Calf muscle-tendon properties and postural balance in old age

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Onambele, Gladys L., Marco V. Narici, and Constantinos N. Maganaris. Calf muscle-tendon properties and postural balance in old age. J Appl Physiol 100: 2048–2056, 2006. First published February 2, 2006; doi:10.1152/japplphysiol.01442.2005.—We tested the hypothesis that compromised postural balance in older subjects is associated with changes in calf muscle-tendon physiological and mechanical properties. Trial duration and center of pressure (COP) displacements were measured in 24 younger (aged 24 ± 1 yr), 10 middle-aged (aged 46 ± 1 yr), and 36 older (aged 68 ± 1 yr) healthy subjects under varying levels of postural difficulty. Muscle-tendon characteristics were assessed by dynamometry, twitch superimposition, and ultrasonography. In tandem and single-leg stances, trial duration decreased (≥65% lower, P < 0.001) and COP displacements increased (≥90% higher, P < 0.05) with age. Muscle strength, size, activation capacity, and tendon mechanical properties decreased with age by 55, 13, 13, and 36–48%, respectively (P < 0.05). Regressions with these parameters and balance indexes were significant (P < 0.05) for single-leg and tandem (0.69 < r² < 0.90) postures only, indicating that the age-related changes in muscle-tendon characteristics may explain the majority of the variance in balance performance during tasks more difficult than habitual bipedal stance.

The exact physiological mechanisms underlying the increase in COP displacement with ageing and higher incidence of falls are unclear. However, previous studies suggest that a deterioration of the visual, vestibular, and somatosensory systems, as well as the manner in which these three systems integrate both spatially and temporally, may be involved (20). The importance of the musculoskeletal system’s ability to generate and transmit contractile forces to execute a balance task and maintain stance through the above mechanisms is not well understood. Hence, the contribution of musculoskeletal function deterioration with age in increased COP displacement remains unclear so far. However, it is generally thought that the muscles of the lower limbs may play a key role in standing (18, 19, 29, 31), with the calf muscles specifically shortening and lengthening to control sway (30). Appendicular muscle size (total muscle mass in trunk legs and arms) has previously been found to bear no relation to postural stability during single-leg stance in older people (17), but it may be the case that a relation only exists with the size of those lower limb muscles that are relevant to standing. This notion is supported from previous reports on an association of calf muscle strength to postural stability (55, 69). However, the relevance of ageing and task difficulty (determined by the size of the base of support) for the above association has not been examined. Similarly, there is no information on the relation between balance performance and the properties of the tendon of the contracting muscles, which act as force transmitters affecting the speed at which postural adjustments can be made when necessary.

In light of the above considerations, the present study aimed to identify whether muscle-tendon parameters relevant to contractile force production would be associated with age-related balance defects in conditions of different postural demands. We specifically studied maximal joint torque, muscle size, activation capacity (AC), and tendon mechanical properties in the calf muscles. We hypothesized that ageing deteriorates these muscle-tendon characteristics, which, in turn, are associated with, and may partly explain the variance in, postural balance performance, especially in more demanding postural tasks.

METHODS

Subjects

Ninety subjects responded to posters and newspaper advertisements in the local community. We excluded prospective participants with neurological, muscular, metabolic, or cardiovascular diseases or conditions that could affect postural stability, muscle strength, or cutaneous sensation, as well as those with vestibular diseases, foot

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ulcerations, numbness in the foot extremities, Alzheimer’s disease, Parkinson’s disease, and stroke. Our study populations, therefore, included 36 older individuals (17 men, 19 women), 10 middle-aged individuals (5 men, 5 women), and 24 younger individuals (12 men, 12 women) aged 68 ± 1, 46 ± 1, and 24 ± 1 yr (means ± SE), respectively. All participants gave written, informed consent to participate in the study, which was approved by the local institutional ethics committee.

Postural Stability Tests

Three tasks were examined: 1) bipedal stance, 2) single-leg stance, and 3) tandem stance. Tasks 2 and 3 were included as tasks with greater postural demand compared with task 1. Each test was performed three times, and the trial with the longest stance duration was used for further analysis. Trial duration was the period of time during which the subject managed to stay in the required stance. In cases where the trial duration reached 60 s, the trial was ended and taken as the subject’s best trial.

