Journal of Physiology (2002), **542.2**, *pp.* 643–663
© The Physiological Society 2002

DOI: 10.1113/jphysiol.2001.015644
www.jphysiol.org

Journal of Physiology

Age-dependent variations in the directional sensitivity of balance corrections and compensatory arm movements in man

J. H. J. Allum *, M. G. Carpenter *†, F. Honegger *, A. L. Adkin *† and B. R. Bloem ‡

* *Department of Otorhinolaryngology, University Hospital, Basel, Switzerland,* † *Department of Kinesiology, University of Waterloo, Canada and* ‡ *Department of Neurology, University Medical Centre St Radboud, Nijmegen, The Netherlands*

We investigated the effects of ageing on balance corrections induced by sudden stance perturbations in different directions. Effects were examined in biomechanical and electromyographic (EMG) recordings from a total of 36 healthy subjects divided equally into three age groups (20–34, 35–55 and 60–75 years old). Perturbations consisted of six combinations of support-surface roll (laterally) and pitch (forward–backward) each with 7.5 deg amplitude (2 pure pitch, and 4 roll and pitch) delivered randomly. To reduce stimulus predictability further and to investigate scaling effects, perturbations were at either 30 or 60 deg s^{-1}. In the legs, trunk and arms we observed age-related changes in balance corrections. The changes that appeared in the lower leg responses included smaller stretch reflexes in soleus and larger reflexes in tibialis anterior of the elderly compared with the young. For all perturbation directions, onsets of balance correcting responses in these ankle muscles were delayed by 20–30 ms and initially had smaller amplitudes (between 120–220 ms) in the elderly. This reduced early activity was compensated by increased lower leg activity after 240 ms. These EMG changes were paralleled by comparable differences in ankle torque responses, which were initially (after 160 ms) smaller in the elderly, but subsequently greater (after 280 ms). Findings in the middle-aged group were generally intermediate between the young and the elderly groups. Comparable results were obtained for the two different stimulus velocities. Stimulus-induced trunk roll, but not trunk pitch, changed dramatically with increasing age. Young subjects responded with early large roll movements of the trunk in the opposite direction to platform roll. A similarly directed but reduced amplitude of trunk roll was observed in the middle-aged. The elderly had very little initial roll modulation and also had smaller stretch reflexes in paraspinals. Balance-correcting responses (over 120–220 ms) in gluteus medius and paraspinals were equally well tuned to roll in the elderly, as in the young, but were reduced in amplitude. Onset latencies were delayed with age in gluteus medius muscles. Following the onset of trunk and hip balance corrections, trunk roll was in the same direction as support-surface motion for all age groups and resulted in overall trunk roll towards the fall side in the elderly, but not in the young. Protective arm movements also changed with age. Initial arm roll movements were largest in the young, smaller in the middle aged, and smallest in the elderly. Initial arm roll movements were in the same direction as initial trunk motion in the young and middle aged. Thus initial roll arm movements in the elderly were directed oppositely to those in the young. Initial pitch motion of the arms was similar across age groups. Subsequent arm movements were related to the amplitude of deltoid muscle responses which commenced at 100 ms in the young and 20–30 ms later in the elderly. These deltoid muscle responses preceded additional arm roll motion which left the arms directed ‘downhill’ (in the direction of the fall) in the elderly, but ‘uphill’ (to counterbalance motion of the pelvis) in the young. We conclude that increased trunk roll stiffness is a key biomechanical change with age. This interferes with early compensatory trunk movements and leads to trunk displacements in the direction of the impending fall. The reversal of protective arm movements in the elderly may reflect an adaptive strategy to cushion the fall. The uniform delay and amplitude reduction of balance-correcting responses across many segments (legs, hips and arms) suggests a neurally based alteration in processing times and response modulation with age. Interestingly, the elderly compensated for these ‘early abnormalities’ with enlarged later responses in the legs, but no similar adaptation was noted in the arms and trunk. These changes with age provide an insight into possible mechanisms underlying falls in the elderly.

(Received 18 December 2001; accepted after revision 2 May 2002)

Corresponding author J. H. J. Allum, University HNO-Klinik, Petersgraben 4, CH-4031 Basel, Switzerland.
Email: jallum@uhbs.ch Website: www.unibas.ch/audio/neurooto

Many studies on the effects of ageing on postural responses have emphasized changes occurring in sensory systems and the speed with which information is processed by the CNS to yield appropriate balance corrections. Balance corrections could well be hindered by altered sensory thresholds and age-related decreases in nerve transmission times associated with reduced afferent nerve conduction velocities. Loss of muscle strength and a slowing of contraction speed are also well-known changes with age (Whipple *et al.* 1987) which may alter the capacity to produce a rapid change in force for balance corrections in the elderly. Perhaps more important than loss of force may be the increase with age of joint stiffness, leading to a change in the ability to respond to perturbations using the same interlimb coordination as the young. Although, associations between age-related changes and fall prevalence in the elderly have been suggested (Lord *et al.* 1991, 1994), a strong relationship between these factors has not been directly established.

Many investigators have used posturography (quantified assessment of balance control, using a fixed or a tilting support surface equipped with force transducers) to elucidate the mechanisms associated with falls in the elderly. Although assessment of quiet stance can show clear changes in elderly persons (e.g. an increase of static sway, see Brocklehurst *et al.* 1982; Lord *et al.* 1991; Gill *et al.* 2001), many feel that postural control is best probed using controlled perturbations of upright stance (Furman *et al.* 1993). The majority of these ‘dynamic posturography’ studies used postural perturbations in a single direction, usually the anterior–posterior (pitch) plane, and more recently the mediolateral (roll) plane. The results of these studies revealed a host of postural changes in elderly subjects, including an increase of induced sway (Stelmach *et al.* 1989*a, b*), delayed onsets and amplitude changes of automatic postural responses in ankle muscles (Maki, 1993; Nardone *et al.* 1995), delayed and slightly weaker torques about the ankle joint (Shepard *et al.* 1993; Keshner *et al.* 1993; Rivner *et al.* 2001), abnormal compensatory stepping reactions (Maki & McIlroy, 1998), a narrowing of the limits of stability (Murray *et al.* 1975) and an impaired habituation across serial trials (Stelmach *et al.* 1989*b*).

The age-related changes of automatic postural responses to pitch plane perturbations in ankle muscles were generally modest (Woollacott, 1986; Stelmach *et al.* 1989*b*) and it has been questioned whether these small changes are sufficient to produce instability and cause a possible fall (Alexander *et al.* 1992). Indeed, the associations between pitch plane posturography findings and faller status were often weak or even absent in most studies (Overstall *et al.* 1977; Brocklehurst *et al.* 1982; Fernie *et al.* 1982; Bartlett *et al.* 1986; Lichtenstein *et al.* 1988, 1990; Campbell *et al.* 1989; Maki *et al.* 1990, 1991; Fife & Baloh, 1993; Baloh *et al.* 1995*a*, 1998).

One explanation for the poor association between previous posturography findings and falling may be the restricted use of balance perturbations to those along a pitch plane. Recent evidence suggests that perturbations with a roll component may be more representative of conditions which induce falls in everyday life. For example, analysis of spontaneous or induced sway in the mediolateral plane appears to correlate better with faller status than anterior–posterior sway (Maki *et al.* 1994; Williams *et al.* 1997; Lord *et al.* 1999). In fact, a large proportion of falls in the elderly have been found to involve lateral motion (Topper *et al.* 1993; O’Neill *et al.* 1994; Maki *et al.* 1994, 1996) and are associated with the genesis of hip fractures (Greenspan *et al.* 1994). Lateral perturbations may be more destabilizing because they require a more complex coordination of muscle responses in the left and right side of the body (Carpenter *et al.* 1999) and therefore place a greater demand on the processing requirements of the CNS. For example, when the support surface tilts, the ‘downhill’ leg must extend and the ‘uphill’ leg must flex to regain upright stance again. Furthermore the coordination of differing pitch and roll trunk dynamics must be achieved (Carpenter *et al.* 2001). Thus proprioceptive information elicited by multidirectional stance perturbations may well be more difficult for the elderly to process than that coming from a pure pitch plane perturbation. Similarly, adequate balance corrections in two planes may be more difficult to generate.

A further improvement to previous posturographic studies would be to expand the analysis of postural responses beyond the traditionally emphasized ankle muscle responses. Restricted analysis of ankle muscles ignores the contribution of both trunk muscle activity and compensatory arm movements to balance corrections. More rapid trunk roll than pitch movements are required to compensate for falls with both roll and pitch components (Carpenter *et al.* 1999). If the elderly are less flexible in lateral bending than the young, then a study of responses to roll perturbations would provide better insights on changed body mechanics with age than studies of pitch plane perturbations, especially as the trunk appears to be more compliant in roll than pitch in young subjects (Carpenter *et al.* 1999).

Rapid arm movements are also important components of the natural defence against falls. Preliminary work indicates that arm muscle responses can in fact precede those of leg muscles and effectively help to prevent a fall or cushion the impact (McIlroy & Maki, 1994, 1995). Analysis of such arm movements would also be clinically relevant, because wrist fractures are typically due to a fall on the outstretched hand (Melton *et al.* 1988; Nevitt & Cummings, 1993; Chiu & Robinovitch, 1998). A study of ageing effects on the ability to execute appropriate trunk motion and protective arm responses to multidirectional perturbations may provide greater insights into the effects of central nervous system (CNS) slowing on the generation of balance commands than a study on ankle muscle responses alone.

We have, therefore, studied postural responses to randomly delivered multidirectional perturbations in elderly subjects, and compared their responses to those of middle-aged and young subjects. Special emphasis was laid on the analysis of trunk control and protective arm movements after having discovered major differences between the trunk motion of one elderly patient and young controls (Bloem *et al.* 2002). In addition, knowing that persons often adapt to chronic balance impairment we analysed if and how elderly subjects compensated for age-related decline in postural control.

METHODS

We investigated the balance-correcting responses of 36 healthy subjects (18 male, 18 female) divided equally into young (20–34 years old), middle-aged (35–55 years old) and elderly (60–75 years old) groups. All subjects gave witnessed informed and written consent to participate in the experiment according to the Declaration of Helsinki. The Institutional Review Board of the University Hospital in Basel approved the study.

Outcome measures

We obtained EMG and biomechanical outcome measures using previously described techniques (Carpenter *et al.* 1999). To record EMG signals, pairs of silver–silver chloride electrodes were placed ~3 cm apart along the muscle bellies of left tibialis anterior, left soleus, and bilaterally on gluteus medius, paraspinals at the L1–L2 level of the spine, and medial deltoid muscles. EMG amplifier gains were kept constant and pairs of electrodes and lead lengths assigned to individual muscles were not changed between subjects. Support-surface reaction forces of the left foot were measured from strain gauges embedded within the rotating support. The strain gauges were located under the corners of the plate supporting the left foot. From these forces, the anterior–posterior (A–P) and mediolateral ankle torques were calculated for the left foot. Trunk angular velocity in the same pitch and roll planes defined by the planes of support-surface rotation was collected using Watson Industries transducers (±300 deg s^{-1} range) mounted onto a metal plate that hung at the level of the sternum from shoulder straps that wrapped around the shoulders back and chest. Two similar Systron-Donner angular velocity transducers (Inglewood, CA, USA) measured movements of the left upper arm in the pitch and roll directions of support-surface rotation. These transducers had a range of ±200 deg s^{-1} and noise specification of 0.04 deg s^{-1} (average standard deviation). The transducers were attached to a 10 cm long metal plate curved to the radius of the arm. The plate was strapped to the lateral aspect of the left upper arm using an elasticized bandage. To measure lower leg angle in the pitch plane a lightweight metal rod was fixed with an adjustable strap to the lateral aspect of the left tibia, ~4 cm below the level of the lateral condyle. The rod was connected to a potentiometer located on the pitch axis of the platform.

Procedure

The subject's feet were lightly strapped into heel guides fixed to the top surface of the dual-axis rotating platform. The guides were adjusted in the A–P direction to ensure that the ankle joint axis was aligned with the pitch axis of the rotating platform. The roll axis had the same height as the pitch axis and passed between the feet. Just prior to the experiment, subjects were asked to assume their 'preferred' standing posture with their arms hanging comfortably at their sides. At each individual's 'preferred-stance' position, we measured the low-pass filtered (5 Hz) A–P torque from the two strain gauge systems embedded in the surface of the rotating platform. This was then treated as the reference value for preferred stance for the remainder of the experiment.

The experiment consisted of two series of 44 perturbations each. The first trial of each series was excluded from further analysis to reduce habituation effects (Keshner *et al.* 1987). The remaining 86 perturbations consisted of randomized combinations of six different perturbation directions and two different perturbation velocities (either 30 or 60 deg s^{-1}), all at a constant amplitude of 7.5 deg. The six perturbation directions included two that were purely in the pitch plane (forward or 0 deg; and backward or 180 deg in our notation; often called toes-down or toes-up, respectively, in the literature). For the four additional perturbation directions, pitch stimuli were combined with leftward and rightward roll components to form 'forward right' (45 deg), 'backward right' (135 deg), 'backward left' (225 deg) or 'forward left' (315 deg) perturbations (see Fig. 1). Each of the 12 different combinations of perturbation direction and velocity were randomly presented seven or eight times throughout the two series of perturbations. Each perturbation was preceded by a random 5–20 s delay. During this period, subjects were asked to monitor an oscilloscope, which was located at eye level, ~1 m in front. This oscilloscope displayed online the low-pass filtered A–P torque, which was measured as described above. Using this visual feedback, subjects were required to maintain AP ankle torque within a range of ±1 N m from their preferred-stance reference value. The 5–20 s interstimulus delay was initiated automatically once the platform had returned to its original prestimulus position and the subject had regained and maintained his preferred vertical position as monitored by A–P ankle torque reading. In response to each rotational perturbation, subjects were instructed to recover their balance as quickly as possible. Three handrails (generally 80 cm high but adjustable to the hand height of the subject) were located at a distance of 40 cm to the sides and to the front of the platform centre. Subjects were informed they were allowed to grasp the handrails if needed. Two assistants (one behind and one to the side of the subjects) were present to lend support in case of a fall. To minimize fatigue, all participants were given a 2–3 min seated rest after the 22nd trial of each series. A longer seated rest period (5 min) was provided between each series.

