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ORIGINAL RESEARCH

Balance Decrements Are Associated With Age-Related Muscle Property Changes

Christopher J. Hasson,[1] Richard E.A. van Emmerik,[2] and Graham E. Caldwell[2]
[1]Northeastern University; [2]University of Massachusetts Amherst

In this study, a comprehensive evaluation of static and dynamic balance abilities was performed in young and older adults and regression analysis was used to test whether age-related variations in individual ankle muscle mechanical properties could explain differences in balance performance. The mechanical properties included estimates of the maximal isometric force capability, force-length, force-velocity, and series elastic properties of the dorsiflexors and individual plantarflexor muscles (gastrocnemius and soleus). As expected, the older adults performed more poorly on most balance tasks. Muscular maximal isometric force, optimal fiber length, tendon slack length, and velocity-dependent force capabilities accounted for up to 60% of the age-related variation in performance on the static and dynamic balance tests. In general, the plantarflexors had a stronger predictive role than the dorsiflexors. Plantarflexor stiffness was strongly related to general balance performance, particularly in quiet stance; but this effect did not depend on age. Together, these results suggest that age-related differences in balance performance are explained in part by alterations in muscular mechanical properties.

Keywords: biomechanics, muscle, aging, balance, postural control

Postural stability results from the integrated sensory and motor function of the neuromuscular system. It is recognized that older adults exhibit increased postural sway[1–4] and have an increased risk of falling.[5,6] The main physiological changes underlying these balance decrements can be classified into two broad categories: (1) peripheral and central nervous system changes and (2) musculoskeletal system changes. The former has been well studied, and includes less reliable visual, vestibular, and somatosensory information,[7–10] slower sensory integration and cognitive processing,[11–13] increased motor unit discharge variability,[14] and longer neural transmission delays.[15] On the other hand, the effects of age-related alterations in the musculoskeletal system have received less attention.

For a given neural input, muscular force output depends on contractile length[16] and velocity,[17] as well as series elasticity.[18] Age-related changes in these muscular properties will alter the translation of neural commands into muscular force. Although many muscles contribute to postural stability, those surrounding the ankle joint have an important role.[19] Therefore, age-related changes in ankle muscle properties may strongly influence postural control. Onambele et al[20] used regression analysis to examine the influence of calf muscle properties on postural control in the aging population. Together, age-related changes in joint strength, muscle size, activation capacity, and Achilles tendon stiffness could explain up to 70% of the variance in balance performance during the postural challenges of tandem and single leg stance, although the importance of changes in individual muscular properties was not reported. Individual muscles such as the gastrocnemius (GA) and soleus (SO) are each important in the control of upright posture[21] and make unique contributions to joint properties.

With aging there may be differential changes in these plantarflexor muscles that cannot be resolved using joint-level measurements. For example, selective age-related atrophy of the faster-contracting type II muscle fibers[22–24] may cause the GA to be disproportionally weaker and slower in older adults, changing the relative contributions of the GA and SO to postural control. We recently reported that GA muscles in older males displayed altered force-velocity relationships, producing less force at a given velocity compared with younger males, while no such age differences were found for the SO.[25] In general, our results showed that the dorsiflexor and plantarflexor muscles in young and older adults display age-related differences in muscle morphology and mechanical properties. Specifically, our sample of older adults had smaller proportions of contractile tissue relative to total muscle volume and displayed reduced maximal isometric force, slower force-velocity relations, altered force-length properties, and stiffer series elasticity.[25–27]

In the current paper we evaluate the postural control of the same young and older adults to determine if age-related changes in balance responses are correlated with these altered muscular properties. For the dorsiflexors and individual plantarflexor muscles (GA and SO), we sought answers to two questions: (1) Which muscle-specific properties are most related to balance performance on static and dynamic postural tests? (2) Which properties explain the most variation in age-related changes in balance and postural control?

Methods

Postural control data were collected under static and dynamic conditions on the same 12 young (27 ± 3 y; 67 ± 7.4 kg; 1.73 ± 0.07 m; mean ± standard deviation) and 12 older (72 ± 5 y; 82 ± 14 kg; 1.72 ± 0.09 m) participants for whom we previously described ankle joint muscular properties.[25–27] There were an equal number of

Christopher J. Hasson is with the Neuromotor Systems Laboratory in the Department of Physical Therapy, Movement and Rehabilitation Sciences at Northeastern University in Boston, MA. Richard E.A. van Emmerik and Graham E. Caldwell are with the Department of Kinesiology at the University of Massachusetts Amherst in Amherst, MA. Address author correspondence to Christopher J. Hasson at c.hasson@neu.edu.

males and females within each age group. Participants completed an informed consent document approved by the local institutional review board in which all experimental procedures were explained.

For all conditions, participants stood comfortably with the eyes open, hands behind the back, and with the feet placed approximately under the hip-joint centers, parallel with the sagittal plane (no toe-out). Whole-body kinematic and kinetic data were measured with an eight-camera motion capture system (ProReflex; Qualysis, Gothenburg, Sweden) and AMTI force plate (Model BP600; AMTI, Inc., Watertown, Massachusetts). Participants wore a tethered safety harness which remained slack unless a fall occurred. Marker kinematics (200 Hz) and ground reaction forces (1000 Hz) were sampled synchronously using a 16-bit analog-to-digital converter.