COP displacements were also monitored using a piezo-electric force platform (Kistler Instrument, Amherst, NY). Analog force-platform data were recorded at 100 Hz. The total COP displacement (T_d) (mm) was quantified in terms of root mean square (RMS) (3) from the COP displacements in the anterior-posterior (AP_d) and mediolateral directions (ML_d). Since AP_d = \{[\sum(x - x_{\text{mean}})^2]/n\}^{0.5} and ML_d = \{[\sum(y - y_{\text{mean}})^2]/n\}^{0.5}, it follows that T_d = [(AP_d)^2 + (ML_d)^2]^{0.5}, where n is the total number of samples.

Subjects were barefoot throughout the whole exercise and were asked to stand quietly with hands hanging freely at either side, looking straight ahead at a target (black circle 15 cm in diameter against a white background) placed at eye level, ~3 m away (Fig. 1).

Muscle-Tendon Characteristics

Maximal voluntary contraction. Isometric plantar flexion and dorsiflexion maximal voluntary contraction (MVC) torque was recorded while the subject was prone with the knees fully extended and the tested foot (left foot) strapped to the footplate of a dynamometer (Cybex Norm, Phoenix Healthcare Products). The plantar flexion MVCs were used to assess muscle strength, whereas dorsiflexion MVCs were used to quantify antagonistic muscle coactivation and enable the assessment of gastrocnemius (GS) tendon mechanical properties (see below). To emulate the ankle joint angle during the postural tests, all MVC measurements were taken at 0° ankle angle (the foot at 90° with respect to the lower leg axis). The subjects were asked to gradually develop torque and maintain MVC for ~3 s. A short series of three to four warm-up submaximal contractions were carried out at the beginning of the protocol. During all tests, visual and verbal feedback was employed to motivate the subjects. Peak MVC for each subject was taken as the best of three efforts.

Muscle size. The size of the medial head of the GS muscle was measured to obtain an index of calf muscle size differences between groups (50). The thickness of this muscle (Mt) was taken as representative of its volume (47, 48), which, in turn, has been shown to highly correlate with the MVC torque (15). Mt was measured on sagittal-plane ultrasound images taken with a linear 7.5-MHz B-mode probe (Ésaote Biomedica, AU5 Partner, Florence, Italy) as the distance between the muscle’s superficial and deep aponeuroses. The images were taken at rest at midwidth and midlength of the muscle, with the knee joint fully extended and the ankle joint placed at 0°. For each subject, the average of three Mt measurements in the proximal, central, and distal regions of the scan recorded (Fig. 2) was considered for further analysis (39).

AC. To assess muscle AC during the plantar flexion MVCs, the twitch interpolation method was used. Although direct tibial nerve stimulation ensures that all of the plantar flexors are stimulated, this technique, however, was uncomfortable for some of the subjects and was, therefore, not used. Instead, two self-adhesive surface electrodes (8.9 × 3.8 cm anode on the soleus muscle and 7.6 × 13.0 cm cathode on the GS muscle) were placed over the motor point of the muscle.
Elongations were estimated from the equation $F = \frac{\text{displacement of the Achilles tendon insertion in the calcaneum at "tendon"}}{K}$, based on analysis of sonographs showing the elongations for any unwanted shift of the heel during the test were made to ensure that the electrodes were positioned (located using TECA motor-point cards, Versastim, Conmed). A doublet generated by the application of 100 mA above the current producing maximal twitch force was delivered during the plateau phase of the MVC and at rest. Ultrasound images showed no discernible movement of the tibialis anterior (TA) muscle during the above plantar flexor muscle stimulations, thus suggesting the absence of current spread to the antagonist dorsiflexors. The resting twitch-to-MVC ratios in young ($17.2 \pm 3.0\%$), middle-aged ($20 \pm 2.1\%$), and older ($22 \pm 4.3\%$) subjects were not significantly different ($P > 0.05$), indicating that the relative amounts of stimulated muscle in the three groups were similar. AC was calculated as $1 - \frac{\text{IT}}{\text{RT}}$, where IT is the extra torque produced by the doublet superimposed on the MVC, and RT is the torque produced by the doublet at rest (23). In the case where there is no increase in torque during electrical stimulation, the AC is 1.0, and voluntary activation is considered complete.

