

RESEARCH ARTICLE

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Directional sensitivity of stretch reflexes and balance corrections for normal subjects in the roll and pitch planes

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Abstract A large body of evidence has been collected which describes the response parameters associated with automatic balance corrections in man to perturbations in the pitch plane. However, perturbations to human stance can be expected from multiple directions. The purpose of the present study was to describe the directional sensitivities of muscle responses re-establishing disturbed stance equilibrium in normal subjects. The contributions of stretch reflex and automatic balance-correcting responses to balance control, and concomitant biomechanical reactions, were examined for combinations of pitch and roll perturbations of the support surface. More specifically, muscle responses, initial head accelerations and trunk velocities were analyzed with the intention of identifying possible origins of directionally specific triggering signals and to examine how sensory information is used to modulate triggered balance corrections with respect to direction. Fourteen healthy adults were required to stand on a dual-axis rotating platform capable of delivering rotational perturbations with constant amplitude (7.5°) and velocity (50°/s) through multiple directions in the pitch and roll planes. Each subject was randomly presented with 44 support surface rotations through 16 different directions separated by 22.5° first under eyes-open, and then, for a second identical set of rotations, under eyes-closed conditions. Bilateral muscle activities from tibialis anterior, soleus, lateral quadriceps and paraspinals were recorded, averaged across direction, and areas calculated over intervals with significant bursts of activity. Trunk angular velocity and ankle torque data were averaged over intervals corresponding to significant biomechanical events. Stretch reflex (intervals of 40–100, 80–120 ms) and automatic balance-correcting

responses (120–220, 240–340 ms) in the same muscle were sensitive to distinctly different directions. The directions of the maximum amplitude of balance-correcting activity in leg muscles were oriented along the pitch plane, approximately 180° from the maximum amplitude of stretch responses. Ankle torques for almost all perturbation directions were also aligned along the pitch plane. Stretch reflexes in paraspinal muscles were tuned along the 45° plane but at 90° to automatic balance corrections and 180° to unloading responses in the same muscle. Stretch reflex onsets in paraspinal muscles were observed at 60 ms, as early as those of soleus muscles. In contrast, unloading reflexes in released paraspinal muscles were observed at 40 ms for perturbations which caused roll of the trunk towards the recorded muscle. Onsets of trunk roll velocities were earlier and more rapid than those observed for pitch velocities. Trunk pitch occurred for pure roll directions but not vice versa. When considered together, early stretch and unloading of paraspinals, and concomitant roll and pitch velocities of the trunk requiring a roll-and-pitch-based hip torque strategy, bring into question previous hypotheses of an ankle-based trigger signal or ankle-based movement strategies for postural balance reactions. These findings are compatible with the hypothesis that stretch-, force- and joint-related proprioceptive receptors at the level of the trunk provide a directionally sensitive triggering mechanism underlying a, minimally, two-stage (pitch-based leg and pitch-and-roll-based trunk) balance-correcting strategy. Accelerometer recordings from the head identified large vertical linear accelerations only for pitch movements and angular roll accelerations only during roll perturbations with latencies as early as 15 ms. Thus, it appears that balance corrections in leg and trunk muscles may receive strong, receptor-dependent (otolith or vertical canal) and directionally sensitive amplitude-modulating input from vestibulospinal signals.

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Introduction

Falls occur in different directions and at different speeds depending primarily on the original direction and intensity of the perturbation and secondarily on the flexibility of the trunk in both the roll and pitch planes. The conversion of sensory information on the perturbation to appropriate balance corrections is a task the central nervous system (CNS) must rapidly initiate and accurately modulate if a fall is to be prevented. This is accomplished by the CNS initiating bursts of muscle activity with onset latencies around 100–120 ms at a number of body segments thereby providing the effective righting reaction (Allum and Honegger 1992; Allum et al. 1994; Keshner et al. 1987, 1988). Bursts of muscle activity appearing up to 100 ms after onset of the perturbation, generated by proprioceptive stretch reflexes, do not have sufficient strength to prevent a fall (Allum and Pfaltz 1985). From a neurophysiological viewpoint a number of general questions can be raised about these processes. For example, the question arises about the earliest and most directionally specific trigger signal for balance corrections, be it of vestibular or proprioceptive origin. Following initiation of a pattern of responses appropriate for the direction of falling, the responses must be scaled to correct the fall. Again the question is the nature of the underlying sensory signals contributing to this modulation of balance corrections and whether this scaling could be different for different directions of falling.

Previous work on balance corrections has almost exclusively been limited to the pitch plane. This work, which mostly concentrated on lower-leg muscles, established that the latencies of balance corrections occur in a narrow time band of 90–120 ms (Nashner 1977; Allum and Büdingen 1979; Diener et al. 1983). Following the terminology of Melvill Jones and Watt (1971), the observed balance corrections were initially classified as “functional stretch reflexes”, with ankle inputs seen as the primary sensory triggering signal (Nashner 1976, 1977; Diener et al. 1983, 1984). The term “functional stretch reflex” implies that automatic balance corrections are very similar to or even initiated by stretch of leg muscles. Based on this concept, the question arises whether information on the directional sensitivity of balance corrections is best studied using either a constant amount of ankle rotation or other joint rotation.

One common approach used previously for pitch perturbations has been to manipulate different characteristics of the perturbation to destabilize the body while holding ankle rotation at a constant amplitude and observe resultant changes in the automatic responses of biomechanical and muscular variables. For example, translational versus rotational movements of the support surface yield very distinct postural responses regardless of the similarities in ankle joint rotation and stretch responses of ankle musculature (Nardone et al. 1990; Allum and Honegger 1992; Allum et al. 1990, 1993; Schieppati et al. 1995). Allum et al. (1989) observed postural responses to ankle dorsiflexion rotations of the

support surface which were consistent with a two-segment “stiffening strategy” whereas a backward translation elicited a multiple-segment or “multilink” strategy of movement. Observation of stretch-related information at the level of the neck (Keshner et al. 1988) and in intrinsic muscles of the foot (Schieppati et al. 1995) prior to stretch responses in triceps surae muscles provided additional evidence that stretch reflexes and balance corrections consist of distinct neurophysiological entities in contrast to the long-standing hypothesis of an ascending pattern of muscle activation triggered by stretch-related proprioceptive input from the ankle joint muscles (Nashner 1977; Horak and Nashner 1986). To provide further support for the concept that balance corrections can be triggered independent of ankle stretch input, Allum et al. (1995, 1998) utilized combinations of backward translations and plantarflexion rotations of the support surface. This combined perturbation provided a unique condition by nulling any proprioceptive input from ankle joint or lower-leg muscle stretch receptors. With this combination, Allum and colleagues were able to demonstrate that properly timed balance corrections in leg and trunk muscles of normal and vestibular loss subjects were still present in the absence of ankle input.