Data analysis

All EMG and biomechanical recordings were initiated 100 ms prior to perturbation onset and had a sampling duration of 1 s. EMG recordings were band-pass analog filtered between 60–600 Hz, full wave rectified, and low pass filtered at 100 Hz prior to sampling at 1 kHz. All biomechanical data were sampled at 500 Hz after passing through anti-aliasing filters and digitally low-pass filtered off-line at 25 Hz using a zero phase-shift 10th-order Butterworth filter.

Following analog to digital conversion of the data, all biomechanical and EMG signals were averaged offline across each perturbation direction and velocity. Zero latency was defined as the first inflexion of ankle rotation velocity and did not vary with direction or subject. Subject averages were pooled to produce population averages for a single direction and velocity combination (as shown in Figs 2, 3, 6 and 10). Average trunk angular velocity was calculated over time intervals between 90–130 and 180–220 ms. All angular velocities (two each for the trunk and arm) were integrated off-line using trapezoid numerical integration to yield angular displacement. The difference between the angle value at 0 and 700 ms was employed as a measure of the body link angular change caused by the support-surface rotation. The same difference was used to measure angle changes of the lower leg. Angular displacements of the arm were calculated relative to the trunk by subtracting the arm position from the trunk position. Ankle torque changes were calculated between 160–260 and 280–380 ms.

Onset latencies were analysed for directions that elicited primary balance-correcting responses in each particular muscle. For each subject, all the EMG traces for one direction were displayed to the operator on the computer screen. EMG latencies were determined using a semi-automatic computer algorithm that selected the first point at which each trial's profile exceeded and remained longer than 50 ms above a threshold greater than two standard deviations above background muscle activity (BGA), calculated over the 100 ms period preceding perturbation onset. Each latency was first selected by the algorithm and then approved or manually corrected following inspection by the operator.

Small but generally insignificant differences in BGA were noted between the age groups. Effects of prestimulus BGA may confound between-group comparisons for stretch reflex and automatic balance correcting amplitudes (Bedingham & Tatton, 1984; Allum & Mauritz, 1984). Therefore, EMG areas were corrected by subtracting the average amount of BGA (measured over a 100 ms period prior to perturbation onset) from the overall response amplitude. This approach largely eliminates influences of prestimulus BGA (Bloem *et al.* 1993). Corrected EMG areas were calculated using trapezoid integration within predetermined time intervals associated with stretch reflex (40–100 or 80–120 ms from stimulus onset), and balance-correcting responses (120–220 ms) (Carpenter *et al.* 1999). We also analysed secondary balance-correcting responses (240–340 ms) and stabilizing responses (350–700 ms).

Our primary analyses concerned between-groups comparison for ageing effects. To examine differences between different perturbation directions and between different velocities, we used a mixed ANOVA model (group × direction × velocity) for both EMG and biomechanical data after checking that distributions of EMG response areas and biomechanical data were not skewed, but normally distributed. Significant main ageing and interaction effects were further explored using *post hoc* comparisons using Student's t test with a Bonferroni correction to account for the effect of comparing three populations at once. ANOVA and Bonferroni tests with $P < 0.05$ were considered significant.

RESULTS

Ankle muscle responses to backward pitch rotations of the support surface form the overwhelming majority of descriptions in the literature concerning the effect of age on balance corrections. Our description of changes with age commences therefore at the ankle joint, extending the prior knowledge on age-related effects on muscles and torques at this joint to forward pitch and combined roll and pitch directions. Trunk rotations in response to support surface combined roll and pitch proved to be much more age dependent than lower leg responses. These trunk changes, as well as accompanying alterations in responses of the trunk and hip muscles, comprise the next section in our description. Finally, because arm responses were highly dependent on initial trunk roll movement in each age group we tested, these results form the concluding part of our results section.

Changes in pitch plane sensitivity of ankle muscle responses with age

Pure backward rotation of the support surface (180 deg direction in our notation, see Fig. 1) caused the lower leg to be forced backwards and the trunk to pitch forward (Fig. 2). The amount of lower leg rotation (in pitch) over the first 100 ms was the same in all age groups as was the increase in ankle torque over the same time period. Forward, toe-down, rotations caused the lower leg to rotate initially forward and the trunk to pitch backward. As seen with backward rotations of the support surface, there were also no differences across age groups in the initial (first 100 ms) changes in lower leg angle and ankle torque for forward rotations (Fig. 3) which suggests, based on the work of Allum & Mauritz (1984), that ankle stiffness was not different across the age groups. Otherwise age-differences in the rise of ankle torque from stimulus onset to end should have been observed. Thus the small, but non-significant (F(2, 30)=1.37, $P < 0.27$) increase in

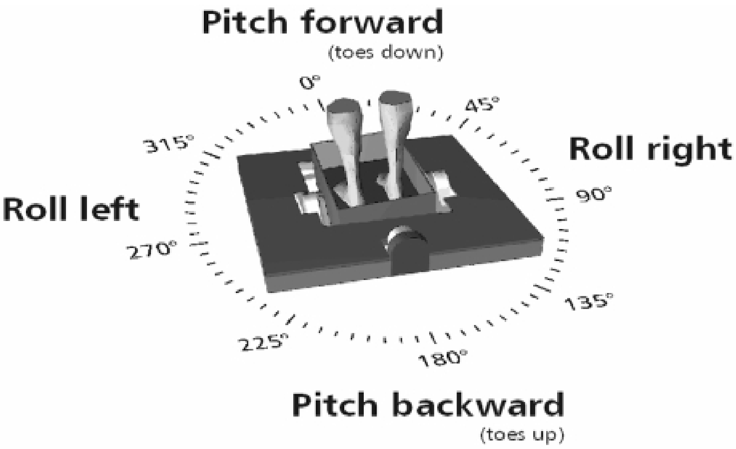

Figure 1. Schematic diagram of the perturbation directions

The angular notation indicates the direction of the stimulus for the polar plots of the other figures.

soleus and decrease in tibialis anterior (F(2, 30)=2.3, $P < 0.77$) background activity (BGA) with age that can be observed prior to stimulus onset in Figs 2 and 3 had no observable effect on muscle stiffness.

After 100 ms both lower leg pitch angle and A–P ankle torque population traces began to show differences between age groups (Figs 2 and 3). Changes in stretch reflex responses and changes in balance corrections (described below) with age may have contributed to this divergence in torque traces. Soleus stretch reflex responses which commence at *ca* 50 ms were smaller in the elderly (over the interval 40–100 ms; $P < 0.05$). In contrast to soleus stretch reflexes, stretch responses in tibialis anterior commence later, at 60–80 ms (Iles, 1976). Tibialis anterior responses to forward rotations (over the interval 80–120 ms) tended to be larger in the elderly than in the young (Fig. 2), but this effect was not significant ($0.05 < P < 0.1$).

Balance-correcting muscle responses to pitch plane support-surface rotations have larger amplitudes in unloaded rather than stretched lower leg muscles (Carpenter *et al.* 1999). These responses in tibialis anterior and soleus, captured by the 120–220 and 240–340 ms measurement intervals, had three characteristic changes with age. Firstly, the response onset was delayed some 20–35 ms in the elderly (Table 1). Secondly, the primary balance-correcting response amplitude (between 120 and 220 ms) was smaller in the elderly ($P < 0.05$). Thirdly, the secondary response (between 240 and 340 ms) was larger

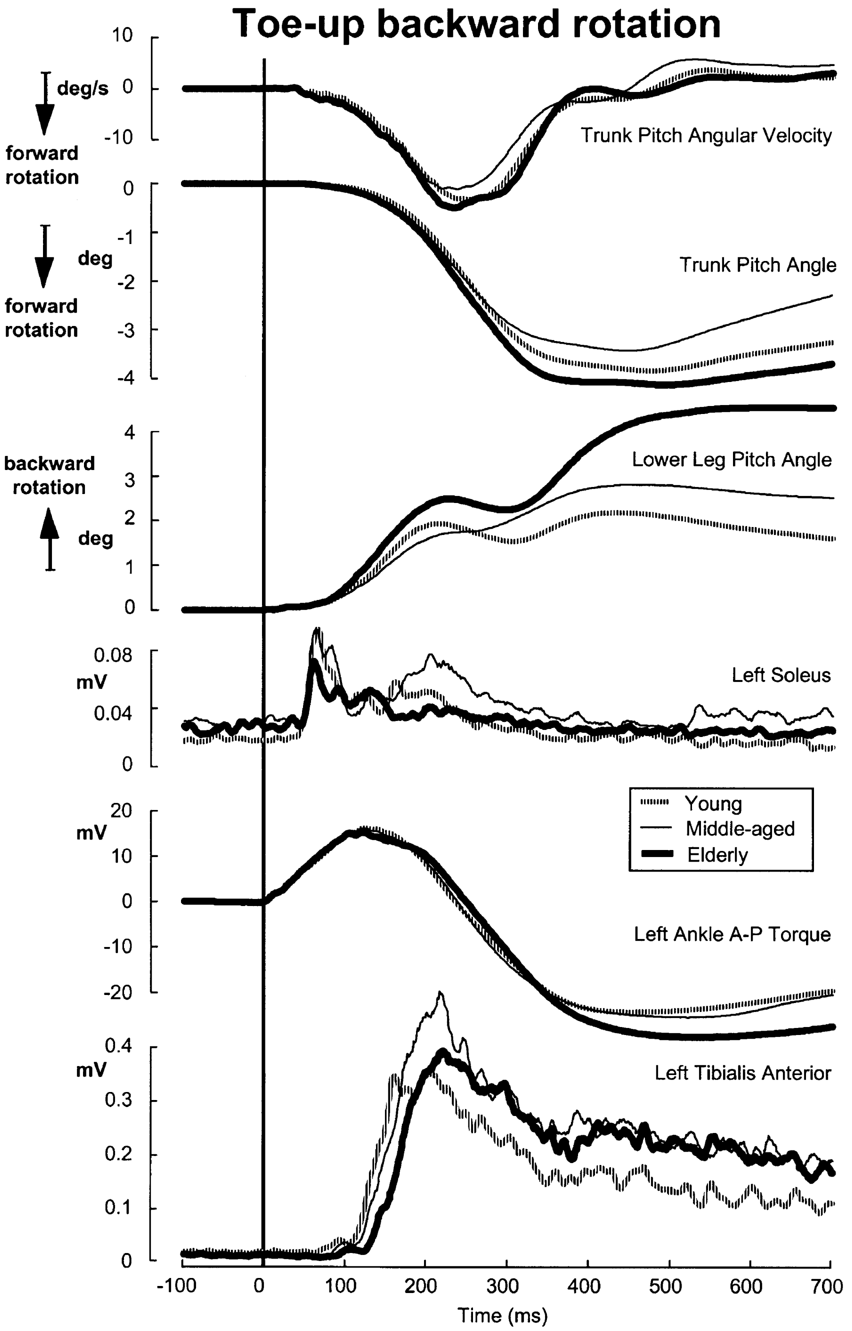

Figure 2. Population responses to a pure toe-up backward pitch rotation (7.5 deg at 60 deg s^{-1}) of the support surface

Each of the traces shown is the average of 12 subjects' responses to seven randomized repetitions of the stimulus yielding a total of 84 responses to the average curve. The thick vertical line at 0 ms represents the onset of the support-surface rotation and is at the first inflexion of the A–P ankle torque trace. A positive deflection of the ankle torque trace represents increased ankle torque imposed on the support surface. The initial increase of ankle torque lasts ~120 ms, the duration of the stimulus. The movement directions for lower leg pitch and trunk pitch are opposite as indicated in the figure. Note the decreased response amplitudes in soleus and delayed onsets of tibialis anterior in the elderly.

Table 1. Mean onset latencies (ms) of balance-correcting responses of left-sided muscles for perturbation directions eliciting maximum response amplitudes in the listed muscle

Muscle	Direction	Young	Middle-aged	Elderly
Tibialis anterior	Backwards (180)	114 (7)	128 (19)*	132 (11)*
Soleus	Forward left (315)	135 (19)	160 (17)*	182 (18)*†
Gluteus medius	Backward left (225)	109 (12)	129 (14)*	129 (12)*
Deltoid	Backward right (135)	109 (8)	114 (12)	134 (18)*†

Standard deviations are shown in parentheses. * Elderly or middle-aged means significantly ($P < 0.05$) different from young. † Elderly means different from middle aged.