**Tendon mechanical properties.** Measurements of GS tendon stiffness ($K$) and Young’s modulus (YM) were taken by ultrasound during the plantar flexion MVCs, using the principles detailed elsewhere (34, 40, 59). Briefly, the ultrasound probe used for $M_t$ measurement was fixed along the midsagittal axis of the medial head of the GS muscle, at the level of its distal myotendinous junction. Subjects performed a ramp isometric plantar flexion contraction up to MVC, during which ultrasound images focused on the myotendinous junction were recorded on a digital video recorder (DVCAM, Sony, Japan). Displacements of the distal myotendinous junction with respect to a fixed skin marker visible on the scans were digitized at 10% torque intervals using computerized image analysis (NIH Image version 1.61/ppc, National Institute of Health, Bethesda, MD). Displacement corrections for any unwanted shift of the heel during the test were made to obtain true distal extramuscular tendon (hereafter referred to as “tendon”) elongations, based on analysis of sonographs showing the displacement of the Achilles tendon insertion in the calcaneum at different intensities (36, 41).

The GS tendon forces ($F$) corresponding to the above tendon elongations were estimated from the equation $F = cTQ \cdot MA^{-1}$, where $cTQ$ is the plantar flexion torque corrected for both antagonistic and synergistic muscle action about the ankle, and $MA$ is the moment arm length of the Achilles tendon. The torque produced by antagonistic coactivation was calculated based on a torque-electromyographic (EMG) model (38, 58), assuming a linear relation between the TA muscle EMG activity and isometric dorsiflexion torque (43). The acquisition and process of EMG signal was done following standard guidelines (77, 78). In brief, EMG data were acquired at 2,500 Hz using surface bipolar Ag-AgCl electrodes 10 mm in diameter (Neuroline, Medicotest, Rugmarken, Denmark), set 20 mm apart along the TA muscle belly. The ground electrode was placed on the lateral side of the knee. Before electrode placement, the skin was shaved and cleaned with abrasive gel to reduce its impedance below 5 KΩ. EMG data were band-pass filtered between 50 and 500 Hz and then processed using a 40-ms running-window RMS. To correct for synergistic muscle action, the relative cross-sectional area (CSA) of the GS muscle with respect to the whole plantar flexor muscle group was assumed to be 25% (16), a constant proportion irrespective of age (51). Sagittal plane magnetic resonance images obtained using a 0.2-T scanner (E-Scan, ESAOTE Biomedica, Genova, Italy) were analyzed to obtain the position of the ankle angle $0^\circ$ as the distance between the tibio-talar center, estimated using the Reuleaux method, as detailed elsewhere (35, 37), and the Achilles tendon action line. The scans were processed using a 40-ms running-window RMS. To correct for synaptic errors, the respective tendon CSA correspond to the position of minimal passive joint torque. For the ankle joint, this is approximated at the neutral position ($0^\circ$ ankle angle) (65). At this ankle position, there were no differences in passive plantar flexion torque between age groups in our subjects ($P > 0.05$, one-way ANOVA). GS tendon resting length was, therefore, measured at $0^\circ$ ankle angle, as the distance between the GS distal myotendinous junction and the insertion of the Achilles tendon in the calcaneum. The corresponding Achilles tendon CSA was measured on three axial-plane sonographs recorded at 1, 2, and 3 cm above the calcaneum, and an average value was considered for further analysis. Clearly, the possibility that some errors have been introduced in our calculations of GS tendon mechanical properties by underestimating the true GS tendon strain cannot be excluded, but the similarities in passive torque at the reference ankle angle indicate that this methodological shortcoming would not impact on the comparative results obtained.