An alternative method commonly employed in searching for the origin of triggered postural responses has been to study the automatic responses of patient populations with “lesions” of the hypothesized triggering sensory system. Observing changes associated with the absence of information from lower-leg proprioceptive systems may help to reveal the relative contributions of proprioceptive information to the triggering and modulation of automatic postural responses that comprise balance corrections. For example, Inglis et al. (1994) found significant differences in the onset latencies of postural responses between patients with selective proprioceptive loss at the level of the ankle and normal controls. However, recent investigations by Bloem and colleagues (Allum et al. 1998; Bloem et al. 1999a), which employed a more vigorous selection procedure to eliminate any confounding effects of muscle strength frequently accompanying selective proprioceptive loss, yielded no evidence of significant differences in onset latencies of automatic postural responses to pure rotation and combined translation/plantarflexion rotation perturbations with nulled ankle inputs. These findings, when considered with earlier evidence from the work of Keshner et al. (1988), Allum et al. (1995, 1998) and Schieppati et al. (1995), provide a substantial body of evidence supporting the position that lower leg stretch reflexes and subsequent balance corrections involve different neurophysiological mechanisms.

Additional directional characteristics of balance corrections in the pitch plane have been discovered. Following the observation of correct postural responses to changes in the forward and backward direction of platform perturbations within a single trial in cats, Rushmer et al. (1983) concluded that these triggered postural responses were sensitive to the direction of the perturba-

tion. In addition, both the amount of information available prior to the perturbation and previous experience with similar perturbations in the pitch plane have been shown to significantly influence the magnitude of the automatic postural response (Horak et al. 1989; Beckley et al. 1991).

Although significant amounts of information regarding the characteristics of balance-correcting responses have resulted from both altered perturbation and lesional studies, the general applicability of these findings to falls in several directions should be seriously questioned. In all of the aforementioned studies, regardless of the type of perturbation (i.e. translational, rotational or combination of both), each has limited the direction of the perturbation to a single plane, specifically the sagittal or pitch plane. However, joint receptors (Rothwell 1994) and vestibular receptors (Tomko et al. 1981) provide directional information in planes other than the pitch plane. Furthermore, the directions of maximum isometric stabilizing activity in neck (Keshner et al. 1988), trunk (Lavender et al. 1994) and elbow muscles (Buchanan et al. 1986) lie in multiple planes. As perturbations to equilibrium can be expected, under normal conditions, to occur in directions other than that of a pure pitch orientation, it seems essential to characterize the properties of the postural control system using perturbations in multiple directions. Aruin and Latash (1995) have demonstrated that anticipatory postural reactions in postural leg muscles are modulated to the direction of fast voluntary arm movements. However, to date only a limited amount of research has been devoted to examining the sensitivity of postural leg and trunk muscle responses to unexpected perturbations in multiple directions. Some studies involving multidirection platform displacements have been performed using human (Maki et al. 1994; Moore et al. 1988; Henry et al. 1998) and cat paradigms (Rushmer et al. 1988; Macpherson 1988a, 1988b, 1994). Experiments from both paradigms have produced evidence supporting the sensitivity of both muscular and biomechanical postural responses to perturbation direction. However, the findings of these multidirectional studies must be weighed against the limitations of the experimental design, including non-randomized and restricted directions and the choice of a single measurement interval overlapping both stretch-reflex and balance-correcting activity. Irrespective of any limitations in protocol, support surface translation studies may also lack the capability to independently observe directionally specific responses in stretch reflex and automatic balance-correcting responses in the lower leg muscles unless the stretch reflex is first nulled out by simultaneous plantarflexion of the support surface (Nashner et al. 1982; Allum and Honegger 1998). Support-surface translation, in contrast to rotation, generally has a slower rise time because of the large mass that must be moved. The slower rise time causes stretch reflex and balance-correcting activity to coalesce in lower leg muscles (Allum et al. 1993). However, in order to understand how directional propriocep-

tive information is used to trigger and/or modulate postural responses, the ability to distinguish between stretch reflex and triggered automatic balance-correcting responses seems vital.

The purpose of the present study was to examine the postural responses of normal healthy adults to support surface rotations in 16 different, randomly presented, pitch and roll combinations. It was hypothesized that biomechanical and muscular activity of lower leg and trunk muscles with respect to stretch reflex and subsequent balance-correcting responses would be sensitive to the direction of the perturbation. It was hoped that observed intramuscular differences in the directional sensitivity of response magnitudes would shed further light onto the relative contributions from the hip, knee and ankle proprioceptive inputs in triggering balance corrections and increase the understanding of how the CNS utilizes vestibular and proprioceptive information to code and modulate responses to the direction of a postural perturbation.

Materials and methods

This study examined the effect of multidirection rotations of the support surface on muscular and biomechanical responses in normal healthy young adults. Seventeen participants (8 male, 9 female; mean age 23 SD 2.6 years; height 1.73 SD 0.08 m; weight 69.5 SD 12.2 kg) volunteered for the study and gave witnessed prior informed consent to participate in the experiment after observing several multidirectional movements of the support surface. All subjects were free from any neurological or previous orthopaedic injuries as verified by self-report and possessed normal balance function as verified by Unterberger and Romberg stance tests.

Subjects were positioned on the force-measuring platform with their feet lightly strapped across the instep to the support surface. Backward movement of the heel was prevented by an adjustable heel bar. This procedure ensured that the lateral malleoli were aligned with the platform's pitch axis of rotation for every trial and was identical to that used in our previous studies (Allum and Pfaltz 1985; Allum et al. 1993, 1994, 1995, 1996; Allum and Honegger 1998). The subjects were asked to assume their normal standing posture, with straight knees and arms hanging comfortably at their sides. Force-plate reaction forces were then reset to zero to establish a reference value for the individual's "preferred stance" position.

Stimulus parameters

The dual-axis rotating force-platform was capable of delivering unexpected rotations through multiple directions in the pitch and roll planes. Platform rotations had a constant amplitude of 7.5° and an angular velocity of 50°/s. A clockwise increasing notation, as viewed from above, was used to specify rotation direction. The 0° rotation direction represented a pure "toes-down" tilt of the platform; conversely, a 180° direction represented a pure "toes-up" rotation. Pure roll movements were assigned angles of 90° to the right and 270° to the left. Combinations of pitch and roll rotations were used to denote 12 other directions, each separated by 22.5°. In order to record electromyographic activity, ankle torque and trunk angular velocity, two sequences of eight directions (0, 45, 90, 135, 180, 225, 270, 315) and (22.5, 67.5, 112.5, 157.5, 202.5, 247.5, 292.5, 337.5) were presented on two separate days (on average, 3 days apart) under eyes-open and eyes-closed conditions on both occasions to 14 subjects (7

female and 7 male). Each series consisted of 44 randomly presented rotational stimuli. Responses to the very first stimulus in each series were ignored in the data analysis to reduce the effects of adaptation (Nashner et al. 1982; Keshner et al. 1987) entering the data, leaving five to six sets of responses per direction and condition in the subject average. The order of presentation of the two directional sequences was counterbalanced between subjects to minimize any ordering effects. Order of visual manipulation (eyes open vs eyes closed) was not randomized to allow future comparisons between normal and subsequently collected patient population data. Although it is acknowledged that the non-random presentation of visual conditions may have invited confounding effects due to order (Keshner et al. 1987), the balance tasks had to be performed in a sequence of increasing difficulty to ensure the safety of patients in future studies. A 5- to 10-min rest period was provided between eyes-open and eyes-closed conditions to try to minimize any confounding effects due to order and/or fatigue. Biomechanical variables, and repeated measures of ankle torque and trunk angular velocity, were recorded in a separate session on average 19 days after the EMG recordings. For this session only the sequence of directions (0, 45, 90, 135, 180, 225, 270, 315) was presented under eyes-open conditions to nine of the subjects (five females and four males) who had had EMG recordings and three female subjects without EMG recordings to have roughly equal numbers of subjects for EMG and biomechanical recordings.