Kinematic and kinetic data were smoothed using a fourth-order zero-lag Butterworth digital filter, with optimal cut-off frequencies determined through spectral and residual analysis.[28] Sagittal plane body center of mass (CoM) motion was computed using standard linked-segment methods, and ground reaction force data were used to compute center of pressure (CoP) position.[28] CoM and CoP positions were referenced to the ankle joint; numerical differentiation was used to compute velocities and accelerations.

CoP and CoM motion variables reflect aspects of postural control that can change with age.[29] CoP displacement is related to the modulation of ankle and hip torque and is indicative of neuromuscular postural control processes.[30] CoM motion relative to the base of support formed by the feet must be controlled for maintenance of stability, and thus reflects performance during balance tasks.[31]

Static Conditions

Quiet Stance. Participants were instructed to stand as still as possible for 30 seconds, with their gaze focused on an eye-level target ~3 m away (Figure 1A). Here, and in other balance tests (unless noted otherwise), two trials were performed; the first serving as an orientation trial and the second for analysis. Although in general, additional trials could have increased the reliability of postural assessments,[32] we were concerned about fatigue effects that could decrease reliability, particularly for the older adults, given the large number of different postural tests. For quiet stance, trial durations of at least 30 seconds have been shown to produce acceptable reliability of balance measures.[33] The instantaneous CoM time-to-contact (TtC) to the anterior (toe) and posterior (heel) support boundaries was calculated as in Slobounov et al:[34]

$$TtC = -v \pm \sqrt{v^2 - 2a\,(p_{\max} - p)}\ /\ a \qquad (1)$$

where p, v, and a are CoM anterior-posterior positions, velocities, and accelerations, respectively, and $p_{\max}$ is the support boundary (toe or heel marker) margin. The shortest time to first boundary contact was considered the instantaneous TtC.

Static Leaning. Participants stood quietly until cued to lean as far as possible without falling, bending at the waist, or lifting their heels, while maintaining their maximal lean position for 30 seconds. Trials were performed in both forward and backward leaning directions (Figures 1B and 1C). The average anterior-posterior CoM position was computed, reflecting postural control at the extremes of a participant's capabilities.

Dynamic Conditions

Rhythmic Sway. At both preferred and imposed (0.25 Hz) frequencies, participants swayed maximally forward and backward around the ankle joint with their feet flat on the floor and their body straight (Figure 1D).[35] In the imposed swaying condition, participants were paced by a metronome. Data were collected for 30 seconds once steady-state sway was achieved. Median CoM displacement frequency was computed using fast Fourier transformation to indicate the stable oscillatory swaying motion[36] and the subject's ability to attain the imposed frequency. Postural control at the limits of dynamic stability, when proper CoM deceleration is needed to prevent destabilizing movement past the support boundary, was quantified by the average extreme forward and rearward CoM positions during each swaying trial.

Maximum Reaching. Three trials were recorded as participants reached forward with their hands together to a predetermined maximal reach target (Figure 1E). Normalized reach distance was computed as maximal anterior wrist marker position relative to the toe divided by participant height. Maximal CoP anterior position was expressed relative to the ankle joint position, reflective of the maximum ankle torque during the reach. Measures were averaged across the three trials.

External Perturbation. Quietly standing participants were perturbed from behind using a pendulum with a backboard apparatus (Figure 1F). In a series of trials, the pendulum was released from increasingly higher positions and release angles (10°–45°) to swing forward, contacting the backboard with the participant in the upper back, and therefore accelerating the body forward. Participants were to resist this acceleration with an ankle strategy,[37] resume quiet stance as quickly as possible, and only step if a fall was imminent. For each trial, a postural challenge was computed as the pendulum impact velocity divided by participant mass. The postural challenge that forced a stepping response reflected the participant's capacity to resist the perturbations, with higher challenge levels meaning better performance. The maximum plantarflexor torque generated during each trial was calculated using standard Newton-Euler equations.[38] A full description of all perturbation data has been previously reported.[39,40]

Muscle Mechanical Properties

Participant-specific estimates of GA, SO, and tibialis anterior (TA) mechanical properties were previously reported.[25] The TA properties included the effects of all anterior compartment dorsiflexor muscles, including extensor hallucis longus, extensor digitorum longus, and peroneus tertius. Each muscle was modeled as a two-component Hill-type model with a contractile element in series with an elastic element.[17] Contractile element behavior was defined by: (1) maximal isometric force P_0, (2) force-length optimal contractile element length L_0 and width coefficient W, and (3) force-velocity coefficients a/P_0 (shape), b/L_0 (maximal shortening velocity) and ε (eccentric plateau). Series elastic element behavior was defined by force-extension stiffness coefficient K and slack length L_S. The stiffness relation was nonlinear and the coefficient K reflects the stiffness (slope) at a force level of 400 N.[25] Force-length, force-velocity, and force-extension parameters are shown in Figure 2. Muscle-specific parameters were obtained by optimizing participant-specific musculoskeletal models to match experimental joint torque-angle, torque-angular velocity, and torque-extension relations. Magnetic resonance and ultrasound imaging data were used to constrain muscle model parameters to realistic participant-specific values.[26,27]

