated fascicle length) = Lf1 + (h/sin p), where h is height] by assuming a linear continuation of the fascicles (4, 36). The thickness of the muscle was measured on both sides of the image, and aponeuroses were considered as parallel if the thickness values did not differ by >2% between the right and the left side of the image. When the two aponeuroses were not parallel, the following equation was used to calculate Lm:

\[ \text{total Lm} = Lf1 (\text{measured fascicle length}) + Lf2 (\text{estimated fascicle length}) = Lf1 + (d \cdot \sin p / \sin b), \text{where d is the height between the fascicle and the superficial aponeurosis; a white dashed line symbolizes d in Fig. 1). The error due to the linear extrapolation has been estimated to be 2–7% (9). Shortening and lengthening of muscle fascicle were defined as negative and positive values, respectively. On average, 65 (range: 44–120) and 59 (range: 48–84) data points for each parameter (Lm and p) have been analyzed per young and elderly subjects, respectively.

The resolved length of the muscular portion of the MTU (Lm) with respect of the deep aponeurosis was calculated by applying the
way (age × vision × sway) ANOVAs with repeated measures on vision and sway. The effect of age and vision on \( \Delta A-P_{\text{max}} \), \( \Delta A-P_{\text{SD}} \), and CoP path length was analyzed by means of two-way (age × vision) ANOVAs with repeated measures for vision. When a significant main effect was found with an ANOVA, a Tukey’s post hoc test was used to identify the significant differences among selected means. The coefficient of determination \( (r^2) \) extracted from Pearson product-moment correlations was calculated for the relation between \( \Delta f \) and the corresponding \( \Delta Mx \). The level of statistical significance was set at \( P < 0.05 \) for all comparisons. Values are expressed as the means ± SD in the text and tables and means ± SE in the figures.

RESULTS

Center of pressure and ankle angle. Regardless of the balance conditions, elderly adults exhibited a lower stability than young adults as indicated by their greater CoP path length (age main effect, \( P = 0.003 \)). For young and elderly adults, the CoP path length increased (vision main effect, \( P < 0.001 \)) during trials performed with eyes closed (24.9 ± 7.0 cm) compared with trials done with eyes open (19.8 ± 8.6 cm). The maximal amplitude of the CoP in the antero-posterior direction \( (\Delta A-P_{\text{max}}) \) was greater in elderly adults (age main effect, \( P = 0.035 \)) but was not influenced by the vision conditions (age × vision, \( P = 0.97 \); Fig. 2). The fluctuations in the antero-posterior displacement of the CoP, as denoted by the SD of the CoP, did not differ between young (0.4 ± 0.1 cm) and elderly adults (0.4 ± 0.1 cm) and vision conditions (age × vision, \( P = 0.55 \)). The rotation of the ankle angle in the sagittal plane was measured for the maximal change in the moment on the x-axis of the platform. No difference was observed between young and elderly adults (age main effect, \( P = 0.54 \)), and the angle ankle was reduced (–0.7 ± 0.3°) during forward sway whereas it increased (0.5 ± 0.2°) during backward sway (sway main effect, \( P = 0.002 \)).

Fascicle length. During upright standing, the fascicle length when the CoP was at the mean value in the antero-posterior direction (see MATERIALS AND METHODS) was longer (Student \( t \)-test, \( P < 0.001 \)) in young (57 ± 9 mm) than in elderly adults (43.5 ± 11 mm). The \( \Delta L_f \) are presented in Table 1. However, to allow more appropriate comparisons between vision conditions and age, changes in fascicle length were expressed as the ratio between variations in the fascicles length and the moment on the x-axis of the force platform \( (\Delta L_f/\Delta Mx) \). The \( \Delta L_f/\Delta Mx \) ratio depended on age and sway direction (age × sway, \( P < 0.001 \); Fig. 3A). In young adults, \( \Delta L_f/\Delta Mx \) differed signifi-
cantly (Tukey’s post hoc test, $P < 0.001$) between forward sways ($-4 \pm 3 \text{ mm/Nm}$) and backward sways ($4 \pm 3 \text{ mm/Nm}$), indicating that during forward sways, fascicle length was shortening whereas it was lengthening during backward sways. Similar qualitative data was obtained in elderly adults and the difference between sway directions tended to be significant (Tukey’s post hoc test, $P = 0.06$). However, the $\Delta L_f/\Delta M_x$ ratio was significantly greater in young compared with elderly adults during forward and backward sways (Tukey’s post hoc test, $P < 0.001$ for both groups; Fig. 3A).