Each perturbation was preceded by a random 5- to 20-s delay. During this delay period subjects were required to maintain anterior/posterior (A-P) ankle torque within a range of ± 1 Nm from the "preferred stance" reference value using online visual feedback from an oscilloscope placed at eye level approximately 1 m away from the subject. During the eyes-closed condition two distinct auditory tones were substituted for visual feedback to monitor variations in A-P ankle torques prior to the stimulus onset. The 5- to 20-s interstimulus delay was initiated automatically once the platform had returned to its original prestimulus position and the subject regained his preferred vertical position.

In response to each rotational perturbation, the subject was instructed to recover their balance as quickly as possible. Handrails were located on the lateral borders of the platform apparatus in case of loss of balance and a spotter was present in close proximity to lend support in case of a fall. No stimuli caused the subject to touch the handrail or to need assistance by the spotter.

Biomechanical and EMG recordings

All biomechanical and electromyographic (EMG) recordings were initiated 100 ms prior to the onset of the perturbation and had a sampling duration of 1 s. Support surface reaction forces were measured from two independent force-plates mounted on the moveable platform. Vertical forces were measured by strain gauges located under the corners of each plate. From these forces A-P and medial lateral (M-L) ankle torques were calculated (Allum and Honegger 1998). Trunk angular velocity in the pitch and roll planes was collected using Watson Industries transducers ($\pm 300^\circ/\text{s}$ range) mounted to a metal plate which hung from shoulder straps at a level on the chest equivalent to the position of the sternum. Pitch and roll angles of the left lower leg were recorded with respect to vertical using a goniometer system consisting of two potentiometers oriented at 90° to one another and attached to a lightweight metal rod strapped to the lower leg just below the knee at 4 cm below the lateral condyle of the tibia. The left upper-leg pitch and roll angular velocities were measured with Watson Industries transducers ($\pm 100^\circ/\text{s}$ range, 0–50 Hz bandwidth). The transducers were mounted perpendicular to one another on a 20-cm-long metal plate moulded to the curvature of the upper leg. The plate was held firmly attached to the upper leg by means of an elasticated bandage. Left knee pitch and roll angular velocities were computed offline from the difference of the upper- and lower-leg angular velocities after differentiating the lower leg angle digitally. All biomechanical data were sampled at 500 Hz and digitally low-pass

filtered offline at 25 Hz using a zero phase-shift 10th-order Butterworth filter.

Surface EMG electrodes were placed bilaterally, approximately 3 cm apart, along the muscle bellies of tibialis anterior, soleus, lateral quadriceps (vastus lateralis) and paraspinal muscles. EMG amplifier gains were kept constant and pairs of electrodes and lead lengths assigned to individual muscles were not changed between subjects. EMG recordings were sampled at 1 KHz, band-pass filtered between 60 and 600 Hz, full-wave rectified, and low-pass filtered at 100 Hz as recommended by Gottlieb and Agarwal (1979).

Data analysis

Following analog to digital conversion of the data, offline analysis was initiated by defining the zero latency point and averaging subject EMG and biomechanical signals for each perturbation direction (five to six stimuli per direction). Zero latency was defined as the first inflexion of ankle rotation velocity and did not vary with direction or subject. For each trial background EMG activity of each muscle recorded 100 ms prior to stimulus onset was averaged and subtracted from the EMG signal before response areas for the trial were calculated. EMG areas were calculated using trapezoid integration within predetermined time intervals associated with previously identified stretch (40–100, 80–120 ms from stimulus onset), balance-correcting (120–220 ms), secondary balance-correcting (240–340 ms), and stabilizing reaction (350–700) responses (Allum et al. 1993, 1994, 1996). Fixed intervals were used rather than alternative terminologies for averaging intervals such as medium- (ML) and long-latency (LL) response intervals (Beckley et al. 1991; Diener et al. 1983, 1984) for two reasons. Often it is difficult to define separate ML and LL periods of activity in a muscle response (Allum et al. 1993) and secondly responses after early stretch reflexes were often active at several body segments simultaneously (see Figs. 4, 6). All biomechanical and muscular profiles were averaged across each direction and subject averages were pooled to produce a population average for each direction. Response latencies were measured on individual trials once it had been determined visually that a consistent activity pattern occurred for all responses from the subject for one direction. A latency was set if the activity pattern diverged for more than 40 ms at least one standard deviation away from the mean EMG activity 100 ms prior to stimulus onset.

Results

Rotation of the support surface induced a direction-specific displacement of body segments during the first 150 ms from onset of the stimulus (Fig. 1). In general, the subsequent balance-corrections enhanced initial movements of the trunk (see Figs. 2, 3, 5). Balance corrections consisted of multisegmental, automatic, muscle activity with onsets in the range of 100–150 ms from stimulus onset (see Figs. 4, 6). Roll displacements of the trunk occurred earlier and were corrected earlier than pitch displacements (see Figs. 2, 3, 5), even though balance-correcting muscle activity did not appear to change in onset between pitch and roll. However, the depth of modulation of muscle activity changed considerably between pitch and roll (see Figs. 4, 6), being stronger and more asymmetric in the trunk muscles, and weaker in the leg muscles for roll (see Figs. 7, 10). The presence of stretch reflex and/or unloading activity after 39, 44 and 73 ms in paraspinal, soleus and tibialis anterior, respectively, was another significant muscle activity pattern change with