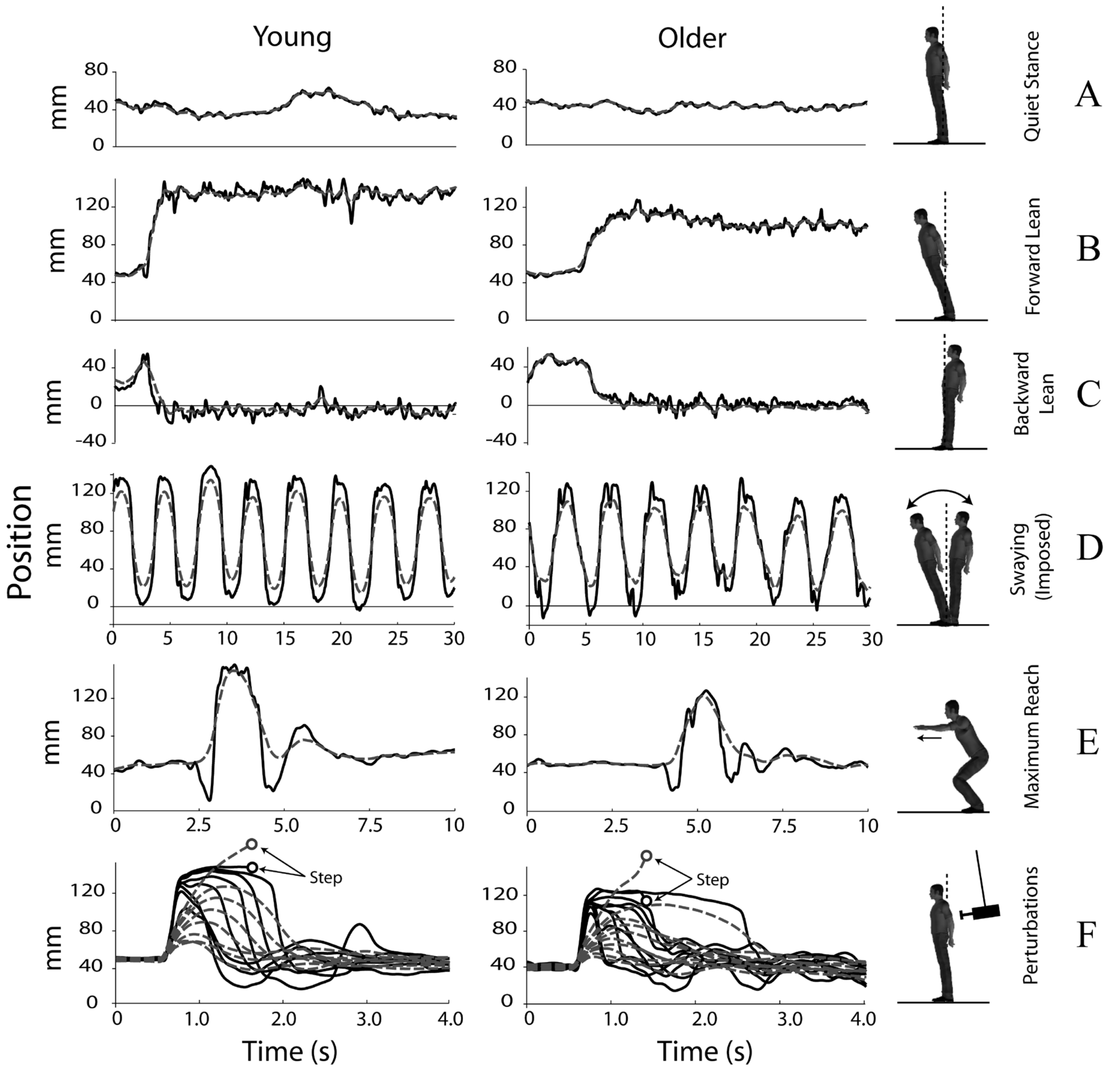

Figure 1 — Representative young (left) and older (right) participant anterior-posterior center of mass (gray dashed lines) and center of pressure (black lines) displacements for the different postural conditions. From top to bottom: (A) quiet stance, (B) forward lean, (C) backward lean, (D) imposed swaying (preferred swaying not shown), (E) maximum forward reach, and (F) sequential external perturbations. In F, center of mass and pressure trajectories are shown for multiple trials and the circles indicate the point at which participants stepped off the force platform. Note that positions are referenced to the ankle joint and that trial durations were 30 seconds in A–D, but shorter in E (10 s) and F (4 s).