**Statistics**

Two-way repeated-measures ANOVA was performed to test for differences in balance indexes between tasks and age groups ($3 \times 3$). One-way repeated-measures ANOVA was performed to test for differences in muscle-tendon properties between the three age groups. Tukey’s post hoc tests were performed where appropriate. To determine the relation between muscle-tendon properties and balance indexes, Pearson correlation analyses were conducted with the balance indexes as dependent variables and the muscle-tendon characteristics as independent variables. Multiple linear regressions (MLRs) were employed to determine the main combination of age and muscle-tendon characteristics of interest that would best predict balance indexes. Durbin-Watson statistics were used to identify any correlation between the independent parameters, and those with the highest variance inflation factor (VIF ≥4.0), i.e., the collinear factors, were removed from the regression. Standardized beta weights coefficients (i.e., $\beta$, or the coefficients of the regression equations standardized to dimensionless values) are also reported, since they explain the relative contributions of each independent variable. Data are displayed as means ± SE. Statistical significance was set at $P < 0.05$.

**RESULTS**

**Trial Duration and COP Displacements in the Three Tests**

In all three groups, the trial duration in the single-leg test was shorter than that in the tandem test (53% shorter, $P < 0.0001$), which, in turn, was shorter than in the bipedal stance test (13% shorter, $P < 0.001$; Table 1). APd, MLd, and Td in the bipedal and tandem stance tests were similar ($P > 0.05$) and significantly lower ($P < 0.001$) than in the single-leg stance test (Table 1). Below are detailed the findings in each specific balance test.

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Table 1. Balance indexes in the three study populations

<table>
<thead>
<tr>
<th></th>
<th>Younger</th>
<th>Middle-Aged</th>
<th>Older</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trial duration, s</strong></td>
<td>60.0±0.0</td>
<td>60.0±0.0</td>
<td>60.0±0.0</td>
</tr>
<tr>
<td>Bipedal</td>
<td>60.0±0.0</td>
<td>47.2±2.9*</td>
<td>19.0±3.2§</td>
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<tr>
<td>Single leg</td>
<td>60.0±0.0</td>
<td>56.4±1.8</td>
<td>45.6±4.5‡</td>
</tr>
<tr>
<td><strong>COP displacement, mm</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bipedal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>APd</td>
<td>4.7±0.3</td>
<td>5.2±0.4</td>
<td>5.3±0.4*</td>
</tr>
<tr>
<td>MLAd</td>
<td>2.1±0.2</td>
<td>2.7±0.2</td>
<td>3.3±0.3*</td>
</tr>
<tr>
<td>Td</td>
<td>5.2±0.4</td>
<td>5.8±0.4</td>
<td>6.3±0.4*</td>
</tr>
<tr>
<td>Single leg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>APd</td>
<td>8.2±0.54</td>
<td>9.7±0.8</td>
<td>11.7±1.1†</td>
</tr>
<tr>
<td>MLAd</td>
<td>6.6±0.5</td>
<td>11.3±0.8*</td>
<td>10.8±1.1†</td>
</tr>
<tr>
<td>Td</td>
<td>10.7±0.6</td>
<td>16.0±1.0*</td>
<td>16.4±1.4†</td>
</tr>
<tr>
<td>Tandem</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>APd</td>
<td>6.2±0.5</td>
<td>6.8±0.9</td>
<td>12.9±1.3‡</td>
</tr>
<tr>
<td>MLAd</td>
<td>4.9±0.2</td>
<td>6.5±0.4*</td>
<td>7.9±0.5†</td>
</tr>
<tr>
<td>Td</td>
<td>8.0±0.5</td>
<td>9.7±0.9</td>
<td>14.5±1.3‡</td>
</tr>
</tbody>
</table>

Values are means ± SE. Trial duration (s) and center of pressure (COP) displacement (mm) are given. Single-leg stance data are average data for the dominant and nondominant leg. Tandem stance data are average data for the dominant leg in front and at the back of the nondominant leg. APd, COP displacement in anterior-posterior direction; MLAd, COP displacement in mediolateral direction; Td, total center of pressure displacement. P < 0.001 for middle-aged vs. older subjects. *P < 0.05 in middle-aged vs. older subjects comparisons.