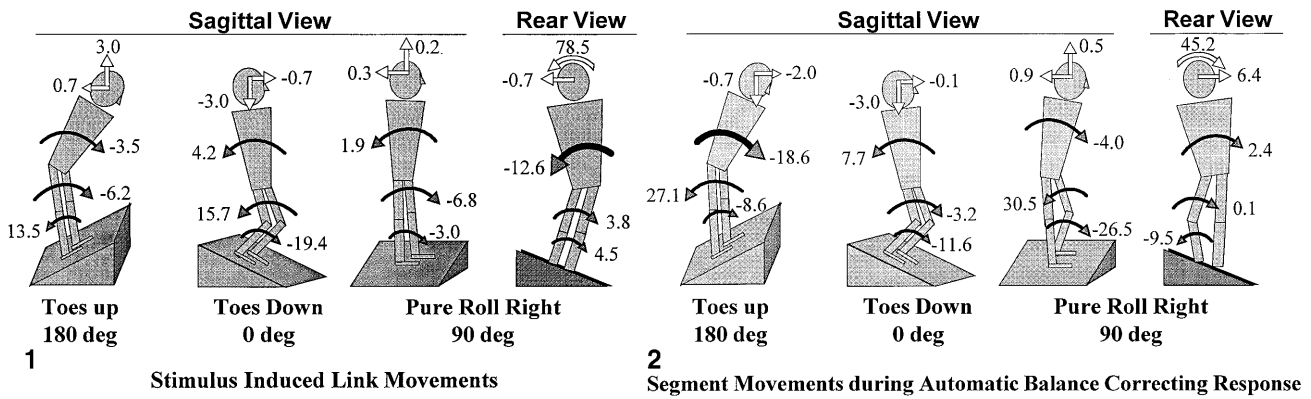


Fig. 1 Initial stimulus-induced link movements in response to rotational perturbations in pure pitch and roll directions. *Curved-filled arrows* and corresponding values represent the direction and average (population) magnitude of trunk, upper leg and lower leg angular velocity in degrees/s calculated over the period 0–150 ms. *The thickened curved arrow* indicates the fastest trunk velocity. *Open arrows* represent average linear (*straight arrows* values in cm/s²) and angular roll (*curved arrows* values in degrees/s²) accelerations of the head between 40 and 90 ms. Toe-up and roll perturbations elicit two-segment, whereas toe-down rotations elicit multilink, reactions

Fig. 2 Biomechanical responses during automatic balance-correcting responses to rotational perturbations in pure pitch and roll directions. *Curved filled arrows* and corresponding values represent the direction and average (population) magnitude of trunk, upper leg and lower leg angular velocity in degrees/s calculated between 240 and 300 ms. *Open arrows* represent average linear (*straight* in cm/s²) and angular roll (*curved* in degrees/s²) accelerations of the head between 180 and 240 ms

direction (see Figs. 4, 6). Our working hypothesis is that these phases of early stimulus-induced and the later occurring, balance-correcting, muscle activity result from different neurophysiological phenomena underlying the postural response to the balance perturbations. Therefore our experimental observations have been presented within the concept of a sequence of such balance-related intervals which together constitute a smoothly executed movement strategy.

Stimulus-induced responses

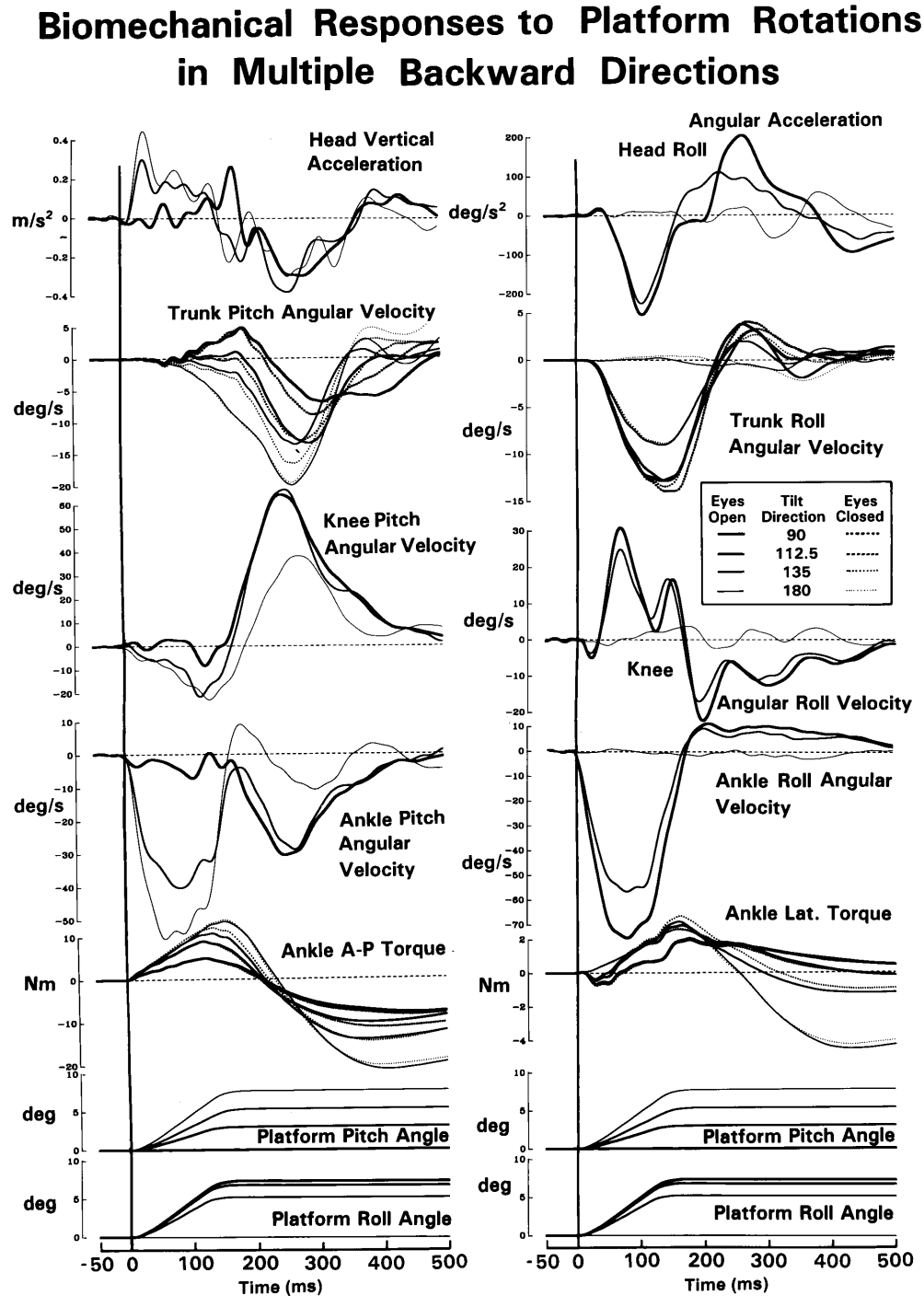
Pitch plane rotations

During the 180° (toes-up) rotational stimuli, the body was forced into movement as a two-segment system (Fig. 1). This two-link motion dominated the subsequent balance correction (see Fig. 2), because the upper and lower legs moved as essentially one link. As observed in Fig. 3, within 50 ms following the onset of platform rotation the ankle was passively dorsiflexed to reach a peak velocity of 60°/s (thinnest set of lines in ankle pitch velocity traces). Corresponding stretch reflexes in soleus muscles were observed (Fig. 4), with an onset latency of 44 ms (SD 3.7 ms). Stimulus onset marked the beginning of a passive backward rotation of

the lower limb segment coupled with forward rotation of the upper leg, thereby forcing the knee into hyperextension with a maximum knee angular-velocity of 20°/s. Forward flexion of the other major link, the trunk segment, was first observed at 50–60 ms, which caused a stretch reflex in paraspinals with onset latency of 68 ms (SD 15 ms). Initial movements of the head were dominated by early upward accelerations at 15 ms followed by smaller horizontal accelerations in the backward direction. Upward accelerations of the head reached a maximum of 0.45 m/s² at a time to peak of 35 ms (Fig. 3). For the purposes of movement strategy conceptualisation, motion of the head as a separate link is not emphasized here (see Allum et al. 1997). These results did not differ from those obtained in our pitch rotation studies (see Fig. 2, Allum and Honegger 1998) for which the feet were also strapped to the support surface.