Statistical Analysis

Statistical analyses (R software[41]) included separate two-way ANOVAs (age × gender) performed on each of the dependent balance variables with a critical value of $p < .05$. Relationships between individual muscle mechanical properties[25] and balance variables were assessed by linear regression. Muscle-specific (TA, GA, and SO) parameters P_0, L_0, W, a/P_0, b/L_0, ε, K, and L_S were regressed against appropriate individual measures from each balance test to determine how well each property could predict postural test performances, and to determine age-group differences, using the regression model form

$$BM = \beta_0 + \beta_1 Age + \beta_2 MP + \beta_3 (Age \times MP) \qquad (2)$$

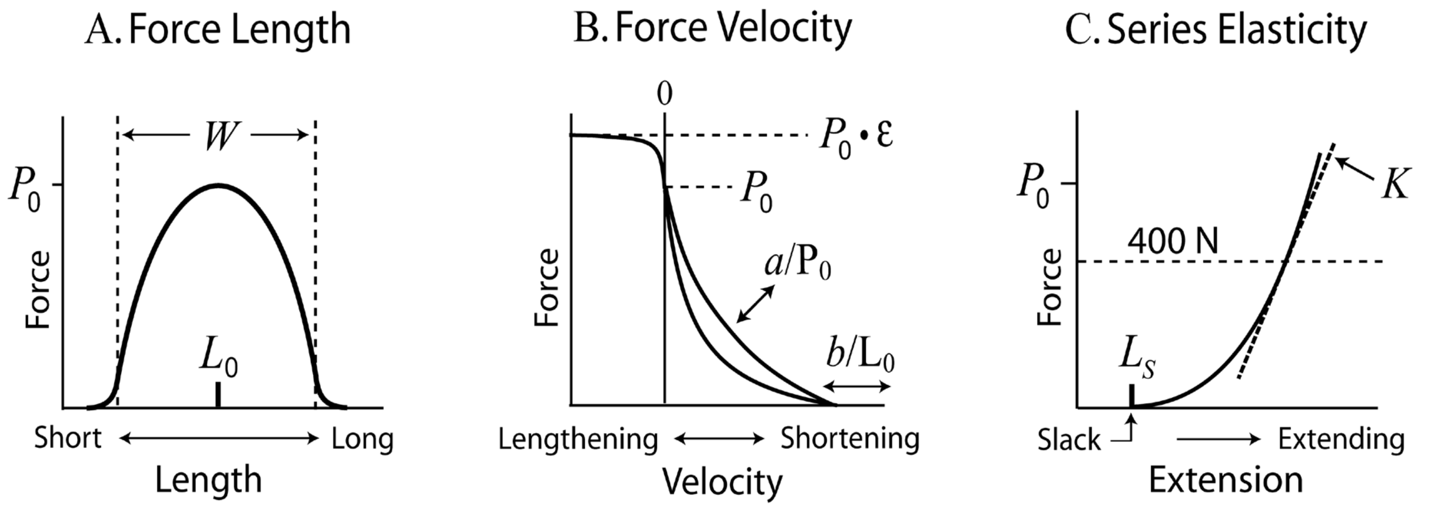

Figure 2 — Schematics showing the characterization of muscle mechanical properties by a set of 8 parameters (P_0, L_0, W, a/P_0, b/L_0, ε, L_S, and K). See text for more details.

where *BM* is the balance measure, *MP* is a single muscle-specific mechanical property, and β_0 through β_3 are the regression coefficients. The *Age* factor is a categorical variable (young or old) that allows separate intercepts and slopes for each age group. Although some gender differences in muscle properties were previously observed,[25] gender was not included as a factor to limit the number of terms in the regression model. Including gender would have created four subgroups of six subjects, and introduced additional unknown model terms (ie, six β coefficients with age and gender main effects and interactions). The resulting ratio between the number of model unknowns and number of data points in each subgroup would have reduced the stability of the regression procedure too much to make useful conclusions. Regression results were screened to form a subset of models that described (a) a slope that was significantly different from zero, indicating that a mechanical property predicts a balance measure, or (b) a significant interaction, indicating that the regression slope was age-dependent (ie, the relationship between balance performance and a muscle property was different for young versus older participants).

Results

As expected, the older adults performed more poorly than the young adults on all static postural tests, with the lone exception of backward leaning (Table 1). During quiet stance, older adults had higher CoP speeds and shorter CoM TtC (both $p < .001$). In forward leaning, the older adults had higher CoP speeds ($p = .016$) and did not lean as far ($p < .001$).

Older adults also performed more poorly on most dynamic postural tests. During rhythmic swaying, the older adults did not sway as far forward as the young (preferred frequency: $p = .005$; imposed frequency: $p = .006$), but they did sway as far backward (preferred: $p = .155$; imposed: $p = .302$). For the imposed frequency, CoM median frequency was closer to the target frequency for the younger participants ($p = .023$). The older participants had greater maximal forward reach ($p = .020$), but with a smaller CoP forward excursion ($p < .001$) compared with the younger participants. During perturbation trials, younger participants could withstand a larger postural challenge than the older adults ($p < .001$). There were no age-specific differences for the maximum plantarflexor torque used to resist the perturbations ($p > .05$). There were a few gender-specific responses. In the preferred swaying condition, males chose lower swaying frequency than females, regardless of age ($p = .039$). During the forward reach condition, males had greater forward CoP shift than females ($p < .001$), perhaps related to their longer feet (29.7 ± 1.1 cm vs. 26.4 ± 0.8 cm; $p < .001$). Finally, in the perturbation tests, males generated larger plantarflexor torques than females ($p < .001$).