Table 2. Relevant muscle-tendon parameters

<table>
<thead>
<tr>
<th></th>
<th>Younger</th>
<th>Middle-Aged</th>
<th>Older</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planar flexion MVC, N-m</td>
<td>144.2±8.9</td>
<td>93.6±9.6*</td>
<td>69.2±3.0†</td>
</tr>
<tr>
<td>Antagonist muscle co-contraction, %</td>
<td>5±1</td>
<td>9±2</td>
<td>23±6†</td>
</tr>
<tr>
<td>AC, %</td>
<td>95±1.5</td>
<td>87±2.0*</td>
<td>824±2.7*</td>
</tr>
<tr>
<td>Maximal gastrocnemius tendon force, N</td>
<td>684±42.4</td>
<td>440±28.1*</td>
<td>375±16.6†</td>
</tr>
<tr>
<td>Maximal gastrocnemius tendon elongation, mm</td>
<td>14.7±1.3</td>
<td>15.1±1.8</td>
<td>17.3±1.6†</td>
</tr>
<tr>
<td>Resting gastrocnemius tendon length, mm</td>
<td>215±2.4</td>
<td>177±5*</td>
<td>180±7.5*</td>
</tr>
<tr>
<td>Resting gastrocnemius tendon CSA, mm²</td>
<td>30.5±2.8</td>
<td>28.5±4.5</td>
<td>24.8±0.5*</td>
</tr>
<tr>
<td>Achilles tendon moment arm, mm</td>
<td>51.6±0.9</td>
<td>50.8±0.8</td>
<td>49.1±1.0</td>
</tr>
<tr>
<td>Maximal gastrocnemius tendon stress, MPa</td>
<td>22.4±1.5</td>
<td>15.2±0.6*</td>
<td>15.1±3.1*</td>
</tr>
<tr>
<td>Maximal gastrocnemius tendon strain, %</td>
<td>6.8±0.4</td>
<td>8.5±0.3*</td>
<td>8.8±0.5*</td>
</tr>
<tr>
<td>K, N/mm</td>
<td>53.3±7.5</td>
<td>39.5±3.9*</td>
<td>32.5±4.1†</td>
</tr>
<tr>
<td>YM, GPa</td>
<td>0.36±0.05</td>
<td>0.26±0.03*</td>
<td>0.26±0.03*</td>
</tr>
<tr>
<td>M, mm</td>
<td>15.9±0.47</td>
<td>14.7±0.98*</td>
<td>13.8±0.93*</td>
</tr>
</tbody>
</table>

Values are means ± SE. Stress is the ratio of tendon force over resting tendon cross-sectional area (CSA). Strain is the ratio of tendon elongation over the tendon resting length. MVC, maximal voluntary contraction; AC, activation capacity; K, tendon stiffness; YM, tendon Young’s modulus; M, muscle thickness. *P < 0.05 compared with the younger group. †P < 0.05 in middle-aged vs. older subjects comparisons.

Bipedal Stance

All three subject groups maintained bipedal stance for the maximum duration set (60 s). Td in this stance test increased gradually with age, reaching in the older group an increment of 21% (P < 0.05) compared with the younger group. ANOVA showed a gradual decrement with age, and in the older group it was 55% lower in older compared with younger subjects (see Fig. 2 and Table 2). AC showed a gradual decrement with age, reaching in the older group 53% (P < 0.0001) and 90% (P < 0.0001), respectively, compared with the younger group.

Single-leg Stance

In single-leg stance, the older group exhibited 65% (P < 0.001) shorter trial durations compared with the younger counterparts. Td in this stance test also increased gradually with age, reaching in the older group a 53% (P < 0.0001) increment compared with the younger group. AC and YM in the older group were increased on average by 63% and 42% (P < 0.001), respectively, compared with the younger group.