As illustrated in Fig. 1, during the 0° (toes down) stimulus the body responded as a three-link system and again this mode of movement comprised the subsequent balance correction (see Figs. 1, 2, 5). The ankles were initially pulled into plantarflexion by platform rotation with a maximum angular velocity of 70°/s (Fig. 5). Stretched tibialis anterior muscles (see Fig. 6) demonstrated reflex responses with latencies of 73 ms (SD 12 ms). Forward rotation of the lower leg segment began at 100 ms. However, backward rotation of the upper leg caused flexion of the knee joint as early as 15 ms with increasing velocity until a maximum of 60°/s was reached at 200 ms (Fig. 5). Corresponding to this period of knee flexion, stretch reflexes were observed in quadriceps muscles with latencies of 85 ms. Backward rotation of the trunk segment was first observed in angular velocity traces, unloading the paraspinal muscles as evidenced by a decrease in stimulus-induced paraspinal EMG activity below prestimulus background levels clearly seen at 70 ms (see, for example, the thin traces in left paraspinals in Fig. 6). The onset latency of the unloading response was on average 45 ms (SD 12 ms). Trunk movement was preceded by early downward vertical linear accelerations of the head peaking at 30 ms and smaller anterior head accelerations at 50 ms (see Figs. 1, 5). Maximum vertical accelerations of the head reached 0.6 m/s².

Fig. 3 Biomechanical responses (average of 12 subjects) to rotational perturbations in multiple backward directions between 90° (pure roll right) and 180° (toe-up) directions for both eyes open (*solid lines*) and eyes closed (*dashed lines*) conditions. The black vertical line at 0 ms represents the onset of ankle rotation. For most recorded variables four traces are shown (for the directions of 90°, 112.5°, 135°, 180°) in decreasing line thickness as the perturbation direction moves from pure roll to pure pitch. In the set of recordings for ankle and knee angular velocities, and head accelerations, only three traces are shown (for 90°, 135° and 180°) because these variables were not recorded for 112.5°. The following traces are plotted positive following the convention of Figs. 1 and 2: trunk pitch backwards, trunk roll right, head linear accelerations upwards, head angular acceleration right (viewed from behind), knee flexion, ankle dorsiflexion, and ankle and knee roll caused by rotation of the lower and upper leg, respectively, to the right. The ankle and knee traces were recorded from the left leg. Note: (1) scaling of all biomechanical variables with respect to direction, (2) early vertical and roll accelerations of the head and (3) early onset of roll compared to pitch angular velocity of the trunk

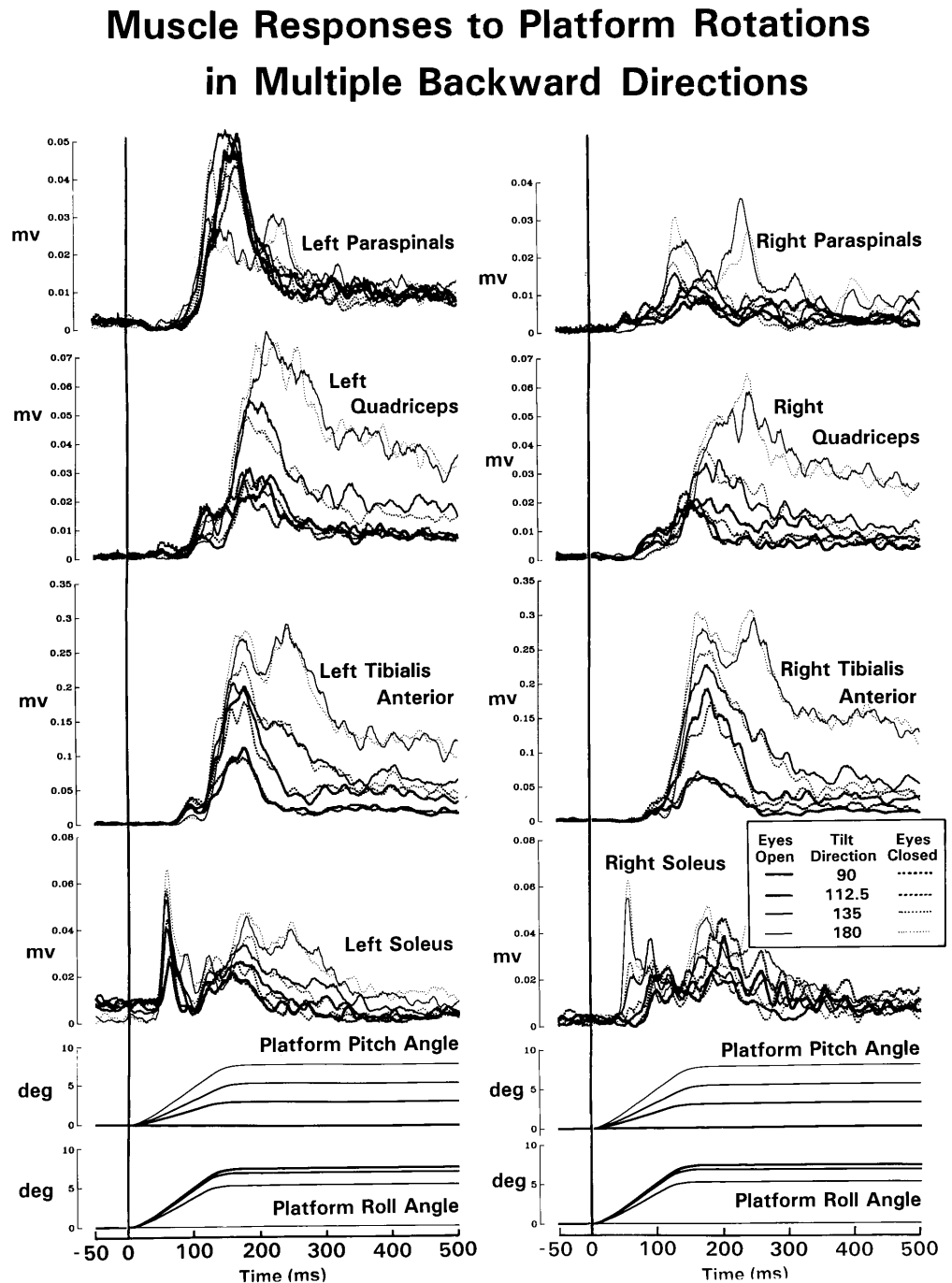


Roll plane rotations

For pure roll conditions to the right (with mirrored responses for left roll stimuli), the lower and upper leg segments initially rotated in the same direction as the platform rotation (see Figs. 1, 3). Interestingly, stretch reflexes were observed in the left soleus muscle with an onset latency of ca. 50 ms, similar to that observed in a pure toes-up rotation, but such early stretch reflexes were not observed in the right soleus (Fig. 4). The trunk segment demonstrated consistent early roll velocities at