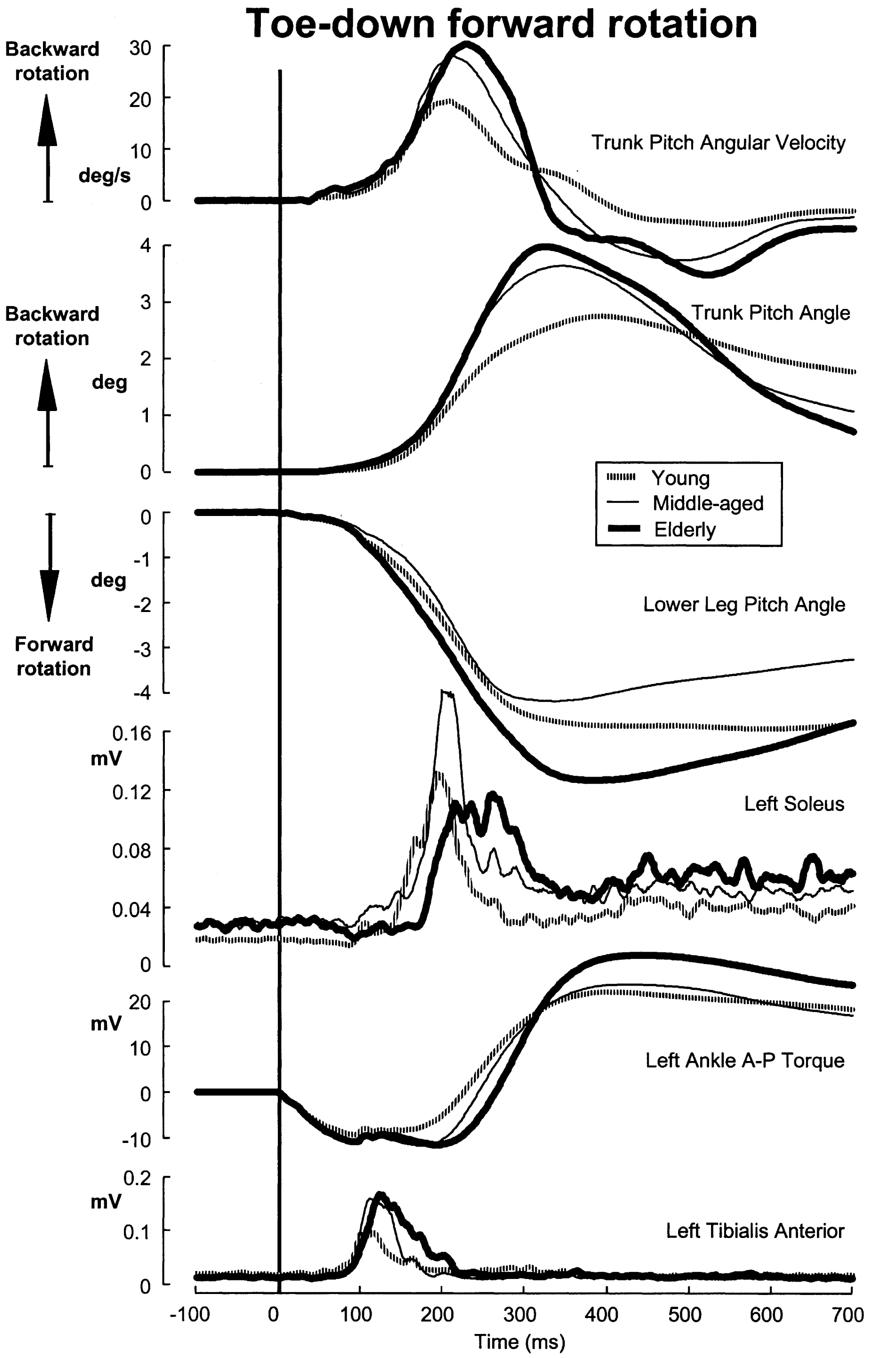

Figure 3. Population responses to a forward toe-down rotation of the support surface

Details of the responses are provided in the legend to Fig. 2. Note the increased early response in tibialis anterior and the delayed decreased response initially in soleus for the elderly compared with the young.

in the elderly ($P < 0.05$) (Figs 2 and 3). For backward rotations the tibialis anterior responses were delayed ($P < 0.05$) in both the middle aged and elderly (Table 1, Fig. 2). For the forward rotations soleus responses were significantly delayed ($P < 0.05$) in the elderly compared with young (Table 1, Fig. 3). The delay in soleus responses was some 35 ms compared with response onsets in the young, and in the middle aged were delayed some 20 ms with respect to the young. The onset delays with age in soleus were longer than those in tibialis anterior (see Table 1).

Changes in roll sensitivity of ankle muscle responses with age

The observed changes in onset delays and reduced early amplitudes of lower leg muscle responses seen with pure pitch plane perturbations were found to be consistent across all perturbation directions. Stretch reflex amplitudes (40–100 ms interval) in soleus were significantly influenced by an interaction between direction and age ($F(10,150) = 1.94, P < 0.05$). Soleus had significantly smaller stretch reflex amplitudes for backward left rotations in left soleus ($P < 0.05$) and correspondingly in the right soleus for backward right rotations ($P < 0.05$). Differences in onset latency of balance-correcting responses in tibialis anterior were found for backward rotations to the left and right ($P < 0.05$) and soleus for forward rotations to the left and right ($P < 0.05$). Both tibialis anterior and soleus balance-correcting responses were significantly delayed in the elderly compared with young and middle-aged groups (Table 1).

While the effects of age on ankle muscle balance-correcting response amplitudes are clearly observable for all directions of platform tilt, backwards rotations for tibialis anterior and forward and left rotations for the left soleus showed the largest differences of all directions (Fig. 4). This result is not unexpected because we found previously that the maximum activity direction is aligned along the pitch plane direction for tibialis anterior and 30 deg off-pitch for soleus (Carpenter *et al.* 1999). Tibialis anterior was significantly influenced by an age by direction interaction for balance-correcting response amplitudes measured between 120–220 ms ($F(10,150) = 3.13, P < 0.002$) As shown in Fig. 4*A*, for backward directions, which cause the largest tibialis

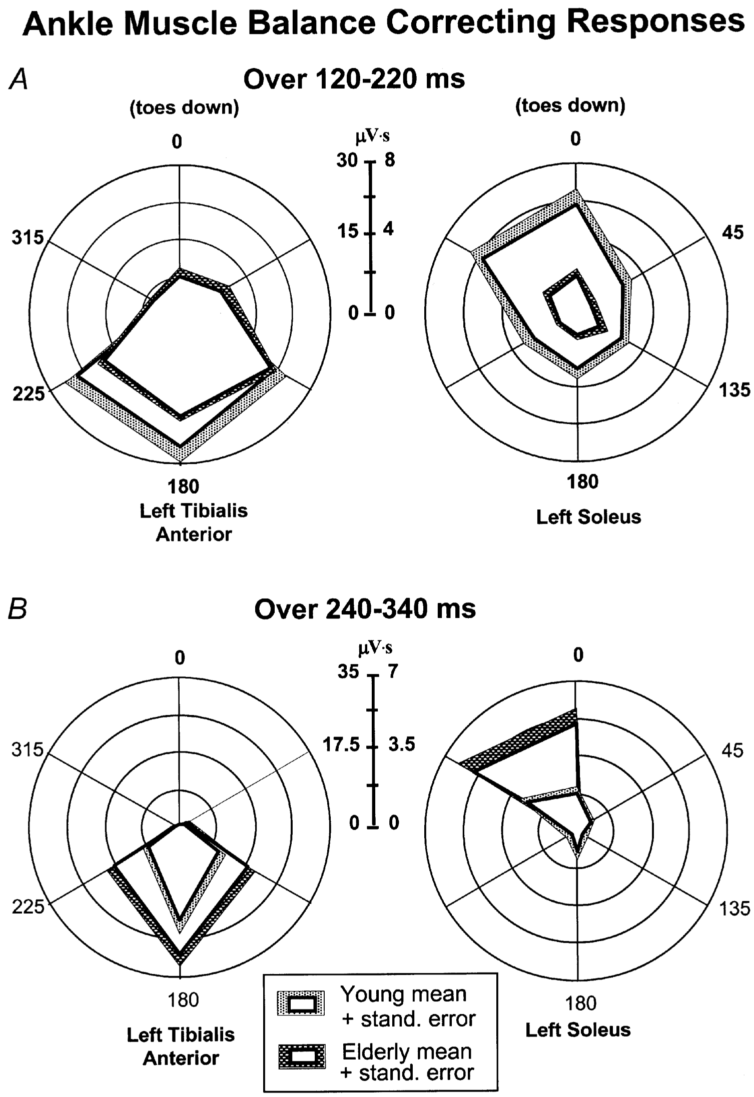

Figure 4. Polar plots for areas of tibialis anterior and soleus EMG responses averaged over two time intervals consisting of balance-correcting (120–220 ms) and secondary balance-correcting (240–340 ms) reactions

Each radial line represents one of the six directions of support-surface rotation (0, 45, 135, 180, 225 and 315 deg). For each direction, mean population values are plotted with amplitude represented as distance from the centre. The standard error of the mean (S.E.M.) has been added to the mean value of the young. The response amplitude is scaled according to the different vertical scales between the set of plots for the two recording sites. Note the slightly off-pitch plane orientation of soleus responses and the smaller, compared with the young, early responses but larger, later response amplitudes in the elderly.

responses in the young adults, elderly individuals had smaller amplitude responses. Similarly, soleus balance-correcting responses over 120–220 ms were significantly influenced by an age by direction interaction ($F(10,150) = 2.35$, $P < 0.02$). As shown in Fig. 4*A*, elderly individuals had significantly smaller balance-correcting responses in soleus for all directions, particularly for forward and forward left directions ($P < 0.05$). Differences with age also occurred for secondary balance corrections (240–340 ms) without a change in directional sensitivity (see Fig. 4*B*). As shown in Fig. 4*B*, these later responses were larger in the elderly than in the young, not smaller. There was a significant interaction between age and direction for amplitudes between 240–340 ms for both tibialis anterior ($F(10,150) = 2.49$, $P < 0.01$) and soleus ($F(10,150) = 2.79$, $P < 0.01$). The differences in muscle response amplitudes with age observed for 60 deg s^{-1} were also present for 30 deg s^{-1} stimuli.

The combined effect of differences in age on stretch reflex and balance correcting on left ankle torques is illustrated in Fig. 5. There was an interaction of age and direction on early balance-correcting torques measured between 160–260 ms ($F(10,150) = 2.83$, $P < 0.033$). Torque changes between 160–260 ms were initially smaller in amplitude for the elderly, specifically for torque changes caused by backward left and all forward perturbations (Fig. 5). Lower initial torque changes were partially compensated by a later (as measured between 280 and 380 ms) larger amplitude of torque in the elderly, which was also significantly influenced by an interaction between age and direction ($F(10,150) = 6.03$, $P < 0.0001$). These characteristics of ankle torque responses with age were also seen for slower (30 deg s^{-1}) stimulus velocities. The directional orientation of ankle torques (the vector direction of anterior–posterior and laterally directed torques) was not different between the young and elderly over the two measurement periods we used. The orientation of these vectors for the left foot was just off the pitch plane as illustrated in the lower part of Fig. 5 by the vector arrows for each stimulus direction. The reversal of the torque direction for one direction (45 deg) over one measurement interval (160–260 ms) was caused by the small reversed amplitude in the lateral torque of the elderly for this direction.

Ageing has no influence on trunk pitch movements

The pitch plane orientation of ankle torque responses described above implies that these torques will generate changes in angular displacements of leg and trunk segments in the pitch plane. Although significant differences in ankle muscles responses and ankle torques were observed in early and late balance-correcting responses between young and elderly subjects, the opposite direction of these age differences yielded no major age differences in the total pitch rotation of the trunk. This finding is best illustrated for pure pitch perturbations which yielded very little initial trunk roll (see Fig. 7, left). The trunk pitch velocity has a

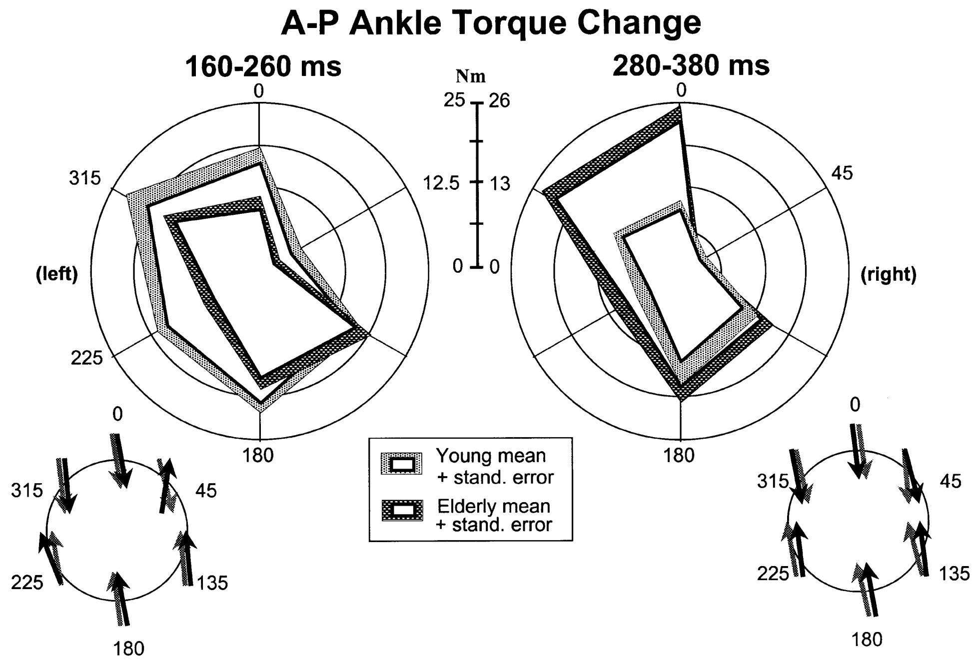

Figure 5. Polar plots for A–P ankle torque changes between 160–260 and 280–380 ms for the left leg

The upper plots are arranged similarly to those of Fig. 4. The two lower plots indicate the vector direction of torque obtained when the lateral torque is taken into account. The resulting torque vector is always oriented just off the pitch direction for each direction and age group except for 45 deg due to a small, sign-reversed, lateral torque for the elderly. Note smaller initial torque amplitude in the left polar plot, but later larger torque for the elderly compared with the young.

maximum around 200 ms for both backward and forward perturbations as shown in Figs 2 and 3. The rearwards pitch velocity of the trunk appeared to be faster initially for the elderly but was also faster forwards after 300 ms (see traces in Fig. 3) resulting in the same total trunk pitch angular displacement as the young at 700 ms.

