Exp Brain Res (2009) 196:413–427
DOI 10.1007/s00221-009-1865-7

RESEARCH ARTICLE

Scaling of plantarflexor muscle activity and postural time-to-contact in response to upper-body perturbations in young and older adults

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Received: 15 October 2008 / Accepted: 14 May 2009 / Published online: 6 June 2009
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Abstract In this study, we describe and compare the compensatory responses of healthy young and older adults to sequentially increasing upper-body perturbations. The scaling of plantarflexor muscular activity and minimum time-to-contact (TtC_{MIN}) was examined, and we determined whether TtC_{MIN} predictions of instability (stepping transitions) for the older subjects were similar to those we previously reported for younger subjects (Hasson et al. in J Biomech 41:2121–2129, 2008). We found that the older subjects stepped at a lower perturbation level than the younger subjects; however, this response was appropriate based on their greater center of mass (CoM) accelerations, which may have been caused by differences in pre-perturbation states between the age groups. Although the CoM acceleration increased linearly with perturbation magnitude, the amount of gastrocnemius and soleus muscular activity increased nonlinearly in both age groups. There were no differences in the maximum plantarflexor torque responses, suggesting that the maximum torque capabilities of the older subjects were not limiting factors. As previously demonstrated in the younger subjects, the older subjects showed a quadratic decrease in TtC_{MIN} with increasing perturbation magnitude. The vertices of the quadratics gave accurate predictions of stepping transitions in both age groups, even though the older subjects stepped at lower perturbation magnitudes. By probing the postural system's behavior through sequentially increasing upper-body perturbations, we observed a complementary nonlinear scaling of muscle activity and TtC_{MIN}, which suggests that subjects could use TtC or a correlate as an informational variable to help determine whether a step is necessary.

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Keywords Aging · Postural control · Balance · Electromyography · Time-to-contact · Plantarflexor · Perturbation

Introduction

Aging is associated with degradation of the neuromuscular system, including declines in maximal isometric muscle strength (Bemben et al. 1991; Frontera et al. 2000) and a slowing of muscle contraction velocity (Larsson et al. 1997; Hook et al. 2001; D'Antona et al. 2003). Such changes are related to decreases in the size and number of muscle fibers (Lexell et al. 1988), shifts towards slower motor units (Larsson and Ansved 1995; Lexell 1995), and a slowing of motor unit axon conduction velocity (Dorfman and Bosley 1979; Kanda et al. 1986). The sensitivity and accuracy of the visual, vestibular, and somatosensory sensory systems also decrease (Woollacott et al. 1986), resulting in delayed and possibly inaccurate information about the environment. Together, these physiological changes result in a system with reduced capacity and slower movements than younger adults.

Thus, it is not surprising that otherwise healthy older adults often have poorer balance control than younger adults, resulting in a decreased ability to respond to postural perturbations. Much of the evidence for age-related degradations of postural control comes from moving platform perturbation studies (Woollacott et al. 1986). Platform perturbations loosely mimic the situation where a person is standing on a bus or train that suddenly accelerates, causing backward or forward sway of the body

(Lin and Woollacott 2002). In response to sudden platform movement, older adults take longer to activate their muscles, and respond with a smaller initial burst of muscular activity (Woollacott et al. 1986; Manchester et al. 1989; Lin and Woollacott 2002). Older adults have also been shown to take compensatory steps to retain balance more frequently, and step in response to smaller perturbations than younger adults (McIlroy and Maki 1996; Pai et al. 1998; Mille et al. 2003).

The responses of individuals to such perturbations are influenced by the details of the platform movement (Brown et al. 2001), and may also depend on the location of the perturbing force. In translating platform experiments, the inertia of the body causes it to lag behind the accelerating feet, so the center of mass (CoM) approaches the base of support boundary. Although a rearward platform translation will cause the CoM and head to move forward relative to the ankle joint, the CoM and head could actually have rearward acceleration in a *global* reference frame (Horak et al. 1994; Runge et al. 1998). In contrast, perturbation forces applied to the upper back above the CoM will directly accelerate the upper body, CoM, and head forward, and the head's linear acceleration may be *greater* than the CoM's (given the head's increased distance from the ankle joint). An upper back perturbation would, therefore, elicit greater vestibular output due to increased head acceleration compared with a platform perturbation. Because the relative body kinematics and the pressure distribution beneath the feet would be similar in the two scenarios,[1] vestibular information may play a greater role in assessing the magnitude of an upper-body perturbation. Considering the age-related declines in vestibular acuity (Rosenhall and Rubin 1975), older adults may have greater difficulty responding to upper-body perturbations, and may need to adjust their muscular activation patterns accordingly.

After a perturbation occurs, one must quickly select an appropriate compensatory response. Presumably, this response is predicated on sensory information and a prediction of imminent postural stability or instability. The CoM time-to-contact[2] (TtC) is a measure which incorporates information about the instantaneous kinematic state of the CoM relative to the base of support boundary, and could be used by the postural control system to predict future instability (Carello et al. 1985; Riccio 1993; Slobounov et al. 1997; van Wegen et al. 2002; Hasson et al. 2008). Schultz et al. (2006) reported that TtC gives good predictions of stepping transitions in response to waist-pull perturbations in unimpaired older females. Recently, we found support for this notion from a dynamical systems perspective when healthy young adults were subjected to sequentially increasing upper-body perturbations (Hasson et al. 2008). In contrast to the randomized perturbation order used in the Schultz study, the sequential perturbation order allowed scaling and transitional behavior to be studied as the postural system was pushed towards its stepping threshold. We found that the minimum TtC (TtC_{MIN}) decreased quadratically with perturbation magnitude, with the minimum vertex of the quadratic relation predicting the transition from a stationary base of support to a stepping strategy. Thus, the quadratic relation described both the stepping transition and the changes in TtC_{MIN} in the perturbation trials leading up to the stepping transition. These results demonstrate that the central nervous system could use TtC_{MIN} information to predict the severity of postural perturbations in younger adults. Considering the neuromuscular system declines that accompany the aging process, we wondered how TtC_{MIN} would scale with perturbation magnitude in older adults, and whether TtC_{MIN} information would still be predictive of stepping transitions.

Therefore, the first aim of this study was to describe and compare the compensatory responses of young and older individuals to sequentially increasing perturbations applied to the upper back. Specifically, we examined how the timing and magnitude of the plantarflexor muscular activity scales with the severity of the perturbation. The second aim was to ascertain if there are differences between the age groups in how the minimum time-to-contact of the CoM relative to the support boundary (TtC_{MIN}) scales with the perturbation magnitude, and to determine whether TtC_{MIN} information predicts the transition from a stationary base of support to a stepping strategy similarly in young and older individuals.

Methods

Subjects

Twelve young [Y: 27 ± 3 years (range 21–31 years); 1.73 ± 0.11 m; 67.1 ± 12.5 kg] and 11 older [O: 71 ± 5 years (range: 66–79 years); 1.71 ± 0.10 m; 81.3 ± 15.0 kg] subjects participated in the experiment. A subset of TtC data on ten of the young subjects was reported earlier in Hasson et al. (2008). All subjects were healthy, were without musculoskeletal or neurological impairments, did not have a history of falls or balance problems, and did not have a fear of falling. The older

[1] However, the shearing forces applied to the subject as the platform accelerates may be different than those from an upper-body perturbation. Also, the upper-body perturbation includes an additional cutaneous sensory input at the location of the perturbing force (i.e. the upper back in the present study).

[2] As used in postural control research, "time-to-contact" has also been referred to as "(virtual) time-to-collision" (e.g. Slobounov et al. 1997) and "time-to-boundary" (e.g. van Wegen et al. 2002).

subjects were all independent community dwellers. All procedures were approved by our Institutional Review Board; subjects gave their written informed consent prior to participating in the experiment (including physician's clearance for all older subjects).