20 ms in the direction opposite to that of the platform rotation (see Figs. 1, 3). Between 100 and 150 ms the trunk demonstrated average roll velocities of 12°/s to the left (Figs. 1, 3). Small stretch reflexes in the right paraspinal for right platform, left trunk roll, were observed at ca. 60 ms while an unloading reflex, characterized by decreased EMG activity below background levels, was observed in left paraspinals with latencies as early as 30 ms (Fig. 4). Very large head roll angular accelerations were recorded in the same direction as trunk rotation (to the left in response to a pure right roll stimulus) beginning at 40 ms

Fig. 4 Muscle responses (average of 14 subjects) to rotational perturbations in multiple backward directions between 90° (pure roll right) and 180° (toe-up) directions for both eyes-open (*solid lines*) and eyes-closed (*dashed lines*) conditions. For each set of traces three or four recordings are shown increasing in line thickness with increasing roll component to the stimulus. For other details refer to Fig. 3. Note: (1) scaling of early stretch and balance-correcting activity to perturbations of different directions and (2) comparable latency of stretch reflex activity in right soleus and paraspinal muscles



and reaching peak accelerations of $200^\circ/\text{s}^2$ within 80 ms (Fig. 3). Notice, however, that head vertical accelerations were of a small, almost negligible, amplitude over the first 150 ms (see Fig. 3).

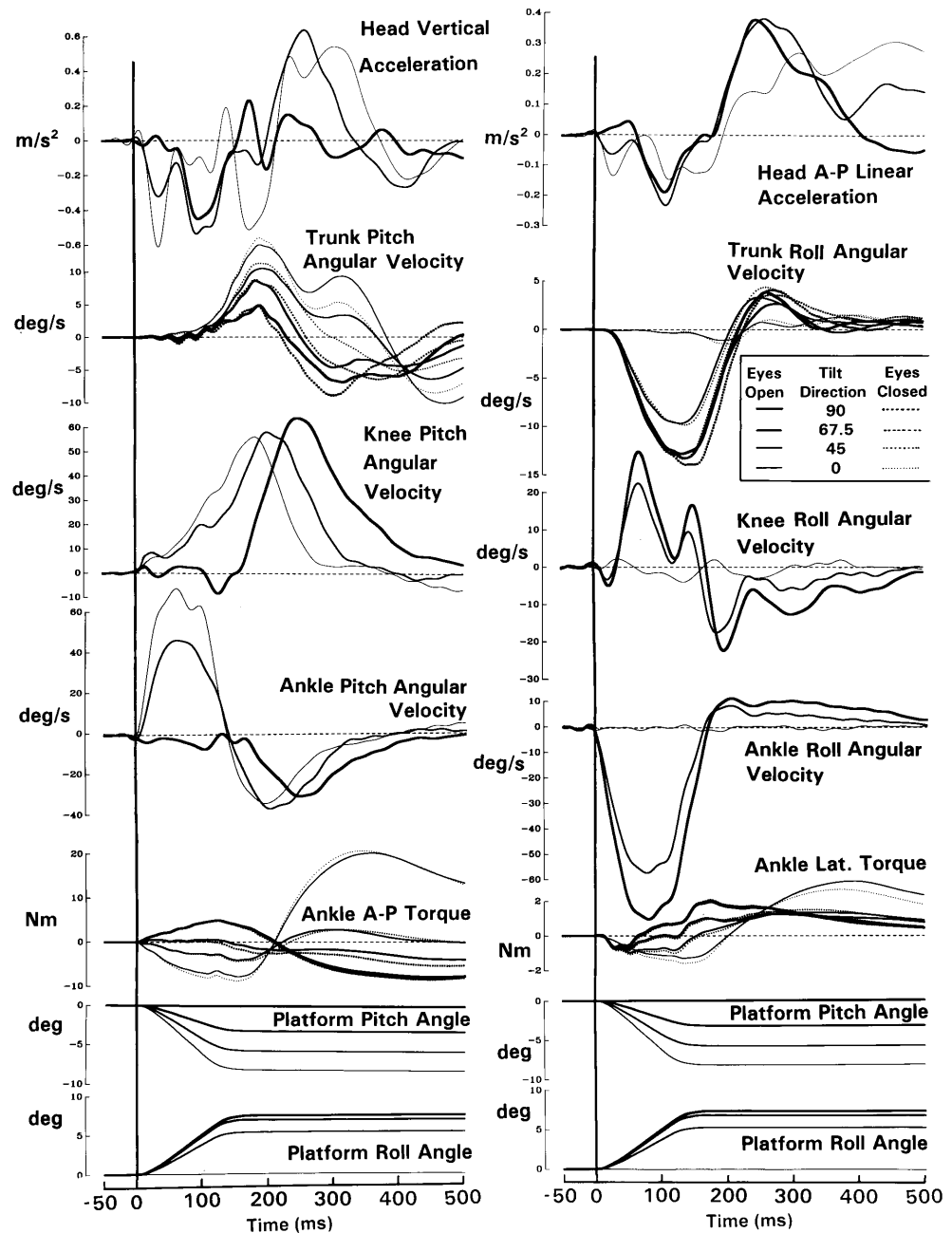
Off-pitch, off-roll rotations

Stimulus-induced movements were unique for each off-pitch and off-roll perturbation direction containing both pitch and roll characteristics; however, certain differences in trunk velocities and head accelerations were observed

with respect to knee and ankle velocities. Generally, clear direction-specific magnitude changes were seen in ankle and knee velocities that were not so well defined in trunk velocities and head accelerations. Generally, roll of the support surface induced little pitch of the ankle and knee and vice versa for pitch displacements. Between these two extremes a stepwise progression in the amount of roll and pitch was noted, consistent with the direction of support-surface motion. This information on the direction of roll was not encoded into soleus stretch reflexes (see Fig. 8) nor clearly into tibialis anterior stretch reflexes (see Fig. 7) because the sensitivities of these reflexes were aligned

Fig. 5 Population biomechanical responses to rotational perturbations in multiple forward directions between 0° (toes down) and 90° (pure roll right) directions for both eyes-open (*solid lines*) and eyes-closed (*dashed lines*) conditions. For details refer to Fig. 3