Linear regression analysis showed that muscle mechanical properties could explain a significant proportion of the variance in several quiet stance performance variables (Figure 3 [TA] and Figure 4 [GA and SO]). The SO P_0 (indicative of maximal isometric strength) was negatively correlated with the mean CoP speed in quiet stance, while the SO force-velocity coefficients a/P_0 and b/L_0 were positively correlated with the mean CoM TtC. Participants with a smaller TA eccentric plateau ε had greater mean CoP speed during quiet stance. Muscle elasticity was also a factor, as GA and SO stiffness K were both positively correlated with quiet stance CoP speed. SO series elastic element slack length L_S was significant too, being positively related to the mean CoP speed but negatively related to the mean CoM TtC.

Strong relationships were also observed for the more challenging balance conditions. In the forward lean condition, GA and SO stiffness K were positively correlated with CoP speed. Performance during swaying was correlated with both plantarflexor and dorsiflexor muscle properties. The TA optimal contractile element length L_0 had positive correlations with the maximum forward CoM position during both imposed and preferred swaying, while the GA L_S had a strong positive relationship with the maximum forward CoM position in imposed swaying and a weaker one in preferred swaying. For maximum reach, two TA muscle properties were predictive of performance. TA stiffness K was directly correlated with maximum reach distance, while participants with a smaller TA eccentric plateau ε had a greater CoP shift during the maximum reach. In the balance perturbation condition, the SO force-length width coefficient W displayed a strong positive relation for the maximum perturbation challenge that participants could withstand, while the GA slack length L_S had a strong positive relationship with the maximum ankle torque produced while resisting the perturbation.

Table 1 Balance measures for static and dynamic postural tasks (mean ± between participants standard deviation)

Condition	Measure	Sig.[a]	Young Male	Young Female	Older Male	Older Female
Quiet stance	CoP speed (mm/s)	A	6.5 ± 2.1	6.3 ± 1.6	14.7 ± 5.7	10.3 ± 2.8
	CoM TtC (s)	A	10.3 ± 0.7	9.5 ± 1.4	7.4 ± 2.0	8.2 ± 1.0
Lean forward	CoP speed (mm/s)	A	19.4 ± 4.2	15.9 ± 6.6	26.2 ± 7.7	22.3 ± 5.6
	CoM pos. (mm)	A	142 ± 14	119 ± 14	101 ± 18	101 ± 18
Lean backward	CoP speed (mm/s)	-	20.6 ± 6.0	15.4 ± 5.6	26.2 ± 9.1	19.5 ± 7.6
	CoM pos. (mm)	-	4.6 ± 13.8	–7.6 ± 12.2	4.4 ± 17.4	0.6 ± 8.8
Preferred swaying	CoM med. freq. (Hz)	G	0.17 ± 0.06	0.23 ± 0.05	0.14 ± 0.08	0.18 ± 0.04
	Ant. CoM pos. (mm)	A	136 ± 6	112 ± 11	106 ± 25	98 ± 20
	Post. CoM Pos. (mm)	-	0.9 ± 17	–4.3 ± 18	–10.2 ± 2	–5.9 ± 19
Imposed swaying	CoM med. freq. (Hz)	A	0.23 ± 0.01	0.22 ± 0.02	0.21 ± 0.03	0.20 ± 0.01
	Ant. CoM pos. (mm)	A	130 ± 12	111 ± 13	100 ± 33	91 ± 18
	Post. CoM pos. (mm)	-	11.6 ± 14	–4.2 ± 12	1.1 ± 21	7.8 ± 14
Reach	Max. reach (% Height)	A	13.0 ± 1.9	13.2 ± 2.7	14.5 ± 3.1	18.2 ± 4.3
	Max. CoP shift (mm)	A, G	172 ± 8	139 ± 10	134 ± 19	122 ± 14
Perturbation	Max. chal. (deg/s/kg)	A	1.92 ± 0.14	1.69 ± 0.27	1.17 ± 0.31	0.97 ± 0.27
	Peak torque (N·m)	G	168 ± 21	105 ± 12	164 ± 25	99 ± 25

Abbreviations: CoP, center of pressure; CoM, center of mass; TtC, time-to-contact; pos., position; med., median; freq., frequency; ant., anterior; post., posterior; max., maximum; chal., challenge.

[a] Indicates significant main effect of either age (A) or gender (G) at $p < .05$ (see text for actual p values).