Instrumentation

Perturbations were delivered using a 15 kg freely swinging pendulum, which incorporated a load cell in-series with a shock absorber (Fig. 1). A lightweight wooden backboard supported by bearings was used to cushion the impact and restrict subjects' motion to the sagittal plane about the ankle joint. Subjects wore a safety harness tethered to the laboratory ceiling to prevent falling. White noise was played through headphones to mask the sound of pendulum release.

Reflective markers on anatomical landmarks (de Leva 1996) of the left side of the body were used to define head, trunk, leg, shank, foot, upper arm, and forearm segment motions. On the feet, bilateral heel and toe markers were used to delineate the base of support boundary and to detect stepping movements. A pair of markers defined the pendulum angle (Fig. 1, θ). Sagittal plane kinematics (sampled at 200 Hz) and ground reaction forces (1,000 Hz) were collected simultaneously using an eight-camera motion analysis system (Qualysis ProReflex^{TM} MCU240) and force platform (AMTI BP6001200-2000).

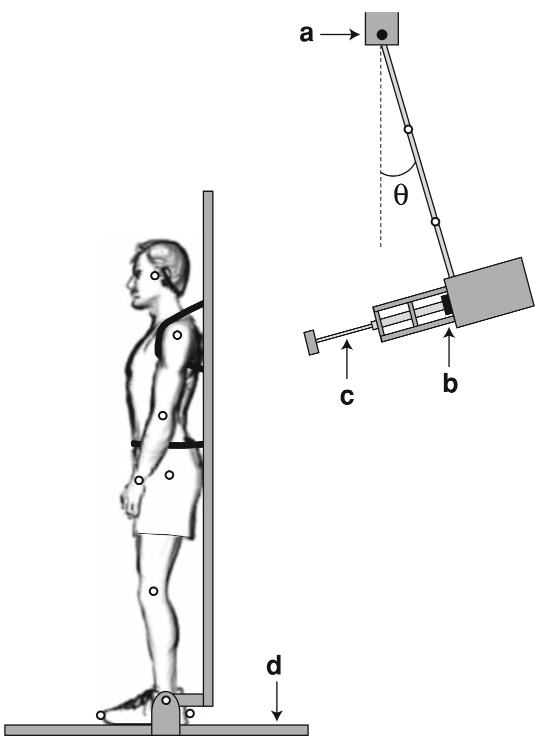

Fig. 1 Illustration of experimental setup showing backboard restraint and perturbation device (pendulum). Passive reflective marker locations are indicated by *small open black circles*. Straps around shoulders and waist were used to secure subject to the backboard. **a** Potentiometer, **b** load cell, **c** shock absorber, **d** force platform, θ pendulum angle. Adapted from Hasson et al. (2008) with permission

Bipolar preamplified (35×) surface electrode pairs (Ag–AgCl; 1 cm diameter; 20 mm interelectrode distance) were placed on the lateral gastrocnemius (GA) and soleus (SO) muscles, according to Cram et al. (1998). GA and SO produce the majority of plantarflexor torque, and are the primary muscles resisting forward postural sway after pendulum impact. The detected voltages were amplified (input impedance: >25 MΩ at DC; CMRR: 87 Db at 60 Hz; Therapeutics Unlimited) and band-pass filtered (20–4,000 Hz). Amplifier ranges were adjusted so that the EMG signal amplitudes within the ±5 V analog-to-digital converter range were maximized without clipping.

Protocol

Subjects were strapped to the backboard at the shoulders and waist, with feet positioned hip width apart and the ankle joint centers aligned with the backboard support bearings (Fig. 1). Foot position was marked to ensure consistency across trials. Subjects were told to fix their gaze on a point located at eye level on a wall 5 m away. They were instructed to resist the perturbations, resume quiet stance as quickly as possible, and only step if they felt a fall was imminent.

The pendulum was positioned at a static release angle with respect to vertical. A light signaled subjects to commence quiet stance; after a random delay of 2–6 s, the pendulum was released to swing forward, contacting the backboard/subject in the upper back region, accelerating the body forward. The first pendulum release angle was 10°. In subsequent perturbation trials, the release angle was increased sequentially in increments of 5° (light subjects, i.e. <70 kg) or 10° (heavier subjects) until subjects needed to step to prevent a fall. The different increments were used so that subjects would receive a similar number of perturbations. The perturbations were impulsive; after the pendulum shock absorber made contact, it rebounded away such that the perturbations were of short duration (~0.25 s). The pendulum only made contact once during each trial. Subjects received two sets of sequentially increasing perturbations; only the second set was analyzed to minimize learning effects. Only one trial was performed at each perturbation level.

Data reduction

Kinematic and kinetic data were smoothed at 10 Hz using a zero-lag fourth-order Butterworth digital filter; 10 Hz was chosen through power spectral analysis of the raw signals. Body segment CoM locations and inertial characteristics were estimated and used to determine the total body CoM position in the sagittal plane (de Leva 1996). The toe base of support boundary was determined from the positions of the toe markers, corrected to account for the marker radii. Foot and pendulum angles in the sagittal plane were calculated and numerically differentiated to compute angular velocities and accelerations. The ground reaction force center of pressure (CoP) was computed and Newton–Euler equations of motion were solved for the reaction forces and torque at the ankle (Elftman 1939). The average ankle torque from the initiation of the perturbation to the reversal of the forward CoM motion was calculated and scaled to each subject's mass.

The stepping trials were well defined for all subjects, with no forward foot motion in non-stepping trials. The initiation of a stepping response was identified by the initial increase in the anterior toe marker velocity of whichever foot moved first.

To control for differing subject inertias, we computed the "postural challenge" by dividing the peak pendulum velocity at impact by each subject's mass. To account for the effects of different CoM height, the pendulum was adjusted to strike each subject at 78% of their standing height.

For each perturbation trial, GA and SO muscle activity onset times were determined from the raw EMG time series using an automated double-threshold detector with parameters $r_0 = 1$, $P_{fa} = 0.01$, $m = 5$ (see Bonato et al. 1998 for details). Visual inspection was used to verify the chosen onset times; only a few manual corrections were necessary. The raw EMG signals were rectified and low-pass filtered at 20 Hz to produce linear envelopes, followed by numerical integration (IEMG) from pendulum impact to the reversal of forward CoM motion. The IEMG for each perturbation level was divided by the integration time to compute average IEMG, and expressed as a percentage of the average IEMG for the penultimate trial (last trial before stepping).

For each trial, a TtC time series was calculated based on the instantaneous anterior–posterior CoM position (distance to toe boundary), velocity, and acceleration. We used CoM rather than CoP for TtC because it is more relevant for these dynamic perturbation conditions (see Hasson et al. 2008 for a brief discussion). Based on the instantaneous CoM kinematics, the CoM trajectory was extrapolated (assuming constant acceleration) to predict the time when the CoM would contact the toe support boundary. From the CoM TtC time series for each perturbation trial, the minimum TtC (TtC_{MIN}) was selected for further analysis. We chose TtC_{MIN} because it provides salient information about the severity of the perturbation (Hasson et al. 2008), i.e. the point of maximum potential instability. See Appendix for more TtC details.

Data analysis

Perturbation magnitudes

For each trial, perturbation magnitude was expressed in three forms: the peak perturbation force in (1) Newtons and (2) as a percentage of body weight, and (3) the scaled postural challenge. The magnitudes of the largest perturbations were averaged across subjects within each age group.

Maximum postural responses

From the stepping trials, the maximum plantarflexor torque, maximum rate of torque development, and maximum anterior CoP position were computed to quantify the maximum postural responses. The maximum anterior CoM position was computed from the penultimate trials, because the CoM position continues forward during the stepping trials. The maximum CoP and CoM positions were expressed as a percentage of the distance from the ankle to the toe.