Changes in trunk roll movements with age

As Figs 6–9 show, major age-related differences in trunk roll responses were observed for combined roll and pitch perturbations. The initial movement characteristics of the trunk in the roll plane were significantly altered in elderly adults. This was accompanied by changes in the timing and amplitude of early stretch and balance-correcting responses in hip and trunk muscles, as well as alterations in the intramuscular coordination. Figure 6 provides population plots for 60 deg s^{-1} backwards left rotations (with similar findings noted for 30 deg s^{-1}). These show that the trunk roll displacement of the young and middle aged commenced within 30 ms after perturbation onset, and was in the opposite direction to that of platform tilt. Both young and middle-aged subjects, had a peak trunk roll velocity which occurred at ~100 ms. In contrast, there was little initial trunk displacement in the elderly until after 150 ms. When the trunk did move in the elderly, the direction of trunk roll displacement occurred in the opposite direction to that of the young and middle-aged

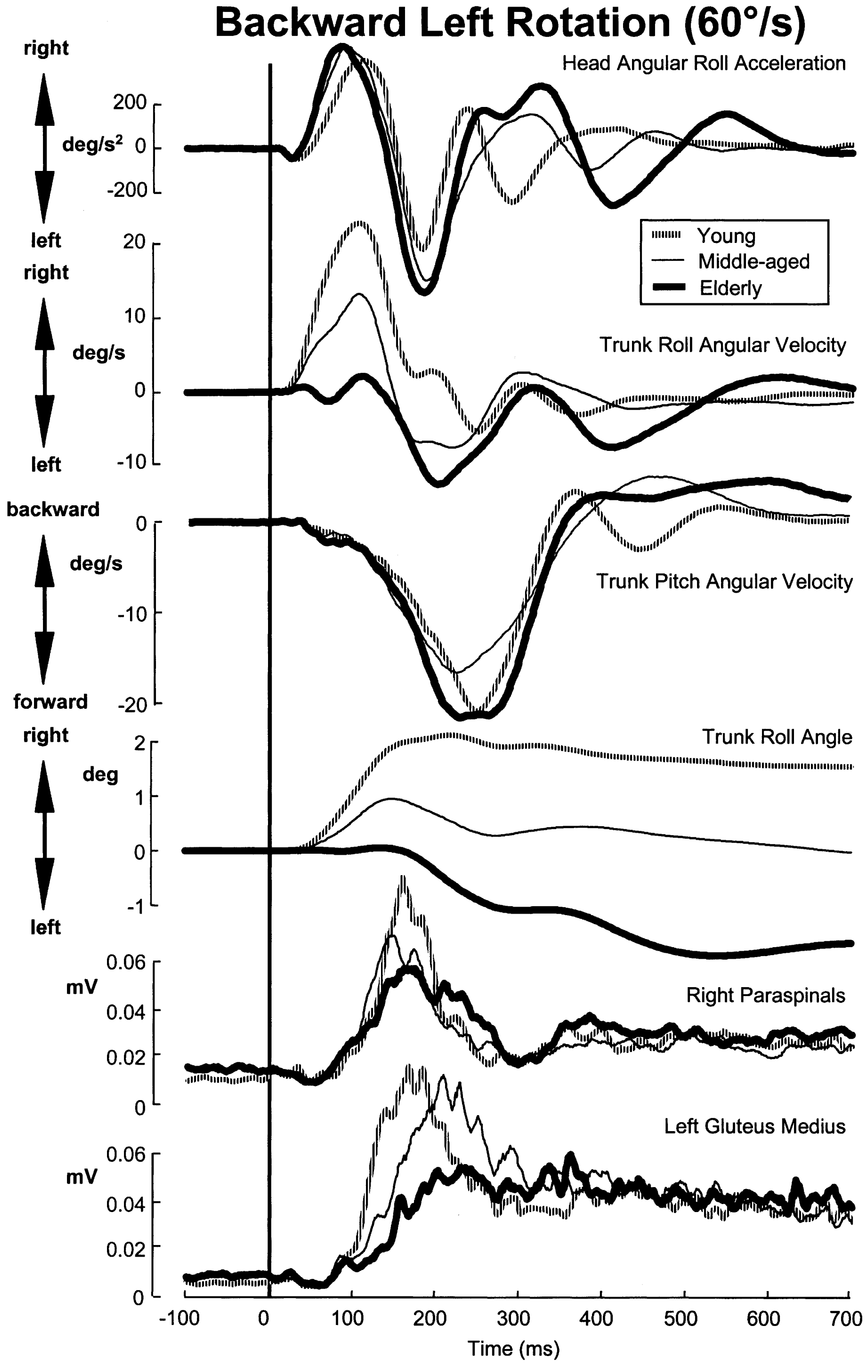

Figure 6. Trunk muscle and velocity population responses to a backward left rotation of 60 deg s^{-1}

Details of the responses have been provided in the legend to Fig. 2. The trunk roll angle traces were obtained by numerically integrating the trunk angular velocity recordings. Note the negligible initial trunk roll velocity in the direction opposite to the support surface tilt and the final trunk roll displacement in the same direction as the tilt in the elderly.

groups (see angular displacement and trunk roll velocity profiles of Fig. 6). The trunk roll angular velocity traces in Fig. 6 show that trunk roll velocity in the elderly reached a peak value much later at ~200 ms and then in the same direction as the support surface tilt. The middle aged had trunk roll velocity profiles between those of the young and elderly, rolling in the direction opposite to support-surface tilt but with velocity amplitudes approximately one-half that seen in the young (Fig. 7, left).

Using the average velocity over a 40 ms period, 20 ms either side of the time when trunk peak velocities occurred in the young (on average 110 ms for roll, 200 ms for pitch, see Figs 2, 3 and 6) we captured changes in trunk velocities for each stimulus direction with age (Fig. 7). In every direction with roll, the young exhibited the greatest early trunk roll, the middle aged less, and the elderly showed lowest velocities consistent with a more rigid trunk response. This group by direction effect was highly significant ($F(10,150) = 27.8$, $P < 0.0001$)). The average roll velocity between 90 and 130 ms for 60 deg s^{-1} stimuli was 21 deg s^{-1} for the young, 12 deg s^{-1} for the middle aged and 1 deg s^{-1} for the elderly. Along each roll direction, roll velocities at 110 ms were significantly different between all three populations ($P < 0.05$). The differences in the early trunk roll velocities coincided with age-related changes in the direction of resultant trunk displacement. As shown by the arrows in the vector polar plots below the velocity amplitude polar plots in Fig. 7, the trunk of the elderly initially moved almost only in the pitch plane whereas the trunk of the young and middle aged moved in roll directions opposite to the roll tilt of the support surface. At and after 200 ms the trunk of the elderly had more roll directed motion than the young, especially for backward roll perturbations (Fig. 7, lower right). Moreover, this trunk roll motion of the elderly was in the same direction as the perturbation (Figs 6 and 8).

Despite this stiffer and differently directed trunk roll response, the elderly were only marginally more unstable, in terms of velocity, than the young after 600 ms. As shown in Fig. 6, trunk roll velocities of the young and elderly are both near zero after 600 ms. The final position of trunk roll displacement was, however, different. As observed in Fig. 8, there was a highly significant group *versus* direction interaction ($F(10,150) = 3.21$, $P < 0.001$) for the trunk roll angular displacement at 700 ms. The age differences in the early roll velocity and the lack of a compensatory movement by the elderly yielded a final trunk roll orientation tilted towards the side of support-surface movement in the elderly. The trunk orientation was in the opposite direction and away from the downward support surface movement in the young, and hardly tilted at all in the middle aged (Fig. 8). The average mean difference in trunk roll at 700 ms for roll stimuli between the elderly and young was 3–4 deg (see Fig. 8) or about 2/3 of the tilt stimulus roll angle. Thus the elderly respond to combined roll and pitch perturbations with trunk roll movements more like those of a stiff inverted pendulum with motion in the same

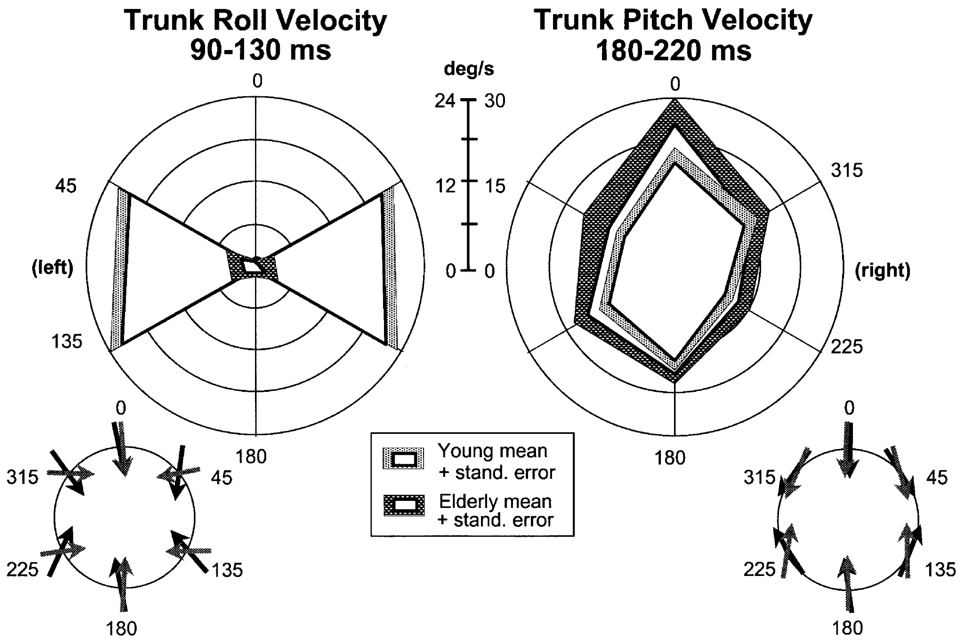

Figure 7. Polar plots of trunk angular velocity with corresponding vector plots

The plotted amplitude of roll velocity is the average between 90–130 ms, and for pitch velocity the average between 180–220 ms. The vector directions of trunk angular velocity at these two times are indicated by the diagrams below to the left and right of the respective polar plots. Note the differences in roll velocities between the two populations and the effect this has on the early direction of trunk roll movement.

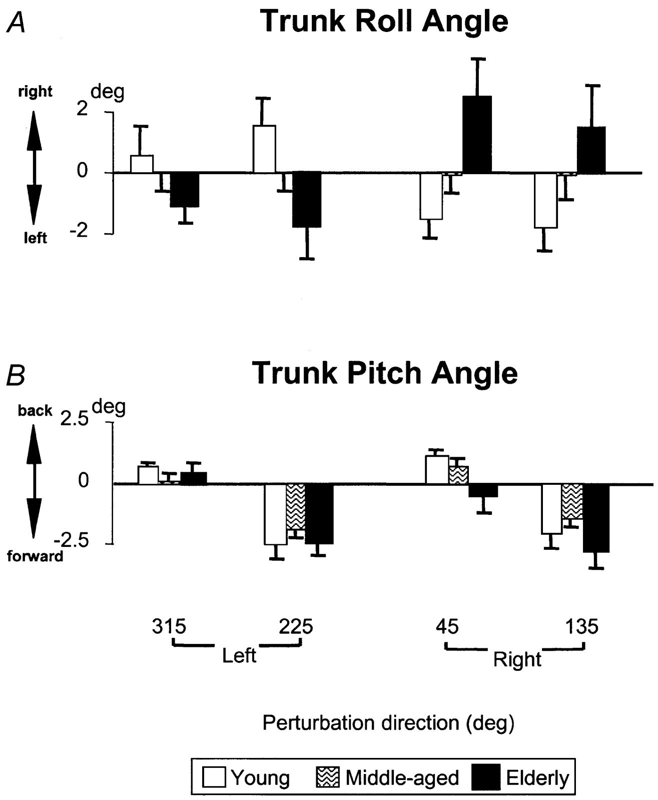

Figure 8. Trunk mean angular changes from stimulus onset to 700 ms later when trunk velocities have stabilized

Mean and standard errors of the mean are shown for each age group. Trunk roll and pitch angles are shown. The direction of support-surface rotation causing the angle changes is indicated by the plot abscissa, leftward directions on the left, rightward on the right. Note the opposite directions of trunk roll changes between the young and elderly populations, but similar directions of trunk pitch rotations.

direction as the tilt. The young responded, instead, with considerably more compliant roll rotation of the trunk about the pelvis and lumbar spine.

Combined roll and pitch perturbations caused stretch and unloading reflexes in both paraspinals and gluteus medius muscles. For example, backward left perturbations caused an initial stretch of the left paraspinals, unloaded the right paraspinals, stretched the right gluteus medius muscle, and unloaded the left gluteus medius muscle (see unloading responses in Fig. 6). Likewise, backward right perturbations unloaded the left paraspinal and the right gluteus medius. The ANOVA analyses of the amplitudes of paraspinal stretch reflex responses measured over the interval 40–100 ms revealed both an age ($F(2,30) = 4.07$, $P < 0.03$) and age by direction interaction ($F(10,150) = 1.85$, $P < 0.06$) for right and left muscles respectively, with smaller responses observed in elderly for backwards roll stimuli. We presume that these early paraspinal responses are highly dependent on the amplitude of early trunk roll velocity. Thus, the reduced responses in the elderly are consistent with their early reduced trunk roll motion. There were no significant differences in stretch reflex amplitudes (over 40–100 ms) of gluteus medius muscles ($F(2,30) = 2.83$, $P < 0.075$) suggesting that there are less age-related changes in pelvis

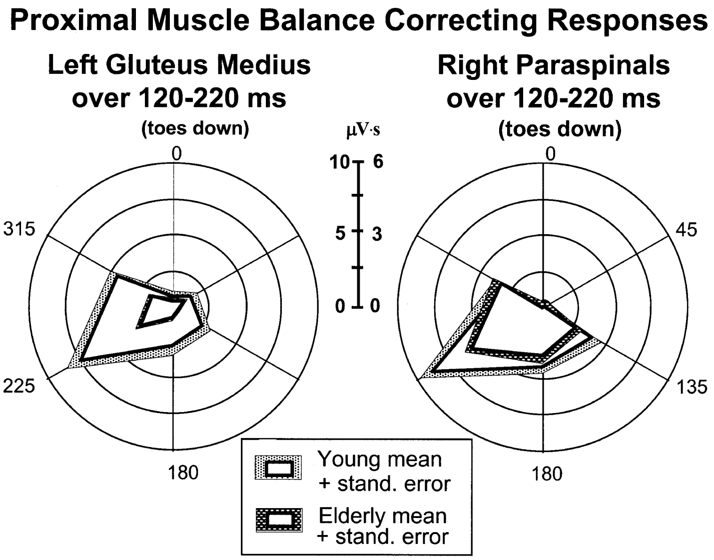

Figure 9. Polar plots for right paraspinals and left gluteus medius mean EMG response areas over the 120–220 ms interval for each direction

The format of the polar plots is identical to that of Fig. 4. Note how the maximum activity directions are the same for right paraspinals and left gluteus medius. These are oriented towards backwards roll. For the backwards roll direction the response amplitudes of the young are clearly larger than those of the elderly.

movement compared with trunk movement (however, this was not directly measured).