Muscle-Tendon Characteristics

Plantar flexion MVC torque decreased gradually with age, and it was 55% lower in older compared with younger subjects (P < 0.05). Middle-aged and older subjects had lower Mt values by 8 and 13% (P < 0.05), respectively, than their younger counterparts (see Fig. 2 and Table 2). AC showed a gradual decrement with age, and in the older group it was lower by 12.6% (P < 0.01) compared with the younger group. YM, K and YM decreased gradually with age (Fig. 3 and Table 2), with the difference between the younger and older groups reaching the level of 36 and 48% (P < 0.05), respectively.

Correlation and Regression Analyses

Age was negatively correlated with planar flexion MVC torque, AC, K, and YM (Table 3). With respect to trial duration, any correlation analyses for bipedal stance became redundant, because, in this test, all subjects were able to outlast the maximum duration set. For both single-leg and tandem tests, however, trial duration was significantly (P < 0.05) associated with plantar flexion MVC torque, AC, and K. In addition, trial duration for single-leg stance was significantly associated with YM (Table 3). With respect to APd, there were no significant correlations in the bipedal stance tests. In single-leg and tandem tests, however, APd was significantly (P < 0.05) associated with plantar flexion MVC torque, AC, and K. Mt, was significantly (P < 0.05) associated with APd only in the tandem test (Table 3).
In the MLRs with balance indexes as dependent factors and 1) age and 2) the five muscle-tendon characteristics as independent variables, YM was removed because it was collinear. In addition, for all balance indexes, except for that relating to APd in bipedal stance, MVC was the highest variance inflation factor and was therefore removed from the final regressions. In bipedal stance, the MLR was not significant (P > 0.05), which meant that no variable accounted for the variability in APd (Table 3). In single-leg stance, MLRs were significant (P < 0.001, Table 3) with age, Mv, and K predicting both trial duration (P < 0.05) and APd (P < 0.001). In addition, AC also predicted single-leg APd (P < 0.001). In tandem stance, MLRs were also significant (P < 0.001, Table 3), with age, AC, and K predicting both trial duration (P < 0.001) and APd (P < 0.05).

Table 3. Pearson correlations and multiple linear regressions of muscle-tendon properties with age and bipedal APd and balance duration and APd in single-leg and tandem stance tests

<table>
<thead>
<tr>
<th>Age</th>
<th>APd</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVC, N·m</td>
<td>-0.76‡</td>
</tr>
<tr>
<td>AC, %</td>
<td>-0.37†</td>
</tr>
<tr>
<td>K, N/mm</td>
<td>-0.36‡</td>
</tr>
<tr>
<td>YM, GPa</td>
<td>-0.27*</td>
</tr>
<tr>
<td>Mt, mm</td>
<td>0.29*</td>
</tr>
</tbody>
</table>

**DISCUSSION**

The present study investigated balance performance indicators during bipedal, single-leg, and tandem stance tests in three age groups. We hypothesized that any age-related deterioration in the ability to maintain a given standing posture would be related to a number of calf muscle-tendon parameters relevant to contractile force development. Our findings confirm this hypothesis for the single-leg and tandem stance tests only.

**Effect of Age on Muscle-Tendon and Postural Parameters**

Our results show that ageing is associated with a gradual reduction in 1) MVC torque, 2) Mv, 3) AC, 4) K and YM, and 5) the ability to maintain single-leg and tandem postures. The findings of deterioration in muscle strength, size, and AC with ageing are in agreement with previous reports (7, 9, 10).
and substantiate that the ability to generate contractile force is compromised in older people due to both peripheral and central factors. The results have also shown that, with aging, there is a stepwise decrement in trial duration in the single-leg and tandem stance tests but not in the bipedal stance test. In agreement with previous reports (3, 4), COP displacements were also affected by age. In contrast to the trial durations, however, $AP_d$, $ML_d$, and $T_d$ increased gradually with age in all three tests. Nevertheless, it should be noted that, except for one case ($AP_d$ comparisons in single-leg and tandem postures), the ageing-related increase in COP was consistently more evident in single-leg stance, less evident in tandem stance, and even less evident in bipedal stance. In agreement with reports of ageing-induced reduction in base of support (68), previous studies indicate that older individuals function in safety limits that are substantially reduced to 15–60% of foot length for anterior/posterior stability during bipedal standing (26). This suggests that the increased postural difficulty imposed by further reducing the base of support in single-leg stance, in particular, may have caused older adults to place their center of gravity close to their stability limits, thereby inducing increased COP displacements and a decreased ability to sustain the required stance for extended periods of time. The finding of a preferential ageing-induced deterioration of balance in more demanding postures has clinical implications. Posturography examinations aiming at assessing the propensity of an older individual to fall (2) should not be limited to habitual postures, but should be extended to stances that impose a relatively high degree of challenge to the postural system.