Scaling of measured variables

Both first (linear) and second (quadratic) order polynomials were used to explore the relationship between the postural challenge level and the following variables: (1) average CoM position 0.5 s before impact, (2) maximum anterior CoP position, (3) average ankle torque, (4) maximum CoM acceleration, (5) GA and SO onset latencies, (6) IEMG, (7) TtC_{MIN}, and (8) TtC_{MIN} latencies. Coefficients of determination (R^2) were computed to assess the strength of all linear and quadratic relations.

Stepping predictions

The vertices of the TtC_{MIN} quadratics represent a prediction for the postural challenge and TtC_{MIN} at which subjects would transition from a stationary base of support to a stepping strategy. The difference between the actual and predicted TtC_{MIN} stepping values was calculated for each subject. Pearson linear correlation coefficients (R_{PC}) were computed between each subject's actual and predicted stepping TtC_{MIN} and postural challenge, and for both the pooled subject data and the separate age groups.

Statistics

Normality was assessed graphically using normal probability plots. The R^2 values characterizing the strength of the relationships between the postural challenge and each of the measured variables were screened to identify variables with strong relationships ($R^2 > 0.8$), which were then evaluated at postural challenges of 0.5 and 0.75 deg/s/kg using a linear mixed effects model (Pinheiro et al. 2007) to determine whether differences existed between the age groups at similar challenge levels. Student's t tests were used to assess differences between the young and older groups for all other comparisons; the associated p values and 95% confidence intervals (CIs) were calculated. Reported standard deviations (SD) are between-subjects.

Results

Kinematics and kinetics

For both young and old age groups, there was no correlation between the CoM position prior to impact and the postural challenge level (Table 1), indicating that subjects did not systematically adjust their CoM position in anticipation of the perturbations. After collapsing across postural challenge levels, the average anterior–posterior pre-impact CoM position was not different between the groups [Y: 13.0 ± 5.7% of ankle to toe distance (toe = 100%); O: 14.8 ± 4.2%; $p = 0.414$, CI = [−6.1, 2.6]]. Post-impact, the CoM moved forward, with a smooth grading of the degree of CoM motion as perturbation magnitude increased (Fig. 2). In contrast, the CoP tended to shift forward quickly in all trials, remaining in this forward position for longer durations as the postural challenge increased.

While there were no differences between the age groups for the maximum forward CoM position in the penultimate trial, the younger subjects were able to shift their CoP farther forward in the stepping trial than the older subjects (Table 2). There were no group differences in the maximum plantarflexor torque or the rate of torque development (Table 2).

The maximum forward CoP position (relative to the ankle–toe distance) and average ankle torque increased nonlinearly as the postural challenge became greater in the young and older subjects (Fig. 3; Table 1); at equivalent challenge levels (0.5 and 0.75) neither variable was different between the age groups (Table 3). There was a linear relation between the maximum CoM acceleration and postural challenge level (Table 1). At the 0.5 challenge levels, the older subjects had higher acceleration values than the young, and there was an interaction effect such that this difference became larger at the 0.75 challenge level (Table 3).

The older subjects were forced to step at lower postural challenge levels that involved smaller body weight scaled pendulum impact forces than the younger group (Table 4). At the initiation of the stepping response, the average position of the CoM was anterior to (i.e. outside) the toe support boundary for the younger group (+35 ± 30 mm), but was posterior to (inside) the toe support boundary for the older group (−35 ± 68 mm; $p = 0.004$, CI = [−115, 25]). Only one younger subject initiated a step while the CoM was still inside the toe support boundary, while eight older subjects did so.

Table 1 Relationships between the postural challenge and selected kinematic, kinetic, and electromyographic (EMG) quantities

Variable	Type of it	Muscle	Young R^2	Older R^2	p value[a]	CI[b]
Challenge vs. pre-perturb. CoM position	Linear		0.15 ± 0.18	0.19 ± 0.21	0.627	[−0.21, 0.13]
Challenge vs. max. CoM accel.	Linear		0.98 ± 0.02[c]	0.93 ± 0.17[c]	0.379	[−0.06, 0.14]
Challenge vs. TtC_{MIN} latency	Linear		0.37 ± 0.47	−0.06 ± 0.52	0.051	[−0.01, 0.86]
Challenge vs. EMG onset latency	Linear	GA	−0.31 ± 0.32	−0.32 ± 0.39	0.946	[−0.30, 0.32]
		SO	−0.17 ± 0.36	−0.07 ± 0.36	0.520	[−0.41, 0.21]
Challenge vs. max. CoP position	Quadratic		0.92 ± 0.06[c]	0.89 ± 0.06[c]	0.227	[−0.02, 0.09]
Challenge vs. avg. ankle torque	Quadratic		0.94 ± 0.05[c]	0.86 ± 0.17[c]	0.115	[−0.02, 0.20]
Challenge vs. TtC_{MIN}	Quadratic		0.96 ± 0.03[c]	0.96 ± 0.03[c]	0.878	[−0.02, −0.02]
Challenge vs. scaled IEMG	Quadratic	GA	0.83 ± 0.20[c]	0.88 ± 0.09[c]	0.413	[−0.19, 0.08]
		SO	0.86 ± 0.22[c]	0.90 ± 0.10[c]	0.658	[−0.18, −0.12]

The coefficients of determination (R^2) are reported. Values are mean ± between-subjects standard deviation

GA gastrocnemius, *SO* soleus

[a] Young vs. older comparison of R^2 values

[b] Confidence intervals for the difference between young and older means

[c] Denotes a strong relationship

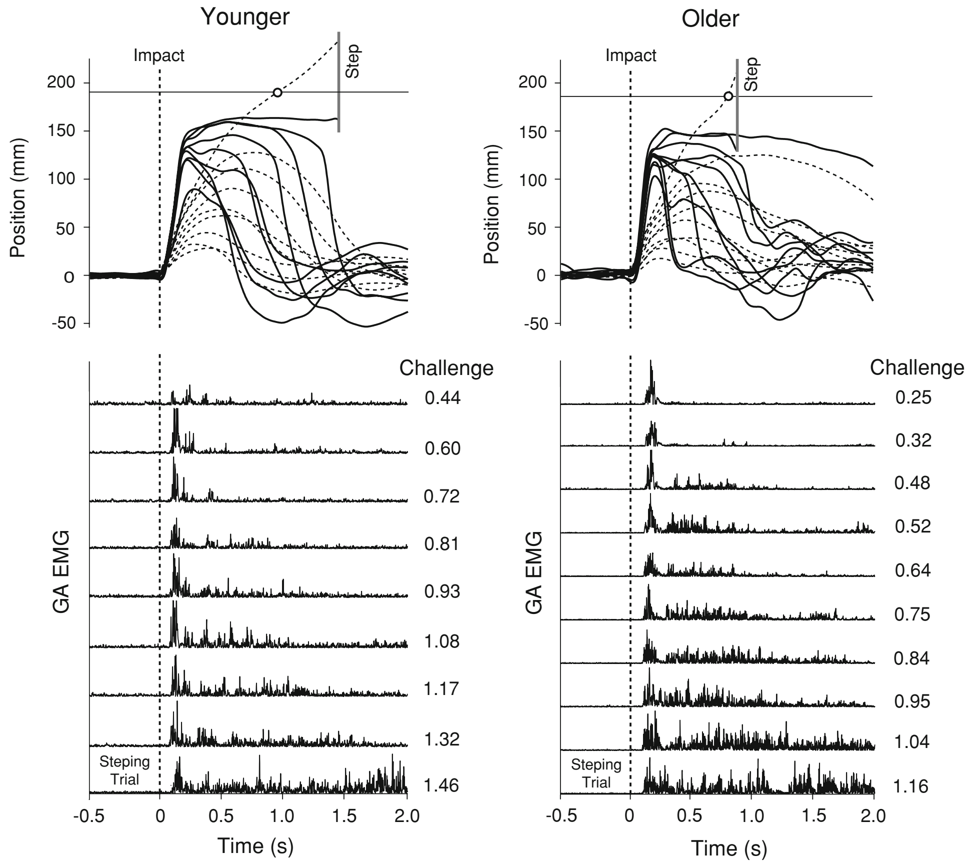

Fig. 2 Example anterior–posterior center of pressure (*solid lines*, *top graphs*) and center of mass (*dashed lines*, *top graphs*) kinematics, and gastrocnemius (GA) rectified electromyographic (EMG) responses to a series of increasing upper-body perturbations for a young (24 years) 56 kg female (*left*) and an older (68 years) 59 kg female (*right*). Position data are given with respect to the ankle joint center (ankle = 0 mm); the EMG data are plotted using the same vertical scale (raw rectified voltages). *Note*: although the majority of the older subjects initiated a forward step before their center of mass crossed their base of support boundary (denoted by *open circles* in *upper graphs*), the older subject shown in the figure did not