There were several significant interactions between age-related changes in muscle properties and balance performance. Most of the strong ($R^2 > .50$) age interactions were observed for quiet stance (Figure 5). Longer SO optimal contractile length (L_0) was related to longer CoM TtC in younger participants but shorter times in older participants, while GA L_0 was positively correlated with mean CoP speed for older, but not younger, participants. The TA also displayed age interactions in quiet stance. Young participants with larger TA b/L_0 (faster) had smaller TtC values, but this relation was reversed for older adults. There was also a strong TA L_S age interaction, positively related to the mean CoP speed for older, but not younger, participants. For the forward lean condition, there were strong age interactions for the maximal isometric force capability P_0, as young participants with stronger plantarflexors (GA and SO P_0) leaned farther forward but stronger older adults did not. Note that in this case, some subjects were relatively far from their group mean and therefore had stronger effects on the correlation coefficients than the other subjects. This was also true for the older subjects' CoM TtC data relationships for the TA (with b/L_0) and SO (with L_0) during quiet stance.

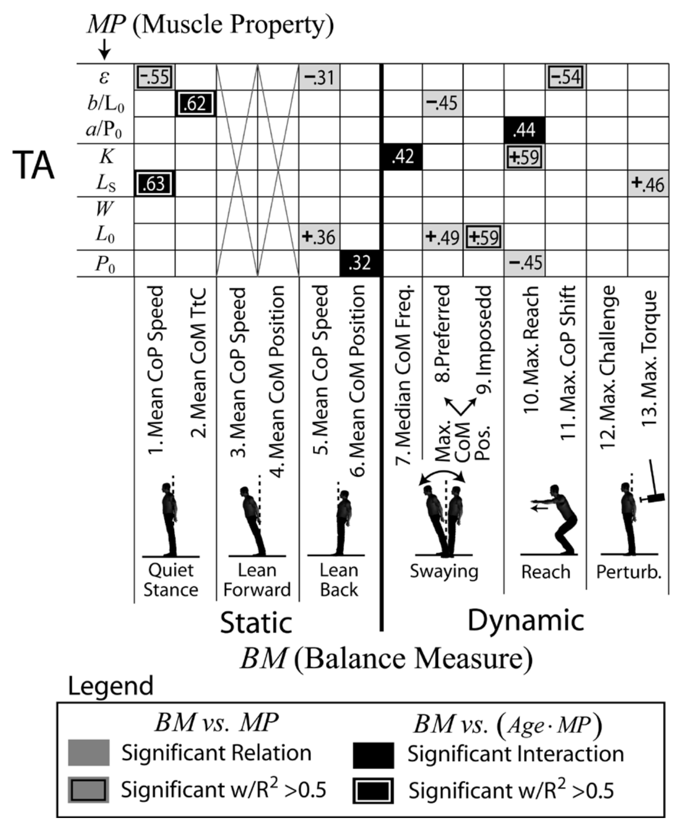

Figure 3 — Matrices showing significant correlations between each static and dynamic balance measure (BM) and each dorsiflexor (TA) muscle mechanical property (MP). Gray shading indicates a significant relation exists between a particular BM and MP (regardless of age), while solid black indicates a significant interaction between age and MP for a given BM. The R^2 values are given inside each shaded box, with an indication of a positive (+) or negative (–) relationship. The strongest significant relationships with $R^2 > .50$ are highlighted with rectangles within the shaded boxes, and are shown in Figure 5. Regressions were not performed for muscles in postural conditions where they have minimal involvement (eg, the TA in a forward lean). CoP, center of pressure; CoM, center of mass; TtC, time-to-contact.

Discussion

The purpose of this study was to explore the relation between individual muscle mechanical properties and balance performance in young and older individuals. To this end, we evaluated the postural control of the young and older subjects for whom we previously estimated muscle mechanical properties.[25–27] As expected, the older adults performed more poorly in almost all static and dynamic balance conditions. We used regression analysis to answer two questions: (1) Which muscle-specific properties are most related to balance performance on static and dynamic postural tests? (2) Which properties explain the most variation in age-related changes in balance and postural control? As we suspected, age-related changes in balance performance were associated with changes in individual muscle mechanical properties.