When $\Delta L_f$ were plotted against the corresponding $\Delta M_x$ (Fig. 4), the two set of data were significantly associated in young ($r^2 = 0.46$, $P < 0.001$) and elderly adults ($r^2 = 0.28$, $P < 0.001$) during upright standing with eyes open (Fig. 4, top). Similarly, $\Delta L_f$ were correlated with $\Delta M_x$ when the upright posture was kept with the eyes closed in young ($r^2 = 0.52$) and elderly adults ($r^2 = 0.35$; Fig. 4, bottom). Moreover, in the two vision conditions, the slope of the relations differed between young and elderly adults. In upright stance with eyes open, the slope was $-2.49 \text{ mm/Nm}$ (confidence interval at 95%: $-2.75$ to $-2.23$) and $-0.07 \text{ mm/Nm}$ (confidence interval at 95%: $-0.08$ to $-0.06$) in young and elderly adults, respectively.

### Table 1. $\Delta L_f$, $\Delta \mu$, and $\Delta MTJ$ in the GM for young and old adults in the two vision conditions

<table>
<thead>
<tr>
<th>Vision</th>
<th>Young</th>
<th>No vision</th>
<th>Elderly</th>
<th>No vision</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Forward</td>
<td>Backward</td>
<td>Forward</td>
<td>Backward</td>
</tr>
<tr>
<td>$\Delta L_f$, mm</td>
<td>$-0.90 \pm 0.75$</td>
<td>$0.94 \pm 0.75$</td>
<td>$-1.26 \pm 1.07$</td>
<td>$1.12 \pm 1.08$</td>
</tr>
<tr>
<td>$\Delta \mu$, °</td>
<td>$-3.94-1.20$</td>
<td>$-0.83-3.72$</td>
<td>$-5.30-1.14$</td>
<td>$-0.50-4.23$</td>
</tr>
<tr>
<td>$\Delta MTJ$, mm</td>
<td>$0.24 \pm 0.18$</td>
<td>$0.25 \pm 0.17$</td>
<td>$0.38 \pm 0.26$</td>
<td>$-0.29 \pm 0.18$</td>
</tr>
<tr>
<td>$\Delta$ MTJ, mm</td>
<td>$0.06 \pm 0.16$</td>
<td>$0.08 \pm 0.19$</td>
<td>$0.10 \pm 0.21$</td>
<td>$-0.15 \pm 0.23$</td>
</tr>
<tr>
<td>$\Delta$ MTJ, mm</td>
<td>$0.12-0.27$</td>
<td>$-1.11-0$</td>
<td>$0.14-1.24$</td>
<td>$-1.29-0$</td>
</tr>
</tbody>
</table>

Changes are means $\pm$ SD (and range) in fascicle length ($\Delta L_f$), pennation angle ($\Delta \mu$), and displacements of the muscle-tendon junction ($\Delta MTJ$) in the gastrocnemius medialis (GM) for young and old adults in the two vision conditions.

Fig. 3. Changes in fascicle length ($\Delta L_f$) and pennation angle ($\Delta \mu$) in the GM, both expressed relative to the respective changes in the moment on the $x$-axis of the force platform ($\Delta M_x$) for forward and backward sways in young (open bars) and elderly adults (filled bars). $^*P < 0.05$, significant differences between sway directions. $^\dagger P < 0.05$, significant differences between age groups.

Fig. 4. Relation between changes in $L_f$ and in the moment on the $x$-axis of the force platform ($M_x$) with eyes open (top) and eyes closed (bottom) in young ($\circ$) and elderly adults (●). A total of 420 and 295 data points are included in top and bottom for young and elderly adults, respectively. All the relations are statistically significant ($P < 0.05$).
were closed, the slope was $-3.1$ mm/Nm (confidence interval at 95%: $-3.40$ to $-2.83$) and $-0.06$ mm/Nm (confidence interval at 95%: $-0.06$ to $-0.05$) in young and elderly adults, respectively. These relations confirm that forward sways are associated with a shortening of fascicles whereas backward sways were accompanied by a lengthening of fascicles, and the extent of length changes relative to $M_x$ is larger ($P < 0.001$) for young compared with elderly adults (Fig. 4).