Table 2 Maximum center of pressure (CoP) and center of mass (CoM) positions, and maximum plantarflexor torques and rates of torque development

Variable	Young	Older	*p* value[a]	CI[b]
Max. CoM position (%)[c,d]	77.2 ± 14.5	66.9 ± 17.8	0.142	[−3.7, 24.3]
Max. CoP position (%)[c]	87.4 ± 3.0	76.6 ± 6.4	<0.0001	[6.5, 15.0]
Max. plantarflexor torque (N m)	137 ± 36	134 ± 41	0.880	[−31, 36]
Max. rate of torque development (N m/s)	1,312 ± 504	1,116 ± 307	0.278	[−170, 563]

Values are mean ± between-subjects standard deviation

[a] Young vs. older

[b] Confidence intervals for the difference between young and older means

[c] Expressed as a percentage of the ankle to toe distance (100% = toe)

[d] The maximum CoM position during the stepping trial was not included

EMG latencies and IEMG scaling

There was no clear relationship between the postural challenge and the EMG onset latencies for either age group (Table 1); therefore, the latencies were averaged across the postural challenge levels for each subject. Comparison of the averaged data revealed that GA and SO onset latencies were longer in the older subjects (Fig. 4c).

In contrast, the relationships between postural challenge level and the scaled IEMG were strong (Table 1; Fig. 4a). For ~65% of the subjects, the rate of IEMG increase (slope) became greater with larger postural challenges. However, some subjects produced different nonlinear (~22%), or linear (~13%) relations between IEMG and postural challenge. The changes in IEMG did not always follow the changes in the average ankle torque (Fig. 4d, e). There were no systematic differences between the age groups or muscles with respect to the shape of the relation. At the 0.5 postural challenge level, the IEMG was higher for the SO muscle in the older subjects compared to the

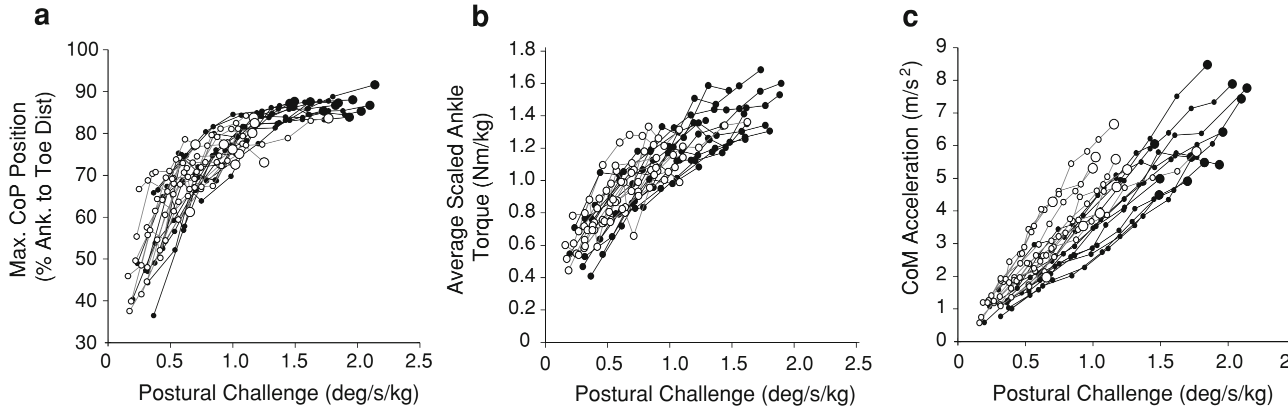

Fig. 3 Young (*black lines*, *filled circles*) and older (*gray lines*, *open circles*) relationships between the postural challenge and **a** maximum anterior center of pressure (CoP) position (expressed as a percentage of the distance from the ankle to the toe, 100% = toe); **b** average ankle torque (scaled to subject mass); **c** maximum center of mass (CoM) acceleration. *Enlarged circles* indicate stepping trials

young, and at the 0.75 challenge level, the IEMG for both GA and SO muscles was higher in the older subjects (Table 3; Fig. 4b).

Scaling of time-to-contact information and step prediction

As with the EMG latencies, there appeared to be no relationship between the postural challenge and the TtC_{MIN} latency (i.e. small R^2 values, Table 1). The TtC_{MIN} latency data were collapsed across postural challenge levels for each age group, but no age differences were observed (Y: 77 ± 5 ms; O: 76 ± 9 ms; $p = 0.711$, CI = [−5, 7]). The older subjects stepped at a lower postural challenge (Table 4; Fig. 5b), and their minimum TtC was longer than the younger subjects (Y: 196 ± 21 ms; O: 237 ± 37 ms; Fig. 5b). Overall, the quadratic functions fit the young and older experimental data equally well, with similar stepping prediction errors for both TtC and postural challenge (Fig. 6b). The correlations between the actual and predicted stepping minimum TtC were strong for the pooled data ($R_{PC} = 0.97$), and also for the separate young ($R_{PC} = 0.95$) and older ($R_{PC} = 0.97$) groups (Fig. 6b). The correlations between the actual and predicted stepping postural challenge were also strong for the pooled data ($R_{PC} = 0.92$); however, the correlation for the young subjects alone ($R_{PC} = 0.55$) was lower than for the older group ($R_{PC} = 0.90$). Across all challenge levels, the older subject data were shifted to the left (Fig. 6a), with shorter minimum TtCs for similar postural challenge levels (Table 3). For both younger and older subjects, the scaling patterns for TtC_{MIN} with increased postural challenge were opposite to IEMG; as the TtC_{MIN} decreased, the GA and SO IEMG increased (Fig. 7).

Discussion

Main findings

The perturbation responses clearly show that the older adults used a stepping strategy at a lower postural challenge than the younger subjects, which agrees with other studies (Pai et al. 1998; Mille et al. 2003). While this could be attributed to a deteriorating postural control system, the older subjects underwent larger CoM accelerations when subjected to equivalent postural challenges as the younger group. From this perspective, the need to step earlier was justified. Analysis of scaling behavior revealed that the CoM acceleration increased linearly with postural challenge level, but that plantarflexor muscle activity increased *nonlinearly* in both young and older subjects. This nonlinear scaling of muscular activity was coincident with changes in the average ankle torque and the maximum anterior displacement of the CoP, which together reflect the constraint imposed by the finite foot length distance over which the CoP can be shifted. As previously shown in younger subjects (Hasson et al. 2008), older subjects demonstrated quadratic scaling of TtC_{MIN} with postural challenge level, and the vertices of the quadratics gave accurate predictions of when the older subjects needed to take a compensatory step, albeit at lower postural challenge levels.