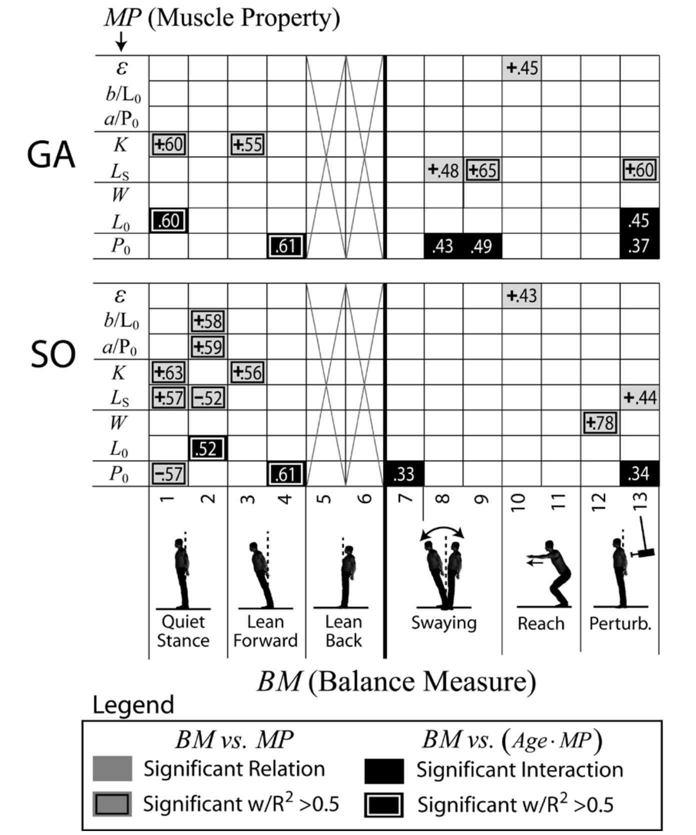

Figure 4 — Matrices showing significant correlations between each static and dynamic balance measure (BM) and each gastrocnemius (GA) and soleus (SO) muscle mechanical property (MP). Gray shading indicates a significant relation exists between a particular BM and MP (regardless of age), while solid black indicates a significant interaction between age and MP for a given BM. The R^2 values are given inside each shaded box, with an indication of a positive (+) or negative (–) relationship. The strongest significant relationships with $R^2 > .50$ are highlighted with rectangles within the shaded boxes. See Figure 3 for details about the specific balance measures for each condition. MPs include: force-length optimal contractile element length L_0 and width coefficient W; force-velocity coefficients a/P_0 (shape), b/L_0 (maximal shortening velocity), and ε (eccentric plateau); and force-extension stiffness coefficient K and slack length L_S.

Regardless of age, plantarflexor (GA and SO) stiffness and force-velocity properties exhibited strong associations with quiet stance performance. This is notable given the debate on the role of ankle stiffness in the control of posture.[21,42–47] The GA and SO stiffness K values were positively correlated with the mean absolute CoP speed during quiet stance and leaning. This is congruent with the behavior of a mass-spring system, where increased stiffness raises natural frequency and induces faster fluctuations in the system CoM. The SO force-velocity properties were also positively correlated with the CoM TtC during quiet stance. Participants with faster SO muscles (larger a/P_0 and b/L_0) had longer TtC, indicating better modulation of CoM motion to keep it farther from spatiotemporal stability limits.[40] At a given swaying speed, the faster SO muscles could produce more force and thus better control CoM movement.

In the dynamic postural tests, properties that affect the operating range of muscle (both L_S and L_0) were associated with balance performance, irrespective of age. Both GA slack length L_S and TA optimal contractile length L_0 were positively related to the maximum forward CoM position during swaying. Because both L_S and L_0 affect the operating range of the force-length relation, we probed these results by performing isometric simulations with the musculoskeletal model using the optimized participant-specific muscular parameters.[25] With the ankle angle at its average position in quiet stance (8 ± 4° forward), the modeled GA was operating beyond optimal length (from 132 ± 27% to 115 ± 32% L_0 as force ranged between 0% and 75% P_0). An increase in L_S will shift the GA contractile element to shorter lengths operating closer to L_0, meaning better control of CoM motion during a forward sway when the dominant muscle action is eccentric plantarflexion, which is necessary to decelerate and reverse forward motion. The same simulations showed the model TA contractile element operating on the ascending limb of its force-length relation (from 79 ± 13% to 68 ± 12% L_0 as force ranged from 0% to 75% P_0). An increase in L_0 would move the TA *farther* from its optimum, making the TA weaker in more forward postures. However, TA force here would produce antagonistic torque that would reduce the net plantarflexor torque, reducing the effectiveness of the plantarflexors. The shift to a longer TA L_0 would allow TA preactivation late in forward sway to prepare for the subsequent backward movement, without interfering with plantarflexor control of the forward movement.

Among the muscle properties that had significant age interactions, the strongest relationships involved the static postural tests.