Biomechanical Responses to Platform Rotations in Multiple Forward Directions

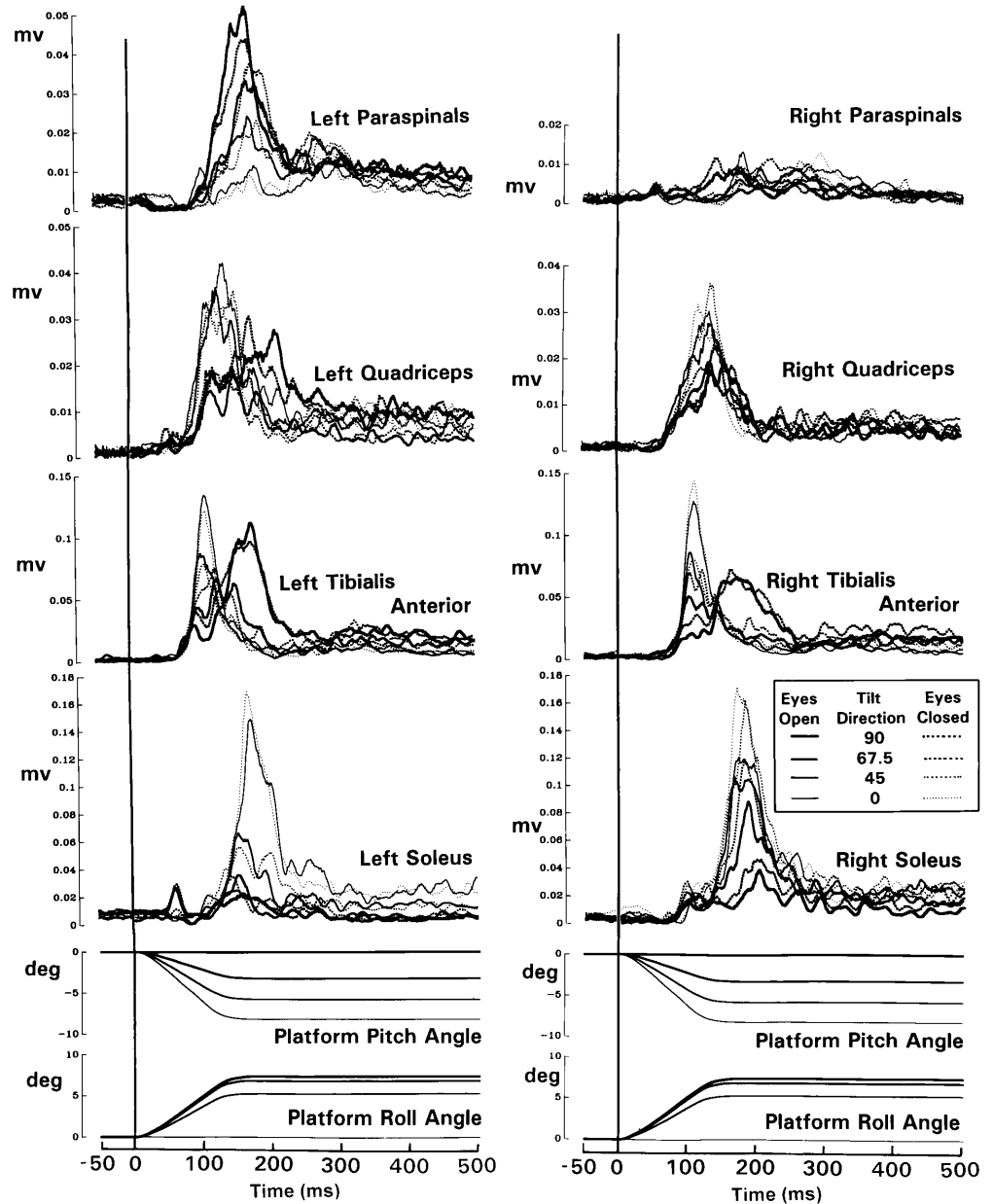


along the pitch axis. In contrast, trunk velocities showed a strong pitch component for roll rotations of the support surface, but no trunk roll velocity was observed following pitch rotations of the support surface. Furthermore, the change in trunk velocity vector between the 67.5 and 112.5 directions of roll was encoded more in trunk pitch velocity (compare trunk roll and pitch velocity traces in Figs. 3, 5). Perturbations with a right roll component (between 22.5° and 153°) induced trunk roll velocities to the left with latencies of 20–30 ms (see Figs. 3, 6). Pitch rotations of the trunk followed with longer latencies of 60 ms and slower

accelerations, pitching backward during toes-down combinations (for directions in the range 270°–90°), and forward in response to toes-up combinations except 112.5° and 247.5° for which no early pitch occurred (see Figs. 3, 5). The direction of maximum sensitivity of paraspinal stretch reflexes was observed for backward directions 45° from pure-pitch, with left and right paraspinal muscles having opposite directions (see upper left polar plots in Fig. 9). Also for that matter were those of the unloading reflexes in paraspinals (not illustrated) albeit oriented 180° to the stretch reflexes. The earliest population average stretch re-

Fig. 6 Population muscle responses to rotational perturbations in multiple backward directions between 0° (toes-down) and 90° (pure roll right) directions for both eyes-open (solid lines) and eyes-closed (dashed lines) conditions. For details refer to Figs. 3 and 4. Note: (1) early unloading response in left paraspinals when released by backward rotation of the trunk followed by large balance-correcting response and (2) differences between stretch reflexes and balance-correcting responses in the same muscles

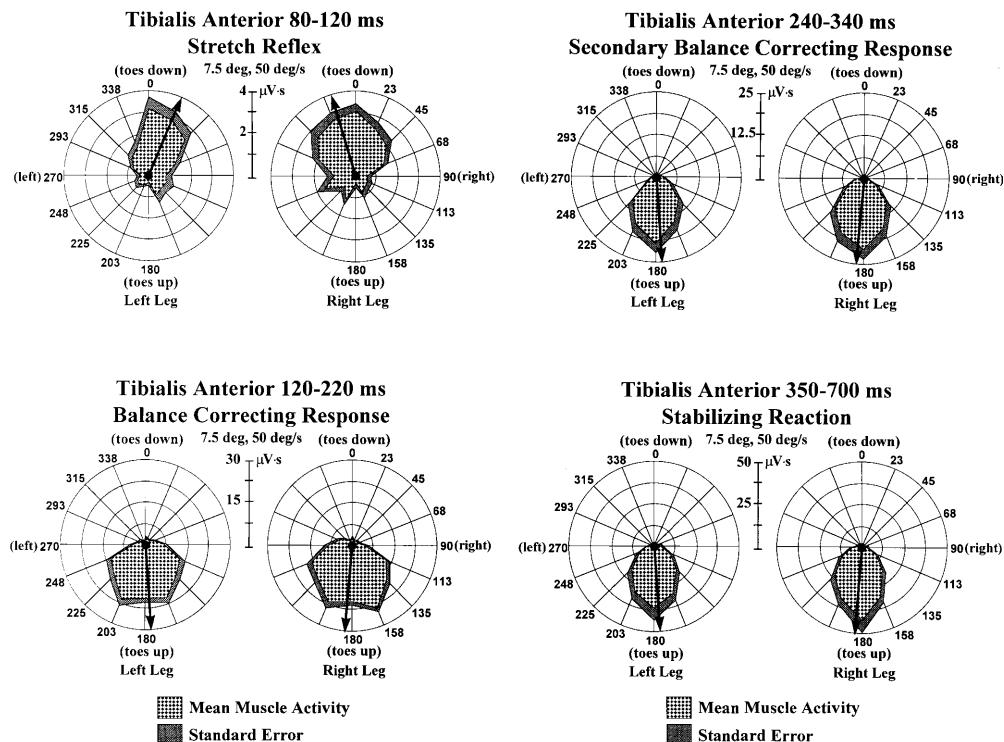
Muscle Responses to Platform Rotations in Multiple Forward Directions