**Pennation angle.** When standing, the pennation angle ($\mu$) of the tracked fascicles when the CoP was at the mean value in the antero-posterior direction was greater (Student $t$-test, $P = 0.002$) in young ($16 \pm 2^\circ$) than in elderly adults ($14 \pm 2^\circ$) and the changes in $\mu$ before the ratio $\Delta \mu/\Delta M_x$ was calculated are given in Table 1. As observed for $\Delta L_m/\Delta M_x$, the $\Delta \mu/\Delta M_x$ ratio depended on both age and sway (age $\times$ sway, $P < 0.001$; Fig. 3B). In young adults, the $\Delta \mu/\Delta M_x$ ratio differed (Tukey’s post hoc test, $P < 0.001$) between forward sways ($1.6 \pm 1.1^\circ$) and backward sways ($-1.5 \pm 0.9^\circ$), indicating that the pennation angle increased during forward sways and decreased during backward sways. Although the $\Delta \mu/\Delta M_x$ ratio exhibited similar behaviors in elderly adults ($0.1 \pm 1.1^\circ$ and $-0.2 \pm 1.9^\circ$ for forward and backward sways, respectively), such difference was not statistically significant (Tukey’s post hoc test, $P = 0.27$). Moreover, the $\Delta \mu/\Delta M_x$ ratio was significantly greater in young compared with elderly adults during forward sways and backward sways (Tukey’s post hoc test, $P < 0.001$ for both sway directions; Fig. 3B).

**Muscular portion of the muscle-tendon unit.** When modifications in fascicle length and pennation angle were expressed as changes in the longitudinal axis of the muscle (resolved length of the muscular portion of the MTU, $L_m$), the combined change induced a $L_m$ shortening of $0.9 \pm 0.5$ mm and a $L_m$ lengthening of $0.9 \pm 0.5$ mm during forward and backward sways, respectively, in young adults. The changes in elderly adults were qualitatively similar as $L_m$ shortened during forward sway ($-0.2 \pm 0.5$ mm) and lengthened ($0.3 \pm 0.5$ mm) during backward sway. When these changes are expressed relative to the variations in $M_x$, changes in $L_m$ depended on age and sway (age $\times$ sway, $P < 0.001$). $\Delta L_m/\Delta M_x$ was greater in young compared with elderly adults for both sway directions (Tukey’s post hoc test, $P < 0.001$; Fig. 5A). Moreover, in young adults, $\Delta L_m/\Delta M_x$ differed significantly (Tukey’s post hoc test, $P < 0.001$) between forward ($-5 \pm 3$ mm/Nm) and backward ($5 \pm 3$ mm/Nm) sways, indicating that during forward sways the muscle portion was shortening whereas it was lengthening during backward sways (Fig. 5A). Similar qualitative data were obtained in elderly adults (shortening during forward sways and lengthening during backward sways) and differences between sway directions tended to reach statistical threshold (Tukey’s post hoc test, $P = 0.08$).

Moreover, the mean distance between the superficial and deep aponeuroses was significantly smaller in elderly adults ($14.4 \pm 2.5$ mm) compared with young adults ($18.9 \pm 2.9$ mm, $t$-test, $P = 0.002$).

**MTJ.** The displacements of the MTJ are reported in Table 1. In contrast to changes in fascicle length and pennation angle, most of the sways were not accompanied by a displacement of the MTJ. When expressed relative to the corresponding

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**Fig. 5.** Change in resolved length of the muscular portion of the muscle-tendon unit ($L_m$; A) and myotendinous junction (MTJ; B) of the GM, both expressed relative to change in the moment on the $x$-axis of the force platform ($M_x$) for forward and backward sways in young (open bars) and elderly adults (filled bars). $^*P < 0.05$, significant differences between sway directions. $^{\dagger}P < 0.05$, significant differences between age groups.
changes in the moment on the x-axis (ΔMTJ/Mx), MTJ depended on age and sway (age × sway, P = 0.05; Fig. 5B). In young adults, the MTJ moved proximally during forward sways (0.52 ± 0.57 mm/Nm) and distally during backward sways (−0.43 ± 0.73 mm/Nm; Tukey’s post hoc test, P < 0.001). These data indicated a lengthening of the tendon during forward sways and a shortening during backward sways. In elderly adults, the mean values for ΔMTJ/Mx indicated similar qualitative changes (0.22 ± 0.57 and −0.21 ± 0.73 mm/Nm for forward and backward sways, respectively) that for young adults, although differences ΔMTJ/Mx were not statistically significant (Tukey’s post hoc test, P = 0.14). Nevertheless, no difference was observed between young and elderly adults as the age main effect was not significant (P = 0.32) and the Tukey’s post hoc test performed for the age × sway interaction did not reveal any significant differences (P values >0.05).