The most prominent age-related aspect of trunk muscle balance-correcting responses was the reduced amplitude of the gluteus medius response between 120 and 220 ms in the elderly compared with both the young and the middle aged. Response amplitude reductions with age were very significant in gluteus medius in both left ($F(10,150) = 3.98$, $P < 0.0001$) and right ($F(10,150) = 5.24$, $P < 0.0001$) muscles. The left gluteus response amplitudes shown in Fig. 9*A* were smaller in the elderly compared with young for all roll directions except forward right. The significant differences in gluteus medius can be partially ascribed to latency differences between the young and elderly subjects. Latencies of left gluteus medius balance-correcting responses commenced on average at 109 ms and were 20 ms earlier in the young than those of the elderly or middle aged (Table 1). Paraspinal balance-correcting responses showed no latency differences with age. As Fig. 6 documents, paraspinal responses had a weaker age effect than in gluteus medius over the 120–220 ms measurement period. In paraspinals a significant direction by age interaction was found for the right paraspinal ($F(10,150) = 1.97$, $P < 0.05$). The polar plots of trunk EMG response amplitudes in Fig. 9 illustrate the interaction of age and direction on gluteus medius and paraspinal responses. The

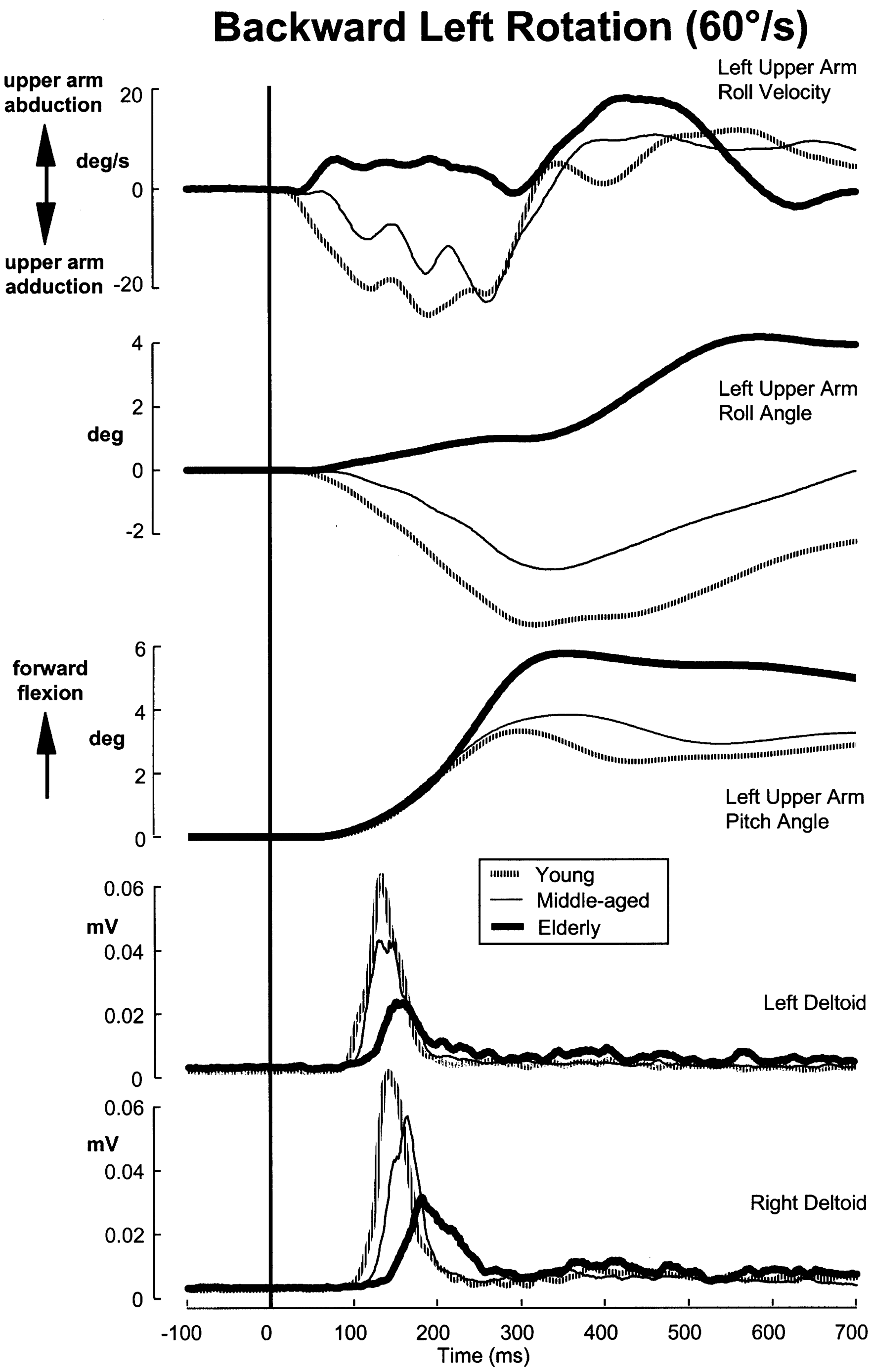

Figure 10. Arm muscle and velocity population responses to a backward left rotation of 60 deg s^{-1}

The relative angular velocity of the arm shown in the roll direction was computed from the difference of the measured angular velocities of the left upper arm and that of the trunk. Left roll angular position of the arm is the numerical integral of this trace. The relative pitch angle of the arm was obtained using the same technique as for roll. Note the different directions of the roll arm movements and the delayed and smaller deltoid responses for the elderly compared with the young.

direction of maximum activity for balance-correcting responses seen in Fig. 9 is at 225 deg for the left gluteus medius and right paraspinal muscles. For the opposite-sided muscles the maximum direction is at 135 deg. As can be seen in Fig. 9 the direction of maximum activity in these muscles did not change with age.

In hip and trunk muscles, there were no observable changes in the amplitude of later muscle responses following attenuated balance correcting responses in the elderly. There were no significant differences in amplitude of responses in gluteus medius or paraspinal muscles ($F(2,30) = 0.36, P < 0.7$) with age between 240–340 ms. As seen in Fig. 6, the dynamic pulse of the balance correcting response was followed after 250 ms by tonic muscle activity which presumably held the body in the tilted position. These tonic activity levels (as captured by our 350–700 ms measurement interval) did not however differ between the young and elderly.

Roll accelerations of the head of the elderly were (over the first 100 ms) always directed, like trunk movements in the young, opposite to the direction of platform rotation (see traces in Fig. 6). That is, despite the age differences in early roll velocities of the trunk, the head roll accelerations followed a pattern expected from being first pulsed in the direction of opposite to that of support-surface roll regardless of age. Consistent however with a stiffer trunk motion, the head accelerations of the elderly were more rapid in onset and peaked earlier than those of the young for both velocities of platform rotation we tested (see traces in Fig. 6 for 60 deg s^{-1} stimuli).

Compensatory arm movements

Arm muscles responses shown in Figs 10 and 11*A* (left) were stronger and earlier in the young than the elderly with the middle aged having amplitudes between the other two age groups. These medial deltoid responses also appear to be more directionally sensitive in the young (Fig. 10*A*, left). Our ANOVA analyses indicated a significant age by direction interaction for both left ($F(10,150) = 2.39$, $P < 0.01$) and right ($F(10,150) = 2.24$, $P < 0.02$) deltoid muscles over the 120–220 ms (Fig. 10). Latencies of deltoid responses were delayed in the elderly for backward left and right directions ($P < 0.05$), but not for pure backwards directions. The difference in latencies between the young and elderly is shown for one direction in Table 1.

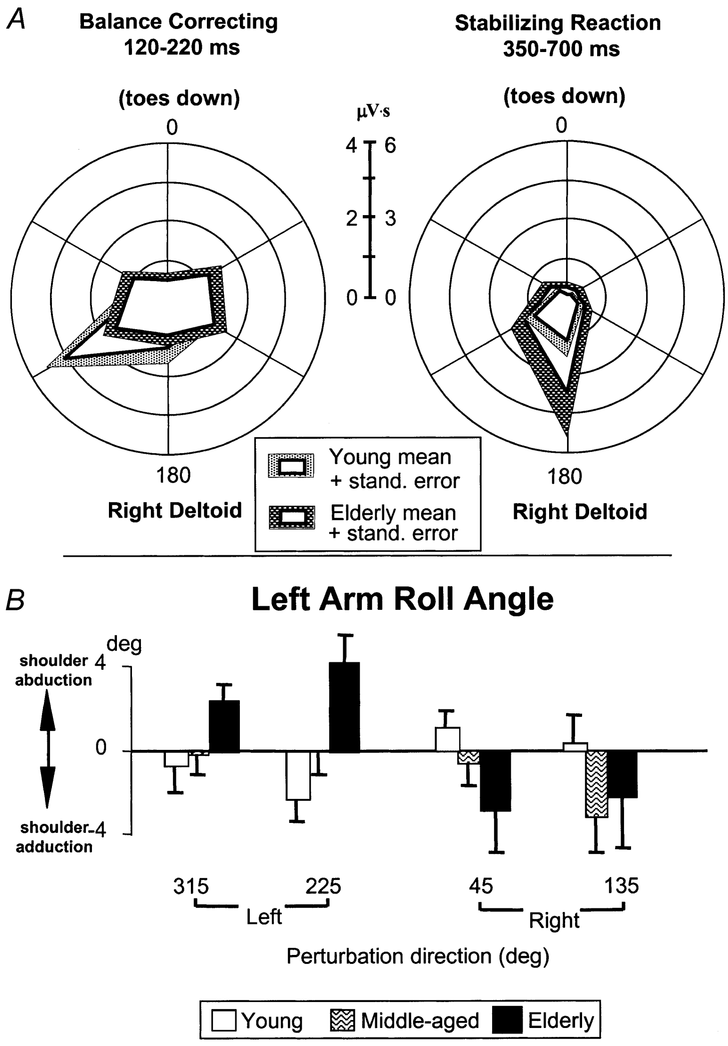

Figure 11

A, polar plots for right deltoid medius mean EMG response areas over the intervals 120–220 and 350–700 ms. *B*, left arm angular displacements with respect to the trunk. The format of the polar plots is identical to that of Figs 4 and 9. Note how the maximum activity is clearly oriented towards back left in the young over the interval 120–220 ms but not in the elderly. In the lower part of the plot angular changes of the left arm relative to the trunk from stimulus onset to 700 ms later are shown for all roll stimuli. The format of the plot is similar to that of Fig. 8. Note the different directions of arm roll between the young and elderly.

We have shown above, that the trunk moves in different roll directions with age. We discovered that differences with age for arm movements were dependent on the greater initial trunk roll compliance in the young. The arm roll velocity traces shown in Fig. 10 have marked similarities in profiles and age effects over the first 200 ms to the trunk roll velocity traces shown in Fig. 6. The amplitude of initial roll velocity of the arms is much greater in the young, less in the middle aged, and even less in the elderly. Furthermore, the direction of arm velocity was initially in the opposite direction in the elderly compared with the directions of the other age groups. The net results of these age differences in early arm roll velocities is illustrated by the left arm roll angle traces which are plotted relative to the trunk in Fig. 10. The roll angle traces of the different age groups clearly diverge from one another 50 ms from stimulus onset in the figure. The left arm for the backward left tilt of the support surface (225 deg direction) was adducted relative to the trunk in the young, but abducted in the elderly. For a backward right tilt (135 deg) the left arm also moves in a different direction for the young and elderly. The difference is, however, not as large nor as significant as the left arm movement for the backwards left directions (compare the columns for 225 and 135 in Fig. 11*B*). Thus, the initial roll velocities initially place the arms in a statically more stable position for the young and middle aged. Early (before 200 ms) pitch velocities of the arms relative to the trunk had no observable age differences. The pitch angle of arm relative to the trunk has a similar profile over the first 200 ms (Fig. 10) for all age groups.

Examining the plots of relative arm roll induced by 700 ms in Fig. 11*B* indicates, for both the young and elderly, that they had moved their arms at this time point in the direction of trunk motion, but like the trunk motion, these directions were different with age ($F(10,150) = 2.23$, $P < 0.02$). For example, for the left arm roll shown in Fig. 9 (direction 225 in Fig. 10*B*) the average arm abduction in the elderly was 3.9 deg and significantly different ($P < 0.05$) from the adduction in the young of 2.3 deg. The trunk and the arms moved towards the ‘downhill’ side in the elderly and towards the ‘uphill’ side in the young (see arm relative roll movements in Fig. 10). The net results of these arm movements placed the body’s centre of mass more downhill in the elderly. Figure 11*B* shows that this difference between the young and elderly in the direction of roll arm movements at 700 ms was observed for all perturbation directions with a roll component (45, 135, 225 and 315 directions). The pitch movements of the arm at 700 ms differed little between age groups except for a tendency at 700 ms for the elderly to flex their arms further forward than the young and middle aged for backward support-surface rotations as shown in Fig. 9. The more extended final position of the arms in the elderly for backward roll directions was correlated with the tendency for increased tonic activity in deltoid muscles of the elderly after 350 ms (see Fig. 11*A*, right). In summary, like trunk movements, arm movements differed with age and these differences were revealed more readily in the elderly by combinations of roll and pitch support-surface rotations than by pitch rotations alone.

DISCUSSION

By employing combined roll and pitch perturbations to upright human stance we have observed three fundamentally different aspects in the first 200 ms of balance reactions in elderly subjects, compared with those of the young. First, the elderly had quite different roll movements of the trunk. Second the elderly had roll arm movements relative to the trunk in the opposite direction to those of the young. Third, balance-correcting muscle responses, that normally protect against an impending fall, were changed in timing, amplitude and coordination in the elderly. We also replicated previous observations of age-related changes in leg muscle synergies induced by pure pitch perturbations, and expanded this knowledge to a multidirectional environment. Finally, we have observed compensatory strategies in elderly subjects that, interestingly enough, were restricted to only certain elements of the postural synergy. These different postural changes with age will be dealt with in separate sections below. Some of these age-related changes could be identified using pure pitch plane perturbations. However the most dramatic changes in upper body and arm responses became evident only when balance perturbations included a roll component.