The present study shows systematically for the first time that ageing also affects negatively the mechanical properties of in vivo tendon. This agrees with several in vitro experimental results (6, 52, 72, 73), although some studies have shown the opposite (62), or that ageing has no effect on tendon mechanical properties (14, 21, 22). An explanation for the above inconsistency may relate to interstudy differences between the population ages examined. For example, Shadwick (62) and Nakagawa et al. (52) included very young animals in their experiments, thus examining the effects of biological maturation and development rather than the ageing process. From studies where senile specimens have been included, however, it emerges that ageing makes the tendons more compliant (6, 52, 72, 73), which is consistent with the present in vivo results. Although our findings do not allow revealing the exact mechanisms responsible for the tendon deterioration with ageing, the reduction in YM by 28% in the older compared with the younger tendons indicates that the material of the tendon undergoes substantial ageing-induced changes. Material property changes in the same direction have recently been found in young in vivo human tendons undergoing short-term unloading (12 wk of bed rest) (57) and chronic disuse (1.5–25 yr) caused by spinal cord injury (42), indicating that the effects of ageing and mechanical unloading on tendons may be mediated by similar mechanisms. Previous studies suggest that a reduction in ground substances, such as water, hyaluronic acid, and glycosaminoglycans (1, 70), a change in the content of elastin (71) and contractile proteins in tendon cells (2), a reduction in the number of longitudinally aligned collagen fibrils (75), and a reduction in collagen fibril diameter (53, 54, 76) may be involved in the deterioration of tendon with ageing/disuse. The latter factor would indicate that, apart from tendon material changes, tendon atrophy may also occur with ageing, which is further substantiated by the differences in tendon CSA between the younger and older groups in the present experiment.

The tendon forces and elongations during the isometric tests for the young subjects agree with previous in vivo results (41). The $K$ and YM values, however, are smaller than previously reported (41), because they have been calculated at a lower tendon force (207 N) to accommodate for the weakest subject in our study. It should be noted that the corresponding tendon elongations required for the calculation of $K$ and YM would not necessarily be equivalent to those experienced during the balance tests. In fact, from the tendon force-elongation curves, the force plate data during the balance tasks (average values across all three tasks) and average moment arms of the ground reaction force, we estimated that the maximal elongations experienced during the balance tasks would be $\sim 0.6\,\text{mm}$ in younger, 0.7 mm in middle-aged, and 1.1 mm in older subjects. These values correspond to only $\sim 10\%$ of the elongations at 207 N and agree with the previously reported tendon elongation of 1 mm during stance obtained from actual, real-time ultrasonic measurements (30). Differences with age in tendon behavior during a given postural task could affect the rate of contractile force transmission to the skeleton and, therefore, influence the ability to make postural adjustments when necessary and maintain balance effectively. The relations found in the ability to maintain single-leg and tandem postures with tendon properties (see discussion below) further support this notion.

Relation Between Muscle-Tendon Properties and Balance

The present study has shown that the calf muscle-tendon parameters studied are not associated with bipedal stance ability. Most of the parameters, however, were independently correlated with single-leg and tandem stance abilities. In addition, the MLRs showed that the combination of age, $M_t$, and $K$ (and for $AP_d$ only) can explain $79–90\%$ of the variance in single-leg stance performance, whereas age, $AC$, and $K$ accounted for $69–82\%$ of the variability in tandem stance performance.