Plantarflexor torque capabilities

The maximum plantarflexor torque and rate of torque development were similar between the age groups, which are in agreement with other postural perturbation studies (Hall et al. 1999; Grabiner et al. 2005). This suggests that

Table 3 Kinematic, kinetic, and electromyographic (EMG) quantities with strong ($R^2 > 0.8$) linear and nonlinear relationships with postural challenge, evaluated at two discrete challenge levels (0.5 and 0.75)

Variable	Young	Older	*p* value
Challenge[a] vs. max. CoM accel. (m/s^2)			
At challenge: 0.5	1.70 ± 0.38	2.34 ± 0.50	
At challenge: 0.75	2.58 ± 0.47	3.49 ± 0.76	
Fixed effects			
Age			<0.001
Challenge level			<0.0001
Age × challenge level			0.005
Challenge vs. max. CoP position[b]			
At challenge: 0.5	60 ± 6	64 ± 4	
At challenge: 0.75	71 ± 4	71 ± 6	
Fixed effects			
Age			0.209
Challenge level			<0.0001
Age × challenge level			0.276
Challenge vs. avg. ankle torque (N m/kg)			
At challenge: 0.5	0.78 ± 0.13	0.86 ± 0.12	
At challenge: 0.75	0.99 ± 0.12	1.00 ± 0.16	
Fixed effects			
Age			0.172
Challenge level			<0.0001
Age × challenge level			0.872
Challenge vs. TtC_{MIN} (ms)			
At challenge: 0.5	433 ± 50	352 ± 45	
At challenge: 0.75	347 ± 36	277 ± 31	
Fixed effects			
Age			<0.001
Challenge level			<0.0001
Age × challenge level			0.738
Challenge vs. scaled IEMG[c]			
At challenge: 0.5			
GA	0.40 ± 0.18	0.54 ± 0.21	
SO	0.34 ± 0.17	0.57 ± 0.24	
At challenge: 0.75			
GA	0.52 ± 0.21	0.79 ± 0.30	
SO	0.44 ± 0.18	0.81 ± 0.36	
Fixed effects			
Age			0.003
Challenge level			<0.0001
Muscle			0.811
Age × challenge level			0.163
Age × muscle			0.077
Challenge level × muscle			0.615
Age × challenge level × muscle			0.906

Means (±between-subjects standard deviation) and the results from linear mixed effects models are reported

GA gastrocnemius, *SO* soleus

[a] Units for the postural challenge are deg/s/kg (mass of subjects)

[b] Center of pressure (CoP) position is expressed as the distance from the ankle to toe (100% = toe)

[c] The integrated EMG (IEMG) is scaled to the stepping trial values

the torque producing capabilities of the plantarflexor muscles is not a limiting factor with respect to the ability of healthy older subjects to resist postural perturbations. However, these results contrast with Thelen et al. (1996), who found age-related declines in the maximal torque and rate of torque development in isometric and concentric dynamometer efforts. This discrepancy may be the result of differing kinematic conditions, because the pendulum perturbations cause the activated plantarflexor muscles to lengthen as the body sways forward. There is evidence that eccentric strength is preserved in older adults (Hortobagyi et al. 1995; Klass et al. 2005), so one would not necessarily expect torque differences between the age groups. However, Loram et al. (2004) have shown that plantarflexor muscle fibers actually shorten during the small amplitude forward sways observed in quiet stance, despite the lengthening of the musculotendon complex. This "paradoxical" behavior is possible because the plantarflexor series elastic components are relatively compliant during the low forces levels acting in quiet stance, and therefore stretch at a greater rate than the entire musculotendon complex, allowing the muscle fibers to shorten. In the present study, subjects' ankle joints moved through a larger range of motion in response to upper-body perturbations compared to that occurring during quiet stance, and produced significantly greater amounts of plantarflexor torque, thus moving the nonlinear series elasticity into a much stiffer region. Therefore, in these perturbations, the muscles fibers would likely need to act eccentrically to contribute to the lengthening of the musculotendon complex.

Plantarflexor EMG latencies

A typical perturbation EMG response involved an initial activity burst from the GA and SO muscles, followed by a period of sustained activity that increased in duration and magnitude as the perturbations became greater. The muscle onset latencies were consistent between perturbation levels, averaging 68 ms for the young (both GA and SO), and increasing to 75 ms (GA) and 84 ms (SO) in the older subjects. These latency values agree with data from platform perturbations (Lin and Woollacott 2002). The onset latencies suggest that short latency monosynaptic reflexes are not visible in the EMG records (Dietz 1992). Instead, the latencies observed may reflect polysynaptic long latency reflexes, mediated by peripheral proprioceptive inputs from slower-conducting secondary (Group II) spindle afferents (Matthews 1984; Lundberg et al. 1987). EMG onset latencies were 7–16 ms longer for the older subjects, again consistent with other studies (Nardone et al. 1995), and possibly due to decreases in peripheral nerve conduction velocity with aging (Dorfman and Bosley 1979; Stetson et al. 1992). However, the functional consequences may be

Table 4 Maximum perturbation magnitudes

Variable	Young	Older	p value[a]	CI[b]
Postural challenge (deg/s/kg)	1.81 ± 0.24	1.08 ± 0.30	<0.001	[0.50, 0.96]
Perturbation force (N)	331 ± 77	300 ± 67	0.322	[−32, 93]
Perturbation force (% BW)	50.7 ± 10.2	38.3 ± 8.8	0.005	[4.1, 20.7]