*aEMG. Figure 6 illustrates the modulation of the aEMG for SOL, GM, GL, and TA in young and elderly adults. In both groups, the SOL aEMG was greater during forward sways compared with backward sways (age × sway, P < 0.001), and the values were greater in elderly adults compared with young adults for both forward (Tukey’s post hoc test, P < 0.001) and backward sways (Tukey’s post hoc test, P = 0.007). Similar results have been obtained for the GM muscle (age × sway, P < 0.001). In contrast, the age × sway interaction was not significant (P = 0.94) for the GL aEMG. However, a sway main effect (P < 0.001) indicated that aEMG for the GL was greater during forward sways (5.9 ± 0.2 μV) than for backward sways (5.1 ± 0.2 μV). Moreover, elderly adults exhibited a greater level of EMG activity than young adults (age main effect, P < 0.001).

The activity of the TA muscle, assumed to be the main dorsiflexor muscle, was influenced by age, vision, and sway (age × vision × sway, P < 0.001). In elderly adults, the TA aEMG was greater during backward sways compared with forward sways during upright standing with eyes closed (Tukey’s post hoc test, P < 0.001) but not with eyes open (Tukey’s post hoc test, P = 0.81). Moreover, in all balance conditions, the TA aEMG was greater in elderly than in young adults (Tukey’s post hoc test, P values < 0.02). However, the activity of the TA did not change across vision conditions and sways in young adults (Fig. 6).

In five young and five elderly subjects, the aEMG activity has been normalized to the maximal aEMG measured during maximal voluntary contractions (MVC) of the plantarflexor and dorsiflexor muscles. The normalized aEMG did not depend on vision and sway but was significantly lower in young compared with elderly adults for SOL (11.4 ± 5.4 vs. 22.3 ± 5.4% MVC; age main effect, P = 0.013) and GM (8.6 ± 8.5 vs. 21.4 ± 8.5% MVC; age main effect, P = 0.041) but not for GL (10.0 ± 6.7 vs. 16.5 ± 6.7% MVC; age main effect, P = 0.13). The normalized aEMG for the TA was significantly greater in elderly (4.7 ± 1.3% MVC) than in young adults (2.5 ± 1.3% MVC; age main effect, P = 0.024) with a trend (Tukey’s post hoc test, P = 0.06) towards a greater TA aEMG during backward sway for elderly adults.

**DISCUSSION**

The main findings of this study indicate that although the amplitude of the sway in the antero-posterior direction is increased in elderly adults during upright stance, the changes in length of the muscular portion of the MTU were less in elderly whereas the displacement of the MTJ did not change significantly with age. Moreover, elderly adults display greater aEMG activity compared with young adults for both plantarflexor and dorsiflexor muscles. These results indicate that,
compared with young adults, elderly adults stiffen the lower leg muscles to maintain upright stance.

Loram et al. (24) have highlighted that the muscular portion of the MTU behaved out of phase with the body sway (paradoxical muscle movement): it shortened during forward sways and lengthened during backward sways. In the current study, we observed similar paradoxical muscle movements in young and elderly adults during quiet upright stance. These movements of the muscle architecture are consistent with aEMG data as plantarflexor muscle aEMG was greater during the forward sways compared with backward sways. Moreover, the MTJ of the GM moved proximally during the forward sway and distally during the backward sway. As the heel remained in contact with the floor and the knee angle did not change, such displacements of the MTJ indicate a slight lengthening of the tendon during forward sways and a shortening during backward sways. Therefore, the muscular portion of the MTU shortens and tendon lengthens during forward sway, and the inverse movements were observed during backward sway. If such mechanical behaviors of the MTU were qualitatively similar in elderly adults, no statistical differences between forward and backward sways were observed for this age group. Nevertheless, it is interesting to notice that the absolute (regardless of the direction of the changes) extent of change in tendon length during isometric voluntary contractions of the plantar flexor muscles at 20, 40, 60, 80, and 100% of the torque developed was 50.2 ± 12.9 and 26.2 ± 5.3 Nm in young and elderly adults, respectively. Despite the tendon compliance may differ between isometric contractions and upright standing, these data are in line with previous studies (8, 33, 37) that reported lower tendon stiffness in elderly adults compared with young adults. The estimated greater tendon compliance in elderly adults, therefore, may contribute to the greater muscle activity for ankle plantarflexor and dorsiflexor muscles in elderly adults compared with young adults (Fig. 6; Refs. 6, 19, 31).