Increased trunk roll stiffness with ageing

The most significant age-related characteristic we observed concerned the initial roll movement of the trunk. This is schematically illustrated in Fig. 12, which is based on our results. In young subjects, the trunk is initially rolled ‘uphill’ when the support surface is tipped to one side, and the legs and pelvis are turned ‘downhill’ (Carpenter *et al.* 1999, 2001*a*). The trunk roll movement in the opposite direction of the impending fall begins as early as 30 ms after onset of platform movements, and this early timing suggests that this characteristic of trunk movement is passive in nature. Our present results show that only minimal initial trunk rotation occurs in the elderly. The progressive nature of these changes in trunk movements is reinforced by the findings in the middle-aged, which acted as an intermediate group between the young and elderly. The validity of the schema of body segment movements illustrated in Fig. 12 is confirmed by the activation pattern of early stretch and unloading responses in hip and trunk muscle. Thus unloading of left gluteus medius (see Fig. 6) and stretch of the right gluteus medius is consistent with rotation of the pelvis in the same direction of tilt. Likewise the unloading of right paraspinals and stretch of the left paraspinals is consistent with rotation of the trunk in the opposite direction to that of the pelvis. Furthermore, the reduction of the paraspinal reflexes in the elderly was also consistent with the reduced trunk motion with respect to the young.

We did not specifically examine why the early trunk movements are reduced in the middle aged, and practically absent in the elderly. Degenerative changes of joints and ligaments likely play a role. Ageing is, among others, associated with a reduced elasticity of peri-articular tissue and with degenerative changes in cartilage or other degenerative arthritic changes (Buckwalter *et al.* 1985). The increased joint stiffness could also result from an increase in intrinsic muscle stiffness. Age-related stiffness has also been observed in other joints, such as the ankle (Kerrigan *et al.* 1998), knee (Bergstrom *et al.* 1985) and hip (Kerrigan *et al.* 1998). The age-related reduction in the range of hip joint motion seems to be quite small (3–5 deg), but lateral motion seems to be more affected than flexion motion (Roach & Miles, 1991), as was the case in our subjects. Interestingly, increased postural stiffness with age has also been reported under different experimental conditions, including quiet stance (Collins *et al.* 1995), sway induced by much slower platform movements in the pitch plane (Maki *et al.* 1990; Accornero *et al.* 1997), reaching or bending forward (Cavanaugh *et al.* 1999; McGill *et al.* 1999), voluntary rotations in the lateral or yaw plane (Schenkman *et al.* 1995; McGill *et al.* 1999) and during gait (Hirasaki *et al.* 1993). Increased viscoelasticity, if severe enough, would be sufficient to explain our observations, because reversed trunk movements highly reminiscent of the pattern observed in elderly persons could be replicated in young healthy subjects who were asked to wear a stiffening corset that strongly reduced movements of the pelvis and trunk (Grüneberg *et al.* 2001).

Is stiffening a protective strategy?

Is it possible that the increased trunk stiffness we observed in the elderly was in fact due to an active stiffening strategy? For example, Maki and colleagues (Maki *et al.* 1990) observed a poor correlation between static sway and sway induced by continuous pitch plane movements of a supporting platform. They attributed this discrepancy to an active stiffening strategy, which was apparently absent under static (low postural threat) conditions, but emerged under the more challenging dynamic conditions. In our experiment it is possible that having the feet fastened to the platform may have been perceived as a more challenging situation for the elderly than the young. Likewise for the stimulus velocities of 60 deg s^{-1} we employed. However, it is noteworthy that the effects of reduced trunk roll were also observed for 30 deg s^{-1} stimuli which were presumably less challenging for the elderly.

Active joint stiffening could be achieved through increases in prestimulus background muscle activity, and this indeed occurred with age but then only with borderline significance in soleus and paraspinals. One possible reason for such a response would be to actively stiffen up because of a fear of falling, which is common in the elderly (Maki *et al.* 1991; Tinetti & Powell, 1993; Arfken *et al.* 1994). Persons who are afraid to fall often stiffen up in anticipation of postural perturbations (Maki *et al.* 1991; Carpenter *et al.* 2001*b*). For example, stiffening strategies could be induced in healthy subjects who were placed on an elevated platform and asked to make voluntary rises onto the toes (Adkin *et al.* 2002) or correct a stance perturbation (M. G. Carpenter, J. S. Frank, A. L. Adkin, A. Patton & J. H. J. Allum, unpublished observations). Stiffening in these subjects was associated with a physiological arousal and a subjective fear of falling, as documented by standard rating scales. Another reason to stiffen-up could be that the limits of stability are narrowed with ageing (Murray *et al.* 1975; Robinovitch & Cronin, 1999), and perception of this narrowing could force older subjects to vigorously maintain their centre of gravity within the safe range. Indeed, healthy subjects start to co-contract when they stand on a narrow surface (Horak & Nashner, 1986). We have recently observed a striking example of a patient with total leg proprioceptive loss (caused by a dorsal root ganglionopathy) who apparently resorted to this stiffening strategy by markedly increasing prestimulus background muscle activity levels (Bloem *et al.* 2002). Interestingly, early trunk movements in roll were completely reversed in this patient in comparison to young controls, and this was associated with considerable postural instability. Finally, we cannot exclude that some of the observed muscle and joint stiffness in the elderly resulted from the presence of

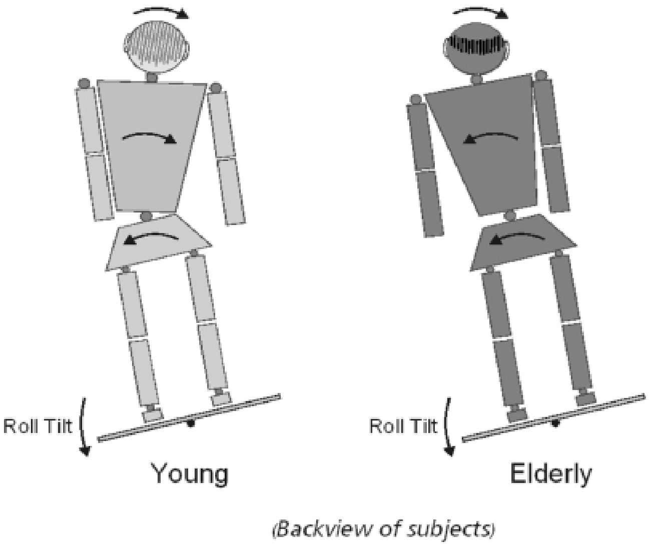

Figure 12. Schematic illustration of body segment movements for leftwards support surface roll tilt as viewed from behind young and elderly subjects

The arrows on the body segments indicate the direction roll velocity at *ca* 100 ms after stimulus onset.

a subtle stooped posture, with some muscles becoming more stretched and showing increased background activity (Bloem *et al.* 1999).

The above considerations suggest that increased trunk stiffness, although perhaps helpful in reducing sway under fairly static conditions, is disadvantageous for postural control under everyday circumstances where continuous dynamic changes occur that call for flexible adaptability across multiple body segments (Hodges *et al.* 2000). Indeed, the early uphill trunk movement in young subjects provides a 'counterweight' to the stimulus-induced downhill displacement of the body's centre of mass (see Fig. 12, left), and loss of this function due to stiffness results in instability because the trunk is now forced into the direction of the induced fall (see Fig. 12, right). We therefore expected that the elderly would try to compensate for their trunk stiffness by adapting their balance-correcting synergy to achieve the same end-stability as young subjects. Specifically, we expected that the elderly, being in a downhill position initially, would have compensated by increasing their later trunk and hip muscle responses and thus 'force' the trunk back uphill. However, it appeared that, following the initially absent trunk movement, the elderly used the same balance-correcting movement synergy of hip and trunk muscle responses as the young, albeit with smaller response amplitudes commencing at 120 ms. Consequently, the elderly continued to move their trunk even further downhill. Thus, our observations indicate that the elderly have not adapted their roll-directed movement strategy to deal with the changed biomechanical response of their body to the postural disturbances.

Compensatory arm movement strategies

Arm responses can perform a number of static and dynamic functions in reaction to a fall. First, arm movements may serve to alter the fall characteristics of the body. In this case the arms may act as a counterweight to change the position of the body away from the direction of fall (Maki & McIlroy, 1997) or to generate reaction torques, through joint coupling, at other joints which are affected by the perturbation (Eng *et al.* 1992). The arms could also serve a protective function. Extending the arm in the direction of the fall may help to absorb the impact of a fall. Similarly, arm movements may be used to reach and grasp for stable objects, either away from or in the same direction of a fall, which may prevent or slow the course of a fall (Maki & McIlroy, 1997).

One age-related difference in arm responses observed between young and elderly subjects was the significantly delayed deltoid response in the elderly. Delayed onsets in deltoid muscles of the elderly with respect to the young may have arisen partially because of having to decide, albeit subconsciously, between continuing to stretch the arms out into the direction of a fall (to grasp support, such as a handrail), or to cushion any possible contact with the floor, or to rapidly activate the arms to help move the trunk uphill. Presumably this decision would be influenced by the anticipated risk of actually losing balance, and possibly also by a fear of falling. Inherent to this assumption is the premise that protective arm movements are at least partially under voluntary control, possibly as 'overlearned' and early occurring reactions. Delays could also occur due to general delays in reaction times, which often occurs in the elderly (Era *et al.* 1986; Calne *et al.* 1991). It should be noted, however, that our conclusions concerning delays in arm muscles and the effect these have in the elderly are based on limited observations. These conclusions may need to be modified once recordings from several arm muscles are available.

The second difference observed between young and elderly subjects was oppositely directed arm movements in the roll plane. In all age groups, the direction of initial arm movements (shown schematically in Fig. 12) was determined by the initial (stimulus-induced) trunk motion. Arm displacement was found to move in the same direction as trunk displacement. Young subjects had initial trunk displacement and subsequent arm displacement towards the uphill side (opposite to platform rotation). Therefore, the rapid arm movements in the young could increase trunk rotation away from the direction of fall (through joint coupling), as well as to put the hands in a position to grasp the uphill rail. In contrast, the elderly had initial trunk and arm movements that were directed in the same direction as platform rotation. The direction of arm movements in the elderly would lead to increased trunk rotation (through joint coupling) toward the direction of the fall while arm movements would be in a position to grasp the downhill rail. The strategy adopted by elderly persons of placing their arms in the direction of a fall would not aid their stability because the weight of the arms and reactive torque generation would aggravate the displaced centre of gravity, and thus increase the likelihood of a fall (see Fig. 11). However, if the goal of the arm movements is to reach and grasp objects closest to the fall direction of the trunk, then arm movements in the elderly are properly directed for the age-related differences they experience with trunk displacement.

Observations of similar arm movements for both forward and backward translations have led some researchers to conclude that arm movements are not primarily used to counterbalance movements of the COM (McIlroy & Maki, 1995). Arm movement trajectories have been shown to be significantly influenced by the position of handrails relative to the direction of a fall, during both standing and seated perturbations (Maki & McIlroy, 1997). Uncertainty about handrail location prior to a perturbation results in variable arm trajectories, however, the onset of arm responses are preserved (Maki & McIlroy, 1997). The present study has provided further evidence that protective arm movement trajectories may be associated with initial trunk movements. Therefore, differences in arm response trajectories between young and elderly subjects may be attributed to oppositely directed trunk movements, which trigger subsequent protective arm movements in the direction of trunk displacement.

Since the direction of trunk movement in elderly is also in the direction of the fall, stretching the arms into the direction of the induced fall increases the risk of wrist fractures, which are typically caused by falls on the out-stretched hand (Melton *et al.* 1988; Chiu & Robinovitch, 1998). Our present results might, at first sight, suggest that young subjects would have a decreased likelihood of fracturing their wrists because their arms move away from the potential contact with the floor. However, we suspect that our perturbations may not have been sufficiently destabilizing for the young subjects compared with the perceptions of the elderly, providing the young the 'luxury' of opting for the counterweight function of the arms. Indeed, if the perturbation size had been decreased in the elderly but increased in the young to produce the same perception of falling, then the arm movement strategy in the young and elderly might have been similar.

Our observations on arm movements may have significance for understanding the mechanisms underlying falls in the elderly, and offer some new approaches for their possible prevention. If young persons can plan different arm movement control when falling as part of judo training, or learn to place their arms pointing downhill in order to enhance dynamic continuous falling downhill while skiing, the question should be asked whether the elderly can be taught to acquire trunk and arm responses which prevent, rather than increase, the likelihood of a fall once tipped. Physiotherapy can be successful in elderly persons (Calne *et al.* 1991).

Altered muscular responses with age

There were several changes seen across body segments with increased age in muscle balance-correcting responses. Changes in the muscular response pattern with age included delayed onset of automatic balance correcting responses, and a decreased amplitude of responses in all postural leg, hip, trunk and arm muscles. These attenuated responses were partially compensated by enhanced later responses in the lower leg muscles between 240–340 ms, but not in the trunk and arms. Ageing thus had dramatic effects on overall movement strategies for trunk control as well as strategies for controlling compensatory arm movements as noted above. We will explore below how these observed changes in balance responses may be related to other neurophysiological changes associated with age.

Delayed onsets of muscle responses. Balance-correcting responses in young subjects had an onset latency around 100 ms. This onset latency emerged more or less simultaneously for arm, hip and ankle muscle responses, suggesting that these balance corrections were centrally timed. The simultaneous activation across many segments during execution of balance corrections has been noted before (Keshner *et al.* 1988; Allum *et al.* 1993; Carpenter *et al.* 1999), but we can now extend these findings to arm muscles and hypothesize that the simultaneous activation arises from the constraint to have righting torques at each of the major joints precisely coordinated. This timing aspect differs from the anticipatory trunk and leg responses which occur prior to voluntary arm movements (Cordo & Nashner, 1982; Friedli *et al.* 1984; Hodges *et al.* 2000).