Values are mean ± between-subjects standard deviation

[a] Young vs. older

[b] Confidence intervals for the difference between young and older means

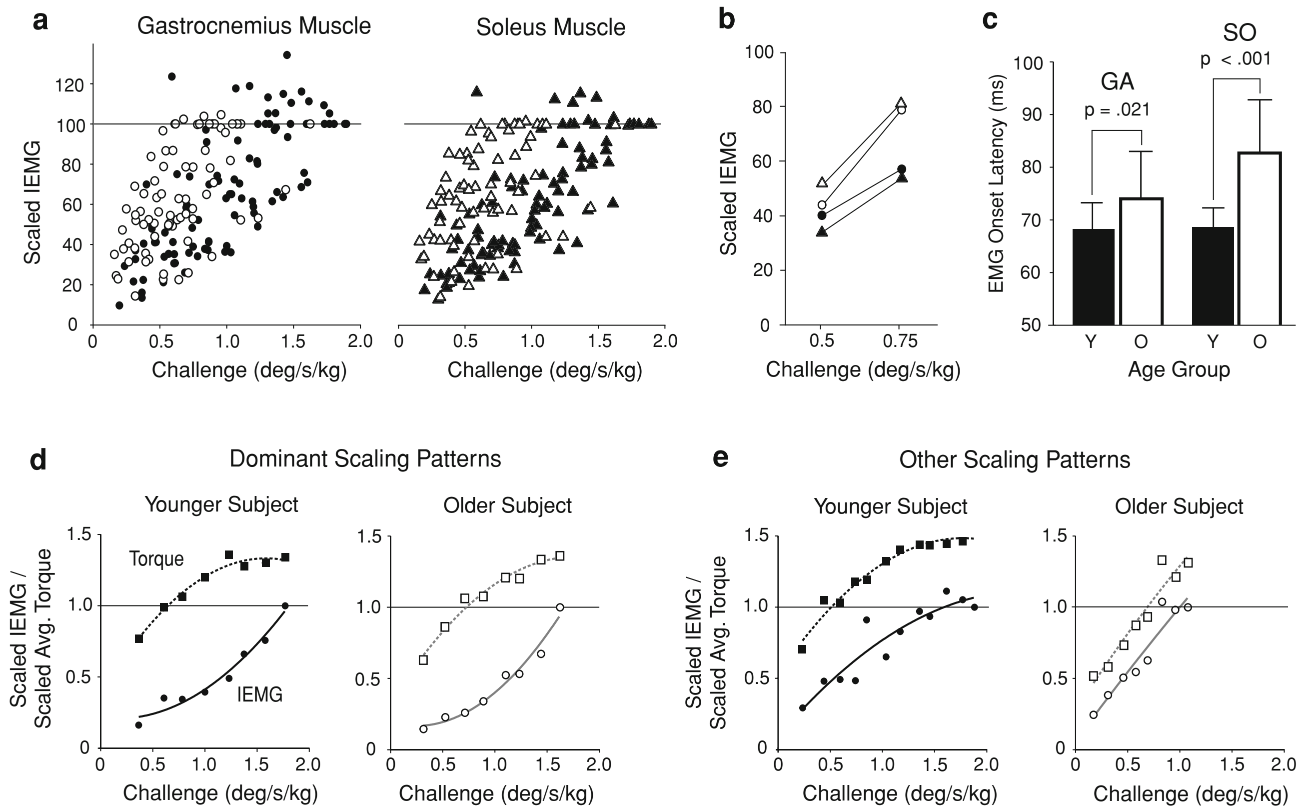

Fig. 4 **a** Scaled gastrocnemius (GA, *circles*) and soleus (SO, *triangles*) integrated EMG (IEMG) for young (*black symbols*) and older (*open symbols*) subjects as a function of postural challenge level. The IEMG was integrated from the initiation of the perturbation to the reversal of forward center of mass motion. **b** Mean GA (*circles*) and SO (*triangles*) scaled IEMG evaluated at 0.5 and 0.75 challenge levels. **c** GA and SO muscle onset latencies, relative to the perturbation onset (Y = young, O = older). Examples of the different relations between the postural challenge and the IEMG for the GA muscle for two young and two older subjects; both dominant (**d**) and non-dominant (**e**) scaling patterns are shown. For comparison, the scaled average torque is also shown (*dashed lines* and *squares*)

small here, as the CoM typically took at least 0.5 s (500 ms) before reaching the anterior base of support in the largest perturbations. Therefore, the 7–16 ms delay represents only a small percentage (<4%) of the available response time.

Scaling of integrated EMG (IEMG)

Both the age groups showed a positive relationship between IEMG magnitude and postural challenge level, which is in agreement with the results of Lin and Woollacott (2002) using rearward platform translations in young and older subjects. We also found that the slope of IEMG activity with respect to postural challenge level was higher in the older subjects. This greater rate of increase was likely due to the larger CoM accelerations experienced by the older adults for any given postural challenge level. Thus, the response strategy displayed by the older subjects was appropriate given the larger CoM accelerations, and should not necessarily be viewed as the result of a declining neuromuscular system.

For both age groups, the IEMG amplitude increased nonlinearly with rising postural challenge. To our knowledge, such a nonlinear relation between IEMG and perturbation magnitude has not been shown previously. Horak

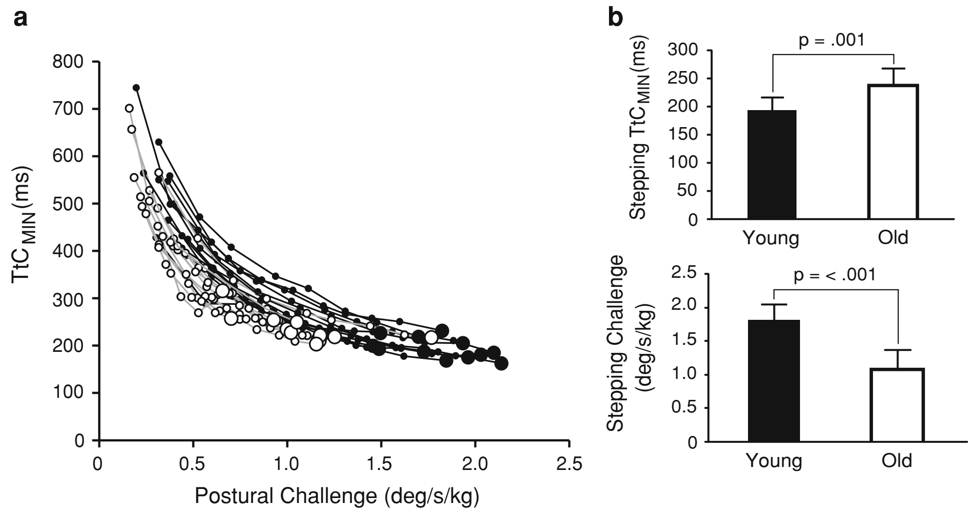

Fig. 5 **a** Individual minimum time-to-contact (TtC_{MIN}) values as a function of postural challenge for young (*black lines*, *filled circles*) and old (*gray lines*, *open circles*) subjects. *Enlarged circles* indicate stepping trials. **b** *Bar charts* showing differences between the age groups for the TtC_{MIN} and postural challenge for the stepping trials (mean + standard deviation)

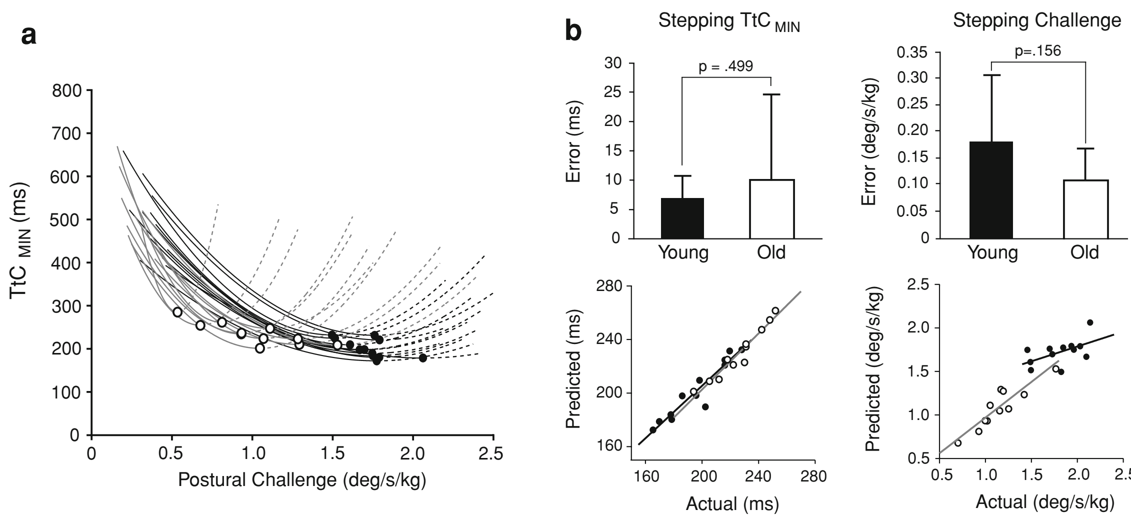

Fig. 6 **a** Quadratic equations fit to experimental data (young: *black lines*, older: *gray lines*). Stepping predictions depicted with *circles* (young: *filled circles*, older: *open circles*). **b** (*upper panels*) TtC_{MIN} and postural challenge stepping trial prediction error for young and older subject groups (mean + standard deviation). **b** (*lower panels*) Pearson linear correlations between the actual and predicted stepping minimum time-to-contact (TtC_{MIN}) (*left graph*) and postural challenge (*right graph*)

et al. (1989) and Horak and Diener (1994) studied postural responses to serially presented platform perturbations, but they assumed linear scaling and used linear regression in their analysis. One possible explanation of these different findings may be that Horak and colleagues used multiple fixed window sizes for the integration of the EMG. In contrast, we integrated the EMG from the perturbation onset to the reversal of forward CoM motion, which we considered to be a functionally relevant time period. Another explanation could be the differing inertial effects in their platform perturbations compared to our pendulum apparatus.

In the present study, for many subjects, the rate of IEMG increase (slope) became greater with larger postural challenges. This scaling pattern was similar in GA and SO muscles for both young and older subjects. This may be a reflection of their rapidly increasing sense of urgency, related to the CoM approaching a fixed base of support boundary with greater acceleration. Further, this scaling pattern closely mirrored the nonlinear decrease in TtC_{MIN} with increasing postural challenge (Fig. 7). However, other subjects had different IEMG scaling patterns but similar TtC_{MIN} patterns with increasing postural challenge.