The greater GM activity likely influences the extent of fascicle length variations. Indeed, Ito and colleagues (17) reported that, in the TA muscle, changes in muscle fascicle length and pennation angle were not linearly associated with the torque developed during ankle dorsiflexion contraction. The shortening of muscle fascicles was more pronounced for low torque levels (up to 20% of the maximal voluntary torque) compared with greater torque level. Consistently, when EMG activity of the plantarflexor muscles was normalized to that recorded during an MVC, our results indicated a relative muscle activity >20% of MVC in elderly adults while it was only ~10% for young adults. Therefore, the greater relative muscle activity observed in elderly adults, that may compensate for sarcopenia and/or changes in tendon compliance, likely reduced the amplitude of the changes in the muscular portion of the MTU.

The greater antero-posterior sway in elderly adults in the absence of differences in the ankle range of motion between age groups suggests a greater contribution of trunk movement in the variation of the center of pressure. In agreement, previous work (3, 15, 16) has indicated that elderly adults tend to use a strategy that involves greater movements of the hip rather than of the ankle to control balance. This shift in movement strategy involves increasing the ankle stiffness. The greater $L_m$ stiffness and EMG activity of agonist and antagonist muscles in elderly adults support the assumption that elderly adults stiffen the ankle during upright stance. Moreover, the increase in antagonist muscle activation (TA) during upright stance with aging (31) has been proposed as a strategy to maintain balance by increasing ankle stiffness (6). Therefore, the current findings suggest an age-related shift in the movement strategy with advancing age such as elderly adults stiffen their lower leg muscle and adjust their balance by increasing the contribution of hip movements. However, in absence of direct measurement of the hip joint angle, such interpretation requires further investigations.

The absence of change in MTU movements between the two vision conditions is consistent with the absence of difference between the two conditions in the amplitude of the body sway in the antero-posterior direction. This indicates that although some adjustments in the mechanisms involved in balance control should occur between these two vision conditions (34), they did not induce large changes in the movements of the MTU structures.
Compared with resting condition, a low level of muscle activity (~10% of maximum) has been shown to improve the sensitivity to detect joint movement due to an increased recruitment and firing rate of afferents originating from muscle spindles (41). Accordingly, Fitzpatrick and colleagues (10, 38) have observed a greater movement sense at the ankle during upright stance compared with rest. In contrast, greater muscle activity (~20% of maximal) has been documented to decrease movement sense due to a possible saturation of the muscle spindle afferents that may reduce their capacity to accurately detect movements (35, 43). In addition to the loss of distal large myelinated sensory fibers and receptors, and impaired distal lower extremity proprioception that have been reported with aging (see for review, Ref. 40), the increased stiffness of the muscular portion of the MTU and the associated greater EMG activity observed for elderly adults presumably contribute to increase the loss of the sensitivity of the muscle spindle pathway. Therefore, these age-related modifications of muscle architecture and activation during upright stance might be involved in the decreased balance stability documented in elderly adults.

In conclusion, this study extends our knowledge on the effect of aging on the behavior of muscle structures during functional tasks. The results show an age-related stiffening of the muscular portion of the MTU and the associated greater EMG activity observed for elderly adults presumably contribute to increase the loss of the sensitivity of the muscle spindle pathway. These findings suggest a shift in the control strategy used by elderly adults to maintain balance.

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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS
Author contributions: S.B. and J.D. conception and design of research; S.B. and G.L. performed experiments; S.B. and G.L. analyzed data; S.B. and J.D. interpreted results of experiments; S.B. prepared figures; S.B. drafted manuscript; S.B. and J.D. edited and revised manuscript; S.B. and J.D. approved final version of manuscript.

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