The onset latencies for automatic balance-correcting responses in arm, hip and ankle muscles were significantly delayed in the elderly compared the the young by some 20 ms. Other investigators also observed delayed onset latencies of monosynaptic spinal stretch responses (Appenzeller *et al.* 1966; Carel *et al.* 1979) and balance-correcting responses with age (Woollacott *et al.* 1982; Woollacott, 1986; Stelmach *et al.* 1989*a*, *b*; Keshner *et al.* 1993; Nardone *et al.* 1995). General cell loss in the CNS is likely to interfere with the speedy generation of appropriately timed balance corrections that avoid a fall (Era *et al.* 1986). These responses could be delayed in the elderly as part of a general reduction in vestibular or other sensory thresholds (Peterka & Black, 1990; Fife & Baloh, 1993; Borger *et al.* 1999), or due to a transmission delay in the peripheral nervous system (Taylor, 1993; Rivner *et al.* 2001), or due to a processing delay of the CNS (Tobimatsu *et al.* 1998; Tanosaki *et al.* 1999). However, evidence of changes in sensory thresholds with age, with concomitant increases in onset times of stretch reflexes and unloading responses, were not found in this study. We only observed reductions in the amplitudes, but no change in the timing of early stretch reflexes in soleus and paraspinals, which were probably related to reduced muscle stretch caused by increased joint stiffness. We therefore feel that central processing and somatosensory integration abnormalities, which commonly occur in the elderly (Stelmach & Worringham, 1985), are the most parsimonious explanation for our results. Such processing abnormalities could result from diffuse white matter lesions, which are not uncommon in otherwise fit elderly persons with gait or balance impairment (Barbeau, 1973; Baloh *et al.* 1995*b*; Tell *et al.* 1998).

Amplitude modulation in muscle responses. Short latency responses were relatively preserved in the lower legs of elderly persons, but balance-correcting responses had delayed onsets and reduced amplitudes. The present study has verified previous reports of reduced amplitude balance-correcting responses in the lower legs which are accompanied by weaker torques about the ankle joint (Keshner *et al.* 1993; Thelen *et al.* 1996). The present study has extended these findings from the lower legs, to encompass muscles in the hips, trunk and arms which have also been shown to have significantly reduced balance-correcting amplitudes. While the amplitude of responses was reduced, the directional sensitivity of the responses was, in general, well preserved with age. These changes could be attributed, in part, to the age-related weakness of older persons (Kerrigan *et al.* 1998). Decreased balance-correcting responses could also be linked to altered vestibular input in the elderly. Loss of vestibular input has been shown to significantly reduce balance-correcting response amplitude in both lower leg and trunk muscles, while the directional sensitivity is preserved (Carpenter *et al.* 2001*a*). As cell loss in the vestibular nuclei occurs with ageing (Alvarez *et al.* 1998), it is plausible that reductions in balance-correcting response amplitudes may stem from a decreased modulation of vestibular inputs.

Leg muscle responses often comprise two bursts of activity (Allum & Pfaltz, 1985; Carpenter *et al.* 1999) suggesting separate generation mechanisms for each. In leg muscles, the secondary balance correcting response (240–340 ms) and corresponding ankle torques were larger in the elderly, suggesting a compensation for the early (120–220 ms) and weaker part of the balance correcting response. Interestingly, we found no evidence for a similar adaptation in trunk muscles. The observation of enlarged secondary balance correcting activity in the elderly compared to young controls in lower leg muscles also parallels changes seen in patients with bilateral vestibular loss (Carpenter *et al.* 2001*a*). The leg muscle responses did not show a changed directional sensitivity with ageing, thus the secondary balance corrections appeared to be scaled with little CNS processing to provide the compensatory additional output. Whether this compensatory mechanism is primarily restricted to leg muscle responses or to pitch plane responses cannot be answered from the current work because we neither recorded from leg muscles responses with a lateral sensitivity, nor from trunk muscles with mainly a pitch sensitivity. Based on our previous work indicating that the CNS processes balance corrections in the roll and pitch planes separately we would hypothesise that the leg muscle compensatory processes are part of the overall pitch plane processing by the CNS. In this respect our results provide an explanation as to why the small age-related changes seen in leg muscles with backwards (toe-up) rotations of the support surface appear to be insufficient to cause a fall (Alexander *et al.* 1992). Further our results would extend this conclusion to forward rotations. It would be when confronted with a perturbation that had a sizeable roll component that the CNS appears unable to compensate for the stiffer environment which places the trunk and arms in danger of causing a fall.

It remains an open question as to why the elderly achieve a considerable degree of adaptation revealed in later responses to earlier weaker responses in leg muscles, but not in trunk muscles. One explanation could be that, in contrast to the changed early stretch reflexes in leg muscles, upper body proprioceptive and vestibular senses provide insufficient or conflicting indications that the trunk of the elderly rolls in an unstable direction. The proprioceptive reflexes that we recorded (stretch and unloading reflexes in gluteus medius and paraspinals) provided some evidence for differences with age in paraspinals. The earlier (with respect to paraspinal reflexes) stretch and unloading reflexes in gluteus medius were generally quite similar for the different age groups, and this seemed consistent with the initial counter-rotations of the pelvis segment with respect to the rotation of the trunk being similar. The differences across age appeared in paraspinal stretch reflex amplitudes with decreased trunk velocities, presumably due to increased trunk stiffness in the elderly. Because we observed reduced stretch reflex amplitudes in paraspinal muscles, but normal stretch reflex amplitudes in gluteus medius muscles, we must assume that proprioceptive systems in the trunk and hips provided information on the differences in velocities of the pelvis and trunk segments to the CNS. Furthermore, reduced amplitudes of early stretch reflexes in more muscles than just paraspinals would presumably be forthcoming from the trunk segment. Finally, our recordings of head roll accelerations confirmed that the initial acceleration of the trunk is in the same direction for all age groups, but is then slowed down rapidly in the elderly by the increased trunk stiffness. As a result, the head of the elderly is whipped faster into a roll angular acceleration, thus providing the CNS of elderly persons a clear indication of an initially slower moving trunk, compared with a faster moving head. This enhanced vestibular information would confirm the evidence provided by reduced proprioceptive input at the trunk. It was therefore surprising that the CNS of the elderly failed to take this differing proprioceptive and vestibular information into account and accommodate the lack of initial trunk roll. We speculate that later compensation was absent because, as mentioned above, trunk stiffening may by itself represent a compensatory strategy that, although perhaps self-perceived to be beneficial, in fact aggravated instability in response to multidirectional perturbations. Further compensation for an inappropriate adaptive strategy may not have been possible, despite the presence of appropriate sensory warning signals.

We did not observe any differences in the ability to scale postural responses to the two different perturbation velocities used in this study. This would suggest that gain control was preserved in our elderly subjects. Other investigators also concluded that elderly subjects could normally scale their postural responses, according to the demands of the postural task at hand (Nardone *et al.* 1995). 'Online' scaling of postural responses to perturbation velocity seems to be a function of the cerebellum (Timmann & Horak, 1997). We were interested to see if we could detect any subtle age-related dysfunction of the cerebellum (Koller *et al.* 1981), but this was not the case.

The fundamental changes in trunk stiffness with age causing different directions of early trunk movement were not modified significantly by age-related alterations in muscle response synergies discussed above. If anything, the changes in muscle synergies with age exaggerated the initial instabilities of the elderly. Thus, overall, changes in balance correcting strategies with age appeared to be linked to inherent changes in roll stiffness of the trunk with ageing. Interestingly, trunk and arm movements in the pitch plane did not differ between the three age groups, and this observation underscores that valuable information on the physiology of ageing can be obtained from the use of combined roll and pitch perturbations to upright human stance.

REFERENCES

Accornero, N., Capozza, M., Rinalduzzi, S. & Manfredi, G. W. (1997). Clinical multisegmental posturography: age-related changes in stance control. *Electroencephalography and Clinical Neurophysiology* **105**, 213–219.

Adkin, A. L., Frank, J. S., Peysar, G. W. & Carpenter, M. G. (2002). Fear of falling modifies anticipatory postural control. *Experimental Brain Research* **143**, 160–170.

Alexander, N. B., Shepard, N., Gu, M. J. & Schultz, A. (1992). Postural control in young and elderly adults when stance is perturbed: Kinematics. *Journal of Gerontology* **47**, M79.

Allum, J. H. J., Honegger, F. & Schicks, H. (1993). Vestibular and proprioceptive modulation of postural synergies in normal subjects. *Journal of Vestibular Research* **3**, 59–85.

Allum, J. H. J. & Mauritz, K.-H. (1984). Compensation for intrinsic muscle stiffness by short-latency reflexes in human triceps surae. *Journal of Neurophysiology* **52**, 797–818.

Allum, J. H. J. & Pfaltz, C. R.(1985). Visual and vestibular contributions to pitch sway stabilization in the ankle muscles of normals and patients with bilateral peripheral deficits. *Experimental Brain Research* **58**, 82–94.

Alvarez, J. C., Diaz, C., Suarez, C., Fernandez, J. A., Gonzalez Del Rey, C., Navarro, A. & Tolivia, J. (1998). Neuronal loss in Human medial vestibular nucleus. *Anatomical Record* **251**, 431–438.

Appenzeller, O., Imarisio, J. J. & Gilbert, J. J. (1966). The effect of age and neurological disease on the ankle jerk. *Archives of Neurology* **15**, 147–150.

Arfken, C. L., Lach, H. W., Birge, S. J. & Miller, J. P. (1994). The prevalence and correlates of fear of falling in elderly persons living in the community. *American Journal of Public Health* **84**, 565–570.

Baloh, R. W., Corona, S., Jacobson, K. M., Enrietto, J. A. & Bell, T. (1998). A prospective study of posturography in normal older people. *Journal of American Geriatric Society* **46**, 438–443.

Baloh, R. W., Spain, S., Socotch, T. M., Jacobson, K. M. & Bell, T. (1995*a*). Posturography and balance problems in older people. *Journal of American Geriatric Society* **43**, 638–644.

Baloh, R. W., Yue, Q., Socotch, T. M. & Jacobson, K. M. (1995*b*). White matter lesions and disequilibrium in older people. I. Case-control comparison. *Archives of Neurology* **52**, 970–974.

Barbeau, A. (1973). Aging and the extrapyramidal system. *Journal of American Geriatric Society* **21**, 145–149.

Bartlett, S. A., Maki, B. E., Fernie, G. R., Holliday, P. J. & Gryfe, C. I. (1986). On the classification of a geriatric subject as a faller or nonfaller. *Medical Biological Engineering and Computers* **24**, 219–222.

Bedingham, W. & Tatton, W.G. (1984). Dependence of EMG responses evoked by imposed wrist displacements on preexisting activity in the stretched muscles. *Canadian Journal of Neurological Sciences* **11**, 272–280.

Bergstrom, G., Aniansson, A., Bjelle, A., Grimby, G., Lundgren-Lindquist, B. & Svanborg, A. (1985). Functional consequences of joint impairment at age 79. *Scandinavian Journal of Rehabilitation Medicare* **17**, 183–190.

Bloem, B. R., Allum, J. H. J., Carpenter, M. G., Verschuuren, J. J. G. M. & Honegger, F. (2002). Triggering of balance corrections and compensatory strategies in a patient with total leg proprioceptive loss. *Experimental Brain Research* **142**, 91–107.

Bloem, B. R., van Dijk, J. G. & Beckley, D. J. (1999). Are automatic postural responses in patients with Parkinson's disease abnormal due to their stooped posture? *Experimental Brain Research* **124**, 481–488.

Bloem, B. R., Van Dijk, J. G., Beckley, D. J., Zwinderman, A. H., Remler, M. P. & Roos, R. A. (1993). Correction for the influence of background muscle activity on stretch reflex amplitudes. *Journal of Neuroscience Methods* **46**, 167–174.

Borger, L. L., Whitney, S. L., Redfern, M. S. & Furman, J. M. (1999). The influence of dynamic visual environments on postural sway in the elderly. *Journal of Vestibular Research* **9**, 197–205.

Brocklehurst, J. C., Robertson, D. & James-Groom, P. (1982). Clinical correlates of sway in old age: sensory modalities. *Age and Aging* **11**, 1–10.

Buckwalter, J. A., Kuettner, K. E. & Thonar, E. J. (1985). Age-related changes in articular cartilage proteoglycans: electron microscopic studies. *Journal of Orthopaedic Research* **3**, 251–257.

Calne, D. B., Eisen, A. & Meneilly, A. (1991). Normal aging of the nervous system. *Annals of Neurology* **29**, 206–207.

Campbell, A. J., Borrie, M. J. & Spears, G. F. (1989). Risk factors for falls in a community-based prospective study of people 70 years and older. *Journal of Gerontology* **44**, M112–117.

Carel, R. S., Korczyn, A. D. & Hochberg, Y. (1979). Age and sex dependency of the Achilles tendon reflex. *American Journal of Medical Sciences* **278**, 57–63.

Carpenter, M. G., Allum, J. H. J. & Honegger, F. (1999). Directional sensitivity of stretch reflexes and balance corrections for normal subjects in the roll and pitch planes. *Experimental Brain Research* **129**, 93–113.

Carpenter, M. G., Allum, J. H. J. & Honegger, F. (2001*a*). Vestibular influences on human postural control in combinations of pitch and roll planes reveal differences in spatiotemporal processing. *Experimental Brain Research* **140**, 95–111.

Carpenter, M. G., Frank, J. S., Silcher, C. P. & Peysar, G. W. (2001*b*). The influence of postural threat on the control of upright stance. *Experimental Brain Research* **138**, 210–218.

Cavanaugh, J. T., Shinberg, M., Ray, L., Shipp, K. M., Kuchibhatla, M. & Schenkman, M. (1999). Kinematic characterization of standing reach: comparison of younger *vs.* older subjects. *Clinical Biomechanics* **14**, 271–279.