Scaling of minimum time-to-contact information (TtC_{MIN})

In both the young and older subject groups, TtC_{MIN} decreased nonlinearly with increasing postural challenge. As expected, the older subjects stepped at a lower postural challenge, but at a longer TtC_{MIN} (Y: 196 ms vs. O: 237 ms). This could reflect a more conservative strategy

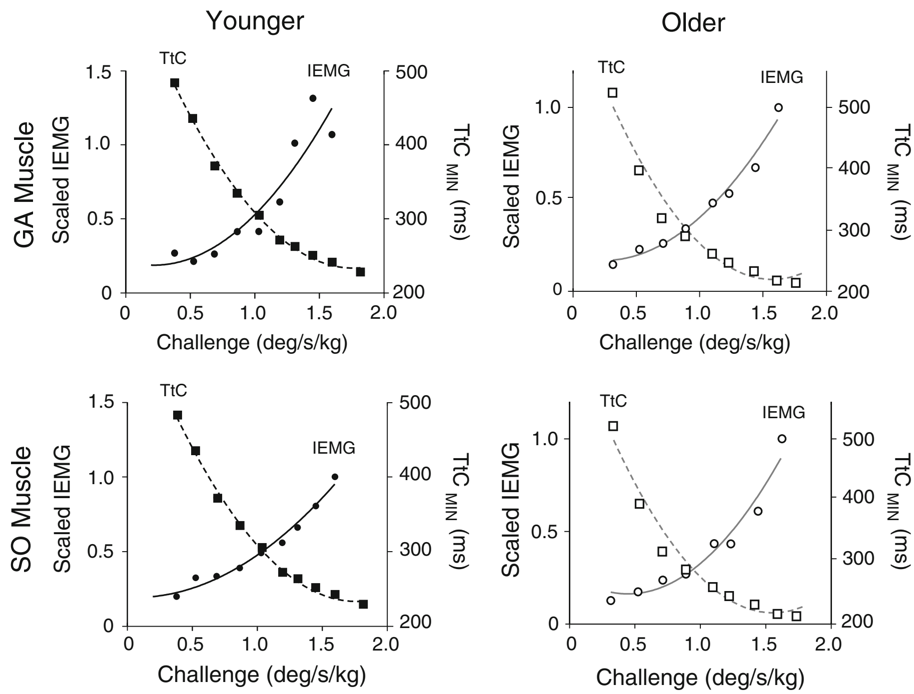

Fig. 7 Exemplar relationships between the postural challenge, minimum time-to-contact (TtC_{MIN}), and gastrocnemius (GA, *top graphs*) and soleus (SO, *bottom graphs*) integrated EMG (IEMG), for a younger (*left side*, *black lines*, *filled circles*) and older (*right side*, *gray lines*, *open circles*) subject. The IEMG was integrated from the perturbation onset to the reversal of the forward center of mass motion, and therefore the stepping trial is not included (however, the stepping trial is present in the TtC_{MIN} data). *Note*: the IEMG data presented in this figure represent the dominant scaling patterns; some subjects displayed other patterns (e.g. Fig. 4e)

used by the older subjects, as would the position of their CoM that was on average 70 mm closer to their ankle joints at the beginning of the stepping movement. The longer stepping TtC_{MIN} of the older subjects is consistent with observations of Schultz et al. (2006), who calculated optimal TtC stepping thresholds of young and older subjects in response to waist pulls. The TtC of their older subjects was about 90 ms longer than in the younger subjects (but not significantly different at $p < 0.05$).

The TtC_{MIN} latency after pendulum impact was similar for both age groups (~76–77 ms), and did not vary with increasing perturbation level. This short latency indicates that TtC_{MIN} information is available soon after the perturbation onset to both young and old subjects. Such early information on perturbation severity would be useful so that adequate time is available to make a compensatory response, such as a forward step, if necessary.

The correlations between the actual and predicted stepping TtC_{MIN} were strong for all subjects. Correlations between the actual and predicted stepping challenge level were strong for the older adults but weaker for the younger subjects. The weaker correlations in the young subjects could be because they withstood a larger range of postural challenges, which caused the quadratic equations to be "stretched" along the challenge axis, making the horizontal position of the vertex more variable. Overall, the TtC results agree with Schultz et al. (2006), who found the critical threshold TtC by optimizing for the greatest number of correct step predictions. Alternatively, we sequentially increased perturbation magnitude, fit quadratic equations to TtC_{MIN} data, and found that the vertices of the quadratic equations were predictive of stepping transitions. Together, these studies demonstrate that TtC information gives good predictions of stepping transitions in both young and older adults.

Pre-perturbation postural state

For the same postural challenge level, the TtC_{MIN} was shorter in the older subjects, primarily because they experienced higher peak CoM acceleration, which heavily influences TtC. Both TtC_{MIN} and peak CoM acceleration occurred ~75 ms after the perturbation, at roughly the same time as the earliest active muscle responses (average EMG onsets ~68–84 ms). Therefore, age-related differences in the TtC_{MIN} are likely due to varying pre-perturbation states, although the CoM position before impact was similar for the two age groups. One possible explanation could be age-related changes in plantarflexor musculotendinous stiffness. Onambele et al. (2006) reported that aging decreases the stiffness of the Achilles tendon, which could adversely affect the initial perturbation response; however, differences in this series elastic stiffness between young and older subjects only became significant at large force levels. Other studies have shown that muscles possess "short-range" stiffness due to series elasticity within the contractile tissue (Hill 1968; Rack and Westbury 1974; Nichols and Houk 1976). Short-range stiffness is greatest for small stretches, and does not have a large dependence on active force production (Loram et al. 2007b). Thus, short-range stiffness could play an important role in the early phases of the perturbation response (Loram et al. 2007a, b). However, we are unaware of studies showing changes in short-range stiffness with aging. Other possible explanations for age-related differences in pre-perturbation states include decreases in the number of active degrees of freedom (Newell 1998), a loss of complexity (Lipsitz and Goldberger 1992), or psychological factors (e.g. increased anxiety; Maki and Whitelaw 1992).

Significance of nonlinear scaling of muscular responses and stability information

In both young and older subjects, we observed nonlinear scaling of both the TtC_{MIN} and the muscular responses to increasing postural perturbations (Fig. 7). In the majority of subjects, these variables scaled together, i.e. as the TtC_{MIN} approached the stepping threshold the magnitude of the IEMG increased sharply. Could it be that the nervous system was using TtC (or a correlate) as an informational variable to scale the muscular response, as suggested by Carello et al. (1985)? Although we cannot answer that question definitively, studying the scaling behavior between TtC and postural responses might provide a way to address whether the nervous system actually uses TtC information to determine future instability. This is important given the growing interest in use of TtC to make assessments of postural control and stability (Haddad et al. 2006; Hertel et al. 2006; Slobounov et al. 2006; Haibach et al. 2007; Hertel and Olmsted-Kramer 2007).

To date, we know of no conclusive evidence that TtC is actually used in postural control, although the present data and our recent study (Hasson et al. 2008) demonstrate that TtC provides accurate estimates of future instability and therefore has the potential to serve as a "control parameter", triggering the shift from a stationary base of support to a stepping strategy in response to perturbations. The generation of such a TtC estimate likely involves sensory information from the visual, vestibular, and somatosensory systems, which may be combined in an internal forward model to predict future postural conditions. However, the degree to which the different sensory systems contribute to TtC estimates is unknown at present, as these were not assessed in this study.