In agreement with previous reports (32, 60, 61), we found that muscle strength is associated with prolonged and steady stance. However, $M_t$ alone had no relation with balance ability in most tests. This finding agrees with a previous report from experiments using indexes of muscle mass less relevant to standing posture (17). This finding is surprising since muscle size is one of the major factors determining contractile force potential, and it has been shown that $M_t$ correlates highly with muscle volume (47, 48), which, in turn, correlates highly with MVC torque (15). One possibility is that $M_t$ differences between groups do not accurately reflect differences in the number of in-parallel sarcomeres. Other possibilities include ageing-related changes in the specific tension of muscle (51) and the ratio of contractile to noncontractile material in the muscle (24). However, we found that $M_t$ was a significant factor when combined with other muscle-tendon characteristics in the multiple-regression analyses, indicating that $M_t$ has some predictive power only in the presence of other more important muscle-tendon parameters.
Two important parameters for postural stance ability were $K$ and YM. Although previous authors have suggested that intrinsic whole ankle stiffness is too low to stabilize human standing (29), this should not be confused with $K$ as we define it here. Similar to muscle strength, the mechanical properties of the GS tendon in the present study also had a significant association with postural sway and trial duration in the single-leg and tandem stance tests but not in the bipedal stance test. This agrees with previous reports showing a lack of influence of “ankle stiffness” on sway during bipedal stance, which would be expected to put a smaller demand on the ankle joint compared with tests requiring a smaller base of support. Our results are also in agreement with an earlier suggestion (56) that calf tendon mechanical properties would be important in sinusoidal, anterior-posterior “sway-like” ankle movements. This makes sense if the mechanisms responsible for balance could be regarded as a feedback loop system in which the timing of the response to disturbances in balance is critical. In such a system, even small delays in the feedback loop would have a negative effect on postural balance. Hence, the correction of the reported “catch and throw” actions (28) about the ankle would be faster in a stiffer unit because force development in an actuator in-series with a compliant unit is inevitably slower than in an actuator in-series with a stiffer unit. In fact, a simulation model (49) has shown that delays of only 50 ms would be sufficient to destabilize the balance control mechanism, while another model (66) showed that time to peak ankle torque is successful at predicting ~80% of failed balance trials. Also, previous work shows that torque about the ankle increases with sway frequency, at least in the high end of sway frequencies (27). These observations, therefore, support our findings that tendon mechanical properties constitute an important factor for maintaining balance.

In addition to $K$ and YM, AC was also found to highly correlate with balance ability. This agrees with suggestions that higher level anticipatory control is used in balance maintenance, since the rapid paradoxical movements observed (30) cannot be generated by stretch reflexes. Models assuming the body to be an inverted pendulum propose that, if the clockwise moment becomes greater than that in the anticlockwise direction, the subject will activate the ankle plantar flexors to correct the forward COP displacement. Here, the main limiting factor is velocity of COP displacements, and the muscle activity control strategy for this mechanism has recently been proposed to work in an anticipatory manner modulated by the central nervous system (46). The significant correlations with AC and postural sway (see Table 3) that we have found in our study agree with the above theorem on requirement for adequately high muscle activation.

Role of Sensory Feedback on Balance Performance

Our experiments deliberately avoided any auditory feedback to remove this extra factor, which has been shown (63) to significantly affect the postural performance of healthy older, but not younger, subjects. Tactile sensation was also controlled by carrying out all tests with the subjects barefoot on a clean, laminated surface. Nevertheless, since previous work has found that sensory measures are good predictors of COP displacement in bipedal stance (13, 33), the addition/manipulation of quantitative measures of tactile sensitivity, vibration sense, and proprioception would have added additional insight into ageing effects and relative contribution to predictors of COP displacement in stance tasks of varying postural difficulty.

In conclusion, the present findings indicate that postural stability decline in old age relates to deteriorations in ankle plantar flexor strength, muscle AC, and tendon mechanical properties. However, these deteriorations seem to be associated with affecting postural tasks that are more challenging than the habitual bipedal stance. The present findings substantiate the involvement of the musculoskeletal system in maintaining balance and have implications for clinical posturography and exercise interventions for fall prevention and/or rehabilitation.

GRANTS

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