Chiu, J. & Robinovitch, S. N. (1998). Prediction of upper extremity impact forces during falls on the outstretched hand. *Journal of Biomechanics* **31**, 1169–1176.

Collins, J. J., De Luca, C. J., Burrows, A. & Lipsitz, L. A. (1995). Age-related changes in open-loop and closed-loop postural control mechanisms. *Experimental Brain Research* **104**, 480–492.

Cordo, P. J. & Nashner, L. M. (1982). Properties of postural adjustments associated with rapid arm movements. *Journal of Neurophysiology* **47**, 287–302.

Eng, J. J., Winter, D. A., MacKinnon, C. D. & Patla, A. E. (1992). Interaction of reaction moments and centre of mass displacement for postural control during voluntary arm movements. *Neurscience Research Communications* **11**, 73–80.

Era, P., Jokela, J. & Heikkinen, E. (1986). Reaction and movement times in men of different ages: a population study. *Perception and Motor Skills* **63**, 111–130.

Fernie, G. R., Gryfe, C. I., Holliday, P. J. & Llewellyn, A. (1982). The relationship of postural sway in standing to the incidence of falls in geriatric subjects. *Age and Aging* **11**, 11–16.

Fife, T. D. & Baloh, R. W. (1993). Disequilibrium of unknown cause in older people. *Annals of Neurology* **34**, 694–702.

Friedli, W. G., Hallett, M. & Simon, S. R. (1984). Postural adjustments associated with rapid voluntary arm movements 1. Electromyographic data. *Journal of Neurology, Neurosurgery and Psychiatry* **47**, 611–622.

Furman, J. M. R., Baloh, R. W., Barin, K., Hain, T. C., Herdman, S. J., Konrad, H. R. & Parker, S. W. (1993). Assessment: posturography. Report of the therapeutics and technology assessment subcommittee of the American Academy of Neurology. *Neurology* **43**, 1261–1264.

Gill, J., Allum, J. H. J., Carpenter, M. G., Held-Ziolkowska, M., Honegger, F. & Pierchala, K. (2001). Trunk sway measures of postural stability during clinical balance tests: effects of age. *Journal of Gerontology* **56A**, M438–447.

Greenspan, S. L., Myers, E. R., Maitland, L. A., Resnick, N. M. & Hayes, W. C. (1994). Fall severity and bone mineral density as risk factors for hip fracture in ambulatory elderly. *Journal American Medical Association* **271**, 128–133.

Grüneberg, C., Allum, J. H. J., Honegger, F. & Bloem, B. R. (2001). The influence of artificially increased trunk stiffness on automatic balance correcting responses. In *Control of Posture and Gait*, ed. Duysens, J., Smits-Engelsman, B. C. M. & Kingma, H., pp. 359–364. *Maastricht Symposium of the International Society for Postural and Gait Research.*

Hirasaki, E., Kubo, T., Nozawa, S., Matano, S. & Matsunaga, T. (1993). Analysis of head and body movements of elderly people during locomotion. *Acta oto-laryngologica. Supplementum* **501**, 25–30.

Hodges, P. W., Cresswell, A. G., Daggfeldt, K. & Thorstensson, A. (2000). Three dimensional preparatory trunk motion precedes asymmetrical upper limb movement. *Gait and Posture* **11**, 92–101.

Horak, F. B. & Nashner, L. M. (1986). Central programming of postural movements: adaptation to altered support surface configurations. *Journal of Neurophysiology* **55**, 1369–1381.

Iles, J. F. (1977). Responses in human pretibial muscles to sudden stretch and to nerve stimulation. *Experimental Brain Research* **30**, 451–470.

Inns, F. J. & Endhold, O. G. (1981). Studies of gait and mobility in the elderly. *Age and Ageing* **10**, 147–156.

Kerrigan, D. C., Todd, M. K., Della Croce, U., Lipsitz, L. A. & Collins, J. J. (1998). Biomechanical gait alterations independent of speed in the healthy elderly: evidence for specific limiting impairments. *Archives of Physical Medicine and Rehabilitation* **79**, 317–322.

Keshner, E. A., Allum, J. H. J. & Honegger, F. (1993). Predictors of less stable postural responses to support surface rotations in healthy human elderly. *Journal of Vestibular Research* **3**, 419–429.

Keshner, E. A., Allum, J. H. J. & Pfaltz, C. R. (1987). Postural coactivation and adaptation in the sway stabilizing responses of normals and patients with bilateral vestibular deficit. *Experimental Brain Research* **69**, 77–92.

Keshner, E. A., Woollacott, M. H. & Debu, B. (1988). Neck and trunk muscle responses during postural perturbations in humans. *Experimental Brain Research* **71**, 455–466.

Koller, W. C., Glatt, S. L., Fox, J. H., Kaszniak, A. W., Wilson, R. S. & Huckman, M. S. (1981). Cerebellar atrophy: relationship to aging and cerebral atrophy. *Neurology* **31**, 1486–1488.

Lichtenstein, M. J., Burger, M. C., Shields, S. L. & Shiavi, R. G. (1990). Comparison of biomechanics platform measures of balance and videotaped measures of gait with a clinical mobility scale in elderly women. *Journal of Gerontology* **45**, M49–54.

Lichtenstein, M. J., Shields, S. L., Shiavi, R. G. & Burger, M. C. (1988). Clinical determinants of biomechanics platform measures of balance in aged women. *Journal of the American Geriatric Society* **36**, 996–1002.

Lord, S. R., Clark, R. D. & Webster, I. W. (1991). Postural stability and associated physiological factors in a population of aged persons. *Journal of Gerontology* **46**, M69.

Lord, S. R., Rogers, M. W., Howland, A. & Fitzpatrick, R. (1999). Lateral stability, sensorimotor function and falls in older people. *Journal of American Geriatric Society* **47**, 1077–1081.

Lord, S. R., Ward, J. A., Williams, P. & Anstey, K. J. (1994). Physiological factors associated with falls in older community-dwelling women. *Journal of American Geriatric Society* **42**, 1110.

McGill, S. M., Yingling, V. R. & Peach, J. P. (1999). Three-dimensional kinematics and trunk muscle myoelectric activity in the elderly spine – a database compared to young people. *Clinical Biomechanics* **14**, 389–395.

McIlroy, W. E. & Maki, B. E. (1994). Compensatory arm movements evoked by transient perturbations of upright stance. In *Vestibular and Neural Front*, ed. Taguchi, K., Igarashi, M. & Mori, S., pp. 489–492. Elsevier, Amsterdam.

McIlroy, W. E. & Maki, B. E. (1995). Early activation of arm muscles follows external perturbations of upright stance. *Neuroscience Letters* **184**, 177.

Maki, B. E. (1993). Biomechanical approach to quantifying anticipatory postural adjustments in the elderly. *Medical Biological Engineering and Computers* **31**, 355–362.

Maki, B. E., Holliday, P. J. & Fernie, G. R. (1990). Aging and postural control. A comparison of spontaneous- and induced-sway balance tests. *Journal of American Geriatric Society* **38**, 1–9.

Maki, B. E., Holliday, P. J. & Topper, A. K. (1991). Fear of falling and postural performance in the elderly. *Journal of Gerontology* **45**, M123–131.

Maki, B. E., Holliday, P. J. & Topper, A. K. (1994). A prospective study of postural balance and risk of falling in an ambulatory and independent elderly population. *Journal of Gerontology* **49**, M72–84.

Maki, B. E. & McIlroy, W. E. (1997). The role of limb movements in maintaining upright stance: The ‘change in support’ strategy. *Physical Therapy* **77**, 488–507.

Maki, B. E. & McIlroy, W. E. (1998). Control of compensatory stepping reactions: age-related impairment and the potential for remedial intervention. *Physiotherapy Theory and Practice* **15**, 69–90.

Maki, B. E., McIlroy, W. E. & Perry, S. D. (1996). Influence of lateral destabilization on compensatory stepping responses. *Journal of Biomechanics* **29**, 343–353.

Melton, L. J., Chao, E. Y. S. & Lane, J. (1988). Biomechanical aspects of fractures. In *Osteoporosis: Etiology, Diagnosis and Management*, ed. Riggs, B. L. & Melton, L. J., pp. 111–131. Raven Press, New York.

Murray, M. P., Seireg, A. A. & Sepic, S. B. (1975). Normal postural stability and steadiness: quantitative assessment. *Journal of Bone and Joint Surgery. American volume* **57**, 510–516.

Nardone, A., Siliotto, R., Grasso, M. & Schieppati, M. (1995). Influence of aging on leg muscle reflex responses to stance perturbation. *Archives of Physical Medicine and Rehabilitation* **76**, 158–165.

Nevitt, M. C. & Cummings, S. R. (1993). Type of fall and risk of hip and wrist fractures: the study of osteoporotic fractures. The Study of Osteoporotic Fractures Research Group. *Journal of the American Geriatric Society* **41**, 1226–1234.

O'Neill, T. W., Varlow, J., Silman, A. J., Reeve, J., Reid, D. M., Todd, C. & Woolf, A. D. (1994). Age and sex influences on fall characteristics. *Annals of Rheumatory Disorders* **53**, 773–775.

Overstall, P. W., Exton-Smith, A. N., Imms, F. J. & Johnson, A. L. (1977). Falls in the elderly related to postural imbalance. *British Medical Journal* **1**, 261–264.

Peterka, R. J. & Black, F. O. (1990). Age-related changes in human posture control: sensory organization tests. *Journal of Vestibular Research* **1**, 73–85.

Rivner, M. H., Swift, T. R. & Malik, K. (2001). Influence of age and height on nerve conduction. *Muscle Nerve* **24**, 1134–1141.

Roach, K. E. & Miles, T. P. (1991). Normal hip and knee active range of motion: the relationship to age. *Physical Therapy* **71**, 656–665.

Robinovitch, S. N. & Chiu, J. (1998). Surface stiffness affects impact force during a fall on the outstretched hand. *Journal of Orthopaedic Research* **16**, 309–313.

Schenkman, M., Hughes, M. A., Bowden, M. G. & Studenski, S. A. (1995). A clinical tool for measuring functional axial rotation. *Physical Therapy* **75**, 151–156.

Shepard, N. T., Schultz, A. B., Alexander, N. B., Gu, M. J. & Boismier, T. (1993). Postural control in young and elderly adults when stance is challenged: clinical *versus* laboratory measurements. *Annals of Otology, Rhinology and Laryngology* **102**, 508–517.

Stelmach, G. E., Phillips, J., Di Fabio, R. P. & Teasdale, N. (1989*a*). Age, functional postural reflexes, and voluntary sway. *Journal of Gerontology* **44**, B100–106.

Stelmach, G. E., Teasdale, N., Di Fabio, R. P. & Phillips, J. (1989*b*). Age related decline in postural control mechanisms. *International Journal of Aging and Human Development* **29**, 205–223.

Stelmach, G. E. & Worringham, C. J. (1985). Sensorimotor deficits related to postural stability: implications for falling the elderly. *Clinical Geriatric Medicine* **1**, 679–694.

Tanosaki, M., Ozaki, I., Shimamura, H., Baba, M. & Matsunaga, M. (1999). Effects of aging on central conduction in somatosensory evoked potentials: evaluation of onset *versus* peak methods. *Clinical Neurophysiology* **110**, 2094–2103.

Taylor, P. K. (1993). CMAP dispersion, amplitude decay, and area decay in a normal population. *Muscle Nerve* **16**, 1181–1187.

Tell, G. S., Lefkowitz, D. S., Diehr, P. & Elster, A. D. (1998). Relationship between balance and abnormalities in cerebral magnetic resonance imaging in older adults. *Archives of Neurology* **55**, 73–79.

Thelen, D. G., Ashton-Miller, J. A., Schultz, A. B. & Alexander, N. B. (1996). Do neural factors underlie age differences in rapid ankle torque development? *Journal of the American Geriatric Society* **44**, 804–808.

Timmann, D. & Horak, F. B. (1997). Prediction and set-dependent scaling of early postural responses in cerebellar patients. *Brain* **120**, 327–337.

Tinetti, M. E. & Powell, L. (1993). Fear of falling and low self-efficacy: a cause of dependence in elderly persons. *Journal of Gerontology* **48**, 35–38.

Tobimatsu, S., Sun, S. J., Fukui, R. & Kato, M. (1998). Effects of sex, height and age on motor evoked potentials with magnetic stimulation. *Journal of Neurology* **245**, 256–261.

Topper, A. K., Maki, B. E. & Holliday, P. J. (1993). Are activity-based assessments of balance and gait in the elderly predictive of risk of falling and/or type of fall? *Journal of the American Geriatric Society* **41**, 479–487.

Whipple, R. H., Wolfson, L. I. & Amerman, P. M. (1987). The relationship of knee and ankle weakness to falls in nursing home residents: an isokinetic study. *Journal of the American Geriatric Society* **35**, 13–20.

Williams, H. G., McClenaghan, B. A. & Dickerson, J. (1997). Spectral characteristics of postural control in elderly individuals. *Archives Physical Medicine and Rehabilitation* **78**, 737–744.

Woollacott, M. H. (1986). Gait and postural control in the aging adult. In *Disorders of Posture and Gait*, ed. Bles, W. & Brandt, T., pp. 325–314. Elsevier Science Publishers B.V. (Medical Division), Amsterdam.

Woollacott, M. H., Inglin, B. & Manchester, D. (1988). Response preparation and posture control. Neuromuscular changes in the older adult. *Annals of the New York Academy of Sciences* **515**, 42–53.

Woollacott, M. H., Shumway-Cook, A. & Nashner, L. M. (1982). Postural reflexes and aging. In *The Aging Motor System*, ed. Mortimer, J. A., Pirozzolo, F. J. & Maletta, J. G., pp. 98–119. Praeger, New York.

Acknowledgements

This work was supported by a grant from the Swiss National Science Foundation (31-59319.99) to J.H.J.A., and a research grant of the Dutch Parkinson Patient Association to B.R.B.; M.G.C. and A.L.A. were also supported by NSERC grants from Canada. We thank Mrs E. Clarke for typographical assistance and Dr J. Visser for graphical assistance.