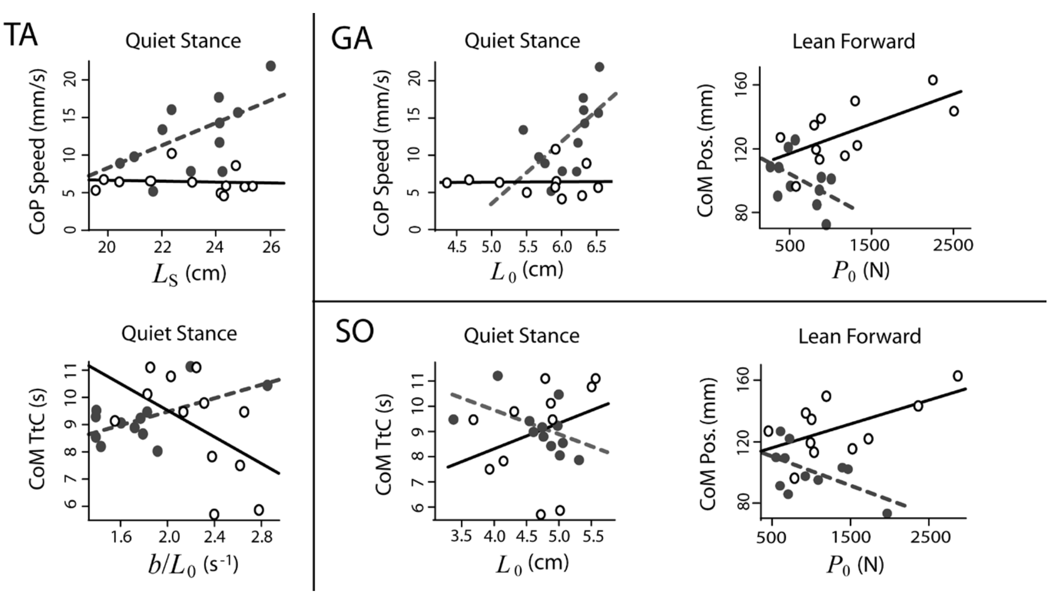

Figure 5 — Significant interactions (with $R^2 > .50$) between age, a muscle mechanical property, and a given balance measure. Muscles shown include dorsiflexors (TA), gastrocnemius (GA), and soleus (SO). Young participants indicated by black open circles and black regression lines. Older participants indicated by gray filled circles and dashed gray regression lines. CoP, center of pressure; CoM, center of mass; TtC, time-to-contact.

Young participants with stronger plantarflexors (larger GA and SO P_0) leaned farther forward, but stronger older adults did not; perhaps indicating a ceiling effect associated with the lower force capabilities in the older plantarflexors.[25] As the forward body lean angle θ increases, there is a nonlinear increase in the gravitational load that the plantarflexors must oppose ($m \cdot g \cdot \sin\theta$). Therefore, even the strongest of the older participants may have not been able to counter the high gravitational torque load of large forward lean angles. In contrast, the significantly stronger young participants were able to produce enough plantarflexor torque to resist falling forward. In the postural perturbations, there was a strong positive correlation between the SO force-length width W and the maximum postural challenge that participants could withstand before stepping. A wider force-length relation (greater W) makes a muscle stronger across a wider range of nonoptimal contractile element lengths, and therefore could facilitate the greater plantarflexor torques needed to prevent a forward fall.

Optimal contractile component length L_0 also demonstrated an age interaction in the quiet stance condition, as younger (but not older) participants with a longer SO L_0 tended to have longer CoM TtC and thus better temporal stability margins. A longer L_0 could shift the SO fibers to operate more on the ascending limb of the force-length relation, a stable position in which a forward sway would make the muscle longer and stronger. This stronger configuration could also support bigger throws within the impulsive catch-and-throw model of postural control,[43] which could explain the positive correlation between the SO L_0 and the mean CoP speed.

Our regression analyses showed that the maximal isometric strength P_0 of the individual plantarflexor muscles was strongly related to age-related differences in balance performance, corroborating the results of Onambele and colleagues.[20] If muscles are viewed as simple linear force transducers, age-related declines in strength could be overcome by increases in neural activation until the strength limit P_0 is reached. If a required task demands more force, then the muscle would need to be strengthened (eg, through resistance training) to increase P_0. However, human skeletal muscle physiology is more complex; the force-length, force-velocity, and force-extension relations filter the relationship between neural input and force output in a nonlinear manner. As our previous results have shown, this filter differs in many ways in older adults,[25] and the current study suggests that these differences may have important consequences for postural control.

Due to the posterior location of the ankle joint within the foot, the plantarflexors (GA and SO) are more effective at counteracting the gravitational toppling torque than the dorsiflexors (TA). Therefore, the CoM position is usually kept in front of the ankle joint, as shown in Figure 1 and elsewhere.[48] Importantly, the plantarflexors show a preferential decline in strength and volume with aging, unlike the dorsiflexors in which volume and torque capability are retained.[26,27,49] In an earlier paper, we showed that older males had weaker and slower GA muscles compared with younger males,[25] consistent with a preferential loss of fast-twitch motor units with aging.[22–24] Therefore, the strong association between age-related plantarflexor muscle property changes and postural control decrements is not surprising. Indeed, compared with the TA, stronger age interactions were found for the GA and SO strength (P_0), optimum fiber length (L_0), force-velocity properties (a/P_0 and b/L_0), and stiffness (K).

In summary, the older adults had poorer performance on a variety of static and dynamic postural tests, and muscle strength (P_0) was strongly related to these age-related decrements. However, significant age interactions in balance performance were observed with other muscle properties as well, including parameters related to the optimal fiber length (L_0), series elastic slack length (L_S), and the velocity-dependent force capability (b/L_0). Although series-elastic stiffness (K) had an important relation with many postural control measures, it was not strongly related to age-related differences. Overall the muscle properties examined accounted for 50% to 60% of the age-related changes in balance properties. Other factors such as age differences in reaction time and sensory thresholds may further explain balance degradations.[50] It remains to be seen whether changes in muscle properties through training[51–53] will improve balance.

Acknowledgments

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