Limitations

Although upper-body perturbations are commonly encountered during everyday activities, our experimental protocol employed restrictions to control confounding variables, and therefore may not replicate perturbations occurring in a more ecological setting. In the present study, a rigid backboard was used to limit motion to the ankle joint and distribute the impact force; the observed responses may be different if more complex body kinematics are permitted (e.g. hip motion). We used a sequential perturbation ordering to study scaling and transitional behavior in response to anticipated perturbations, so the results may not extend to random, unexpected perturbations. Another limitation is that it may not be feasible to give large magnitude perturbations to frail individuals. However, the quadratic scaling of TtC_{MIN} seems robust, and may therefore enable stepping threshold prediction based on a series of small perturbations.

Conclusions

Both young and older subjects demonstrated a nonlinear scaling of the neuromuscular response to upper-body perturbations delivered in a stepwise increasing fashion. The older subjects took a compensatory step at a lower postural challenge level than the younger subjects because they experienced greater accelerations at comparable postural challenge levels. Both age groups appeared to scale their responses appropriately with respect to the perturbation magnitude. As previously shown in the younger subjects, the minimum time-to-contact (TtC_{MIN}) decreased quadratically in the older subjects, and the vertices of the quadratics predicted the transition from a stationary base of support to a stepping strategy.

Acknowledgments The authors would like to thank Catherine Gariépy and Luis Rosado for assistance with data collection and reduction. This research was supported by a Ruth L. Kirschstein National Research Service Award (CJH; National Institutes of Health; 1F31EB005073), and National Institutes of Health Grant R03AG026281 (GEC).

Appendix

The perturbation force, anterior–posterior center of mass (CoM) kinematics, and the corresponding time-to-contact (TtC) for a young subject in response to a postural perturbation are illustrated in Fig. 8a. The TtC was first calculated at each time-step as

$$\mathrm{TtC} = \frac{-v \pm \sqrt{v^2 - 2a(p - p_{\mathrm{toe}})}}{a} \tag{1}$$

where p, v, and a are the instantaneous anterior–posterior positions, velocities, and accelerations of the CoM, respectively, and p_{toe} is the anterior–posterior location of the toe boundary marker. In the present study, we only considered one-dimensional (anterior–posterior) motion in the TtC calculation. However, the TtC can also be calculated in two dimensions (e.g. to anterior–posterior and

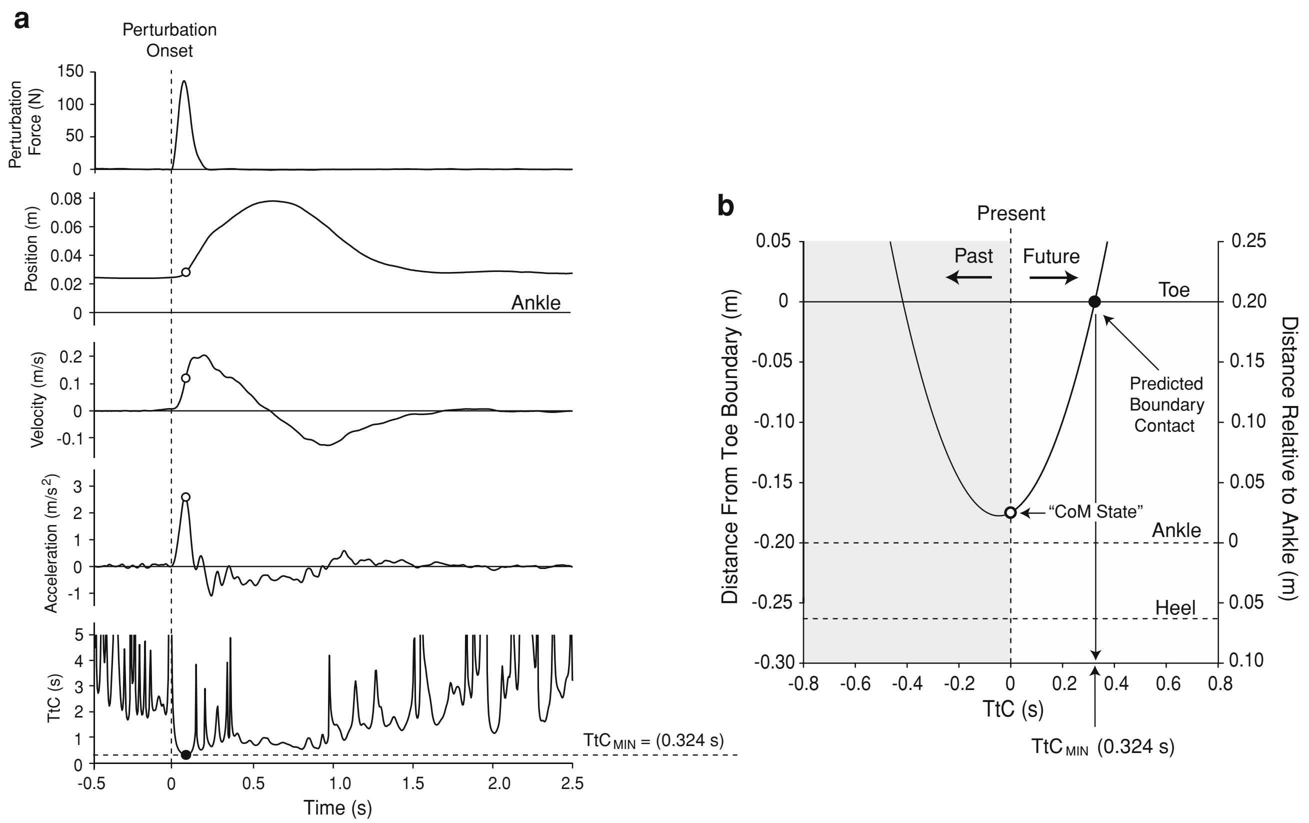

Fig. 8 **a** Perturbation force, anterior–posterior center of mass kinematics, and the time-to-contact (TtC) in response to a postural perturbation (causing forward sway) for a young subject. The *open circles* denote the instantaneous center of mass kinematics associated with the minimum TtC (TtC_{MIN}, *solid circle*). Note that the center of mass position is given with respect to the ankle joint (ankle = 0 m). **b** Schematic representing the TtC calculation for one instant in time, corresponding with TtC_{MIN} indicated by the *solid circle* in the TtC time series. See text for details

medial–lateral base of support boundaries); see Slobounov et al. 1997 for details.

Let us consider an example of the TtC calculation for a single point in time (0.085 s after the start of the perturbation, solid circle in Fig. 8). The instantaneous CoM kinematics (denoted by open circles in Fig. 8) are as follows:

$$p = 0.026\ \text{m},\quad v = 0.120\ \text{m/s},\quad a = 2.59\ \text{m/s}^2 \tag{2}$$

Solving Eq. 1 using a toe boundary position of $p_{toe} = 0.20$ m [the CoM and toe positions are referenced to the ankle in these calculations (ankle = 0 m)] gives a positive and negative solution:

$$\text{TtC} = [-0.416\ \text{s},\ 0.323\ \text{s}] \tag{3}$$

These solutions are depicted graphically in Fig. 8b. The instantaneous CoM state (defined by the given kinematics) is shown as an open circle, and these kinematic conditions are extrapolated in the past (negative time) and future (positive time) directions (the zero crossings indicate the solutions). The negative solution is discarded; the positive solution represents the time it would take the center of mass to contact the toe base of support boundary if it accelerated at a constant rate. This positive solution, denoted by a solid circle, is the predicted TtC for that one instant in time.

Although this example is for a single time point, the TtC calculation is performed at each time point, generating a TtC time series (Fig. 8a). In the present study, the TtC time series was then searched and the minimum selected (TtC_{MIN}) for further analysis. For convenience, in this example, the chosen data point corresponds with TtC_{MIN}, occurring 0.085 s after the perturbation initiation.

Note that it is necessary to calculate the TtC to both the anterior (toe) and posterior (heel) base of support boundaries to have a "complete" TtC time series (as shown in Fig. 8a). In this case, whichever TtC is shorter (to the toe or heel) is chosen at each time point. For the present study, only TtC to the anterior boundary was of interest.

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