flex onsets in the right paraspinals were observed for the 135° direction (63.4 ms, SD 12 ms) and the earliest average unloading response for the 315° direction (39 ms, SD 10 ms). Considering the mean onset for combined stretch reflexes in SOL+TA muscles as one possible trigger source and the mean onset for paraspinal stretch/unloading interaction as another, comparison with a one-way analysis of variance revealed significantly lower onsets for the mean trunk compared to mean leg reflexes ($P < 0.05$). Thus, despite the fact that trunk pitch velocities are observed even during roll perturbations, and limited variation in trunk roll velocities to near pure-roll perturbations, the interaction

between early stretch and unloading paraspinal reflexes on opposite sides of the body provided discriminatory information regarding the direction and onset of trunk movements. Consistent with the observation of uniform trunk roll profiles for different directions, but different trunk pitch profiles, similar amplitudes of head roll angular acceleration profiles were observed for 135° and 90°, in contrast to the large change in head vertical linear acceleration profiles (see upper sets of traces in Fig. 3). Thus the direction of support surface rotation may also be accurately encoded from the combined head angular- and linear-acceleration profiles.

Fig. 7 Polar plots for tibialis anterior EMG activity under eyes-open conditions averaged over four distinct time intervals representative of stretch, balance-correcting, secondary balance-correcting and stabilizing reactions. Each radial line or spoke represents the direction of platform rotation. For each direction, mean muscle activity (pattern) and the mean plus one standard error (shade) of all subjects for eyes closed are plotted for left and right muscles separately. The amplitude is plotted as distance from the centre. The response amplitude represented by each of the concentric circles in the plot is scaled according to the vertical scale between the set of plots for the left and right recording sites. Black arrows represent the direction of calculated maximum activity vector for each averaging interval. Note the alignment of this vector along the pitch axis



Balance-correcting responses

Balance corrections were characterized biomechanically by a reversal from stimulus-induced responses in both A-P and M-L ankle torque records and by a second phase of body segment (lower-leg, upper-leg, trunk) velocity commencing at approximately 160 ms (Figs. 3, 5). Ankle and knee joint pitch velocities rose to a second clearly defined peak around 240 ms for all perturbation directions (see Figs. 3, 5). This phase in angular joint velocity occurred as a result of movement of the upper leg in the opposite direction to that induced by the stimulus (compare leg velocities in Figs. 1, 2). The trunk, in contrast, generally continued to pitch forward or changed to pitching forward except for toe-down stimulus combinations between 315° and 45° (cf. upper and lower parts of Fig. 12). Roll velocities in the legs during balance corrections were of more limited amplitude than those during pitch movements presumably because of the limited joint motion possible in the roll direction. Ankle and knee joint roll velocities during balance corrections were, however, always in the opposite direction to those induced by the stimulus and small compared to pitch velocities (Fig. 3). Trunk roll velocities reversed direction only after 220 ms (see Figs. 3, 12). Thus, trunk motion is fundamentally different during balance corrections from motion of the leg for all perturbation directions in one major aspect. The amplitudes of roll trunk velocities were similar to those of pitch. Due to this difference it might be expected that muscle response amplitudes of automatic balance corrections are highly directionally sensitive and differ in directional sensitivity between trunk and leg muscles. As shown in Figs. 4 and 6,

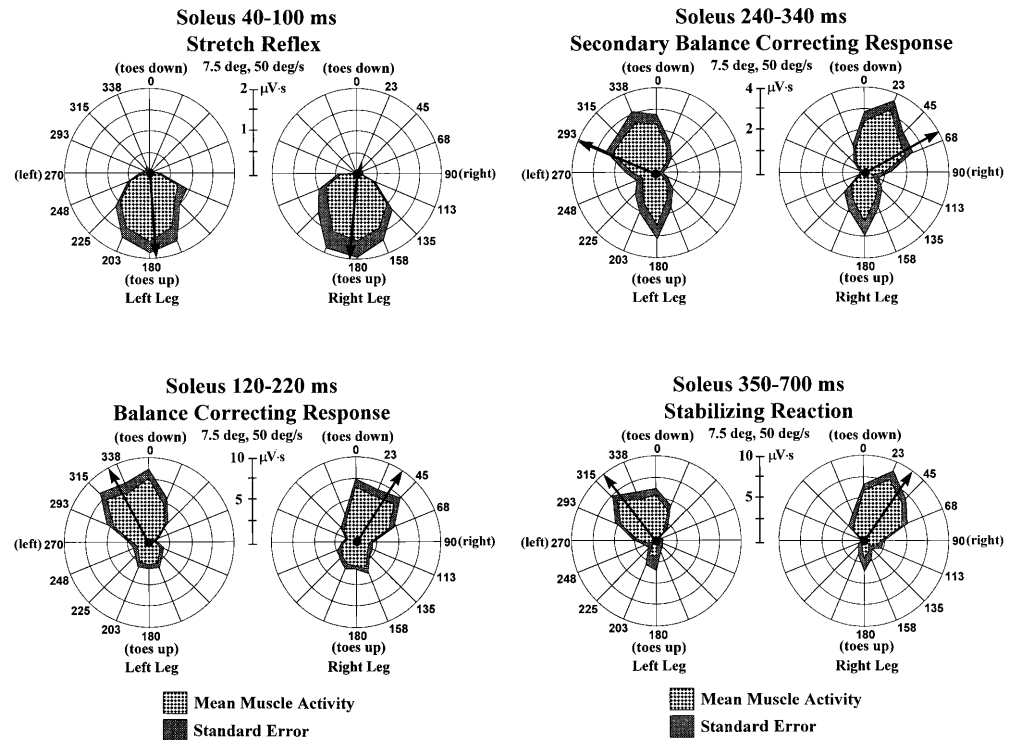
amplitudes of muscle responses rather than muscle response onsets underlie these differences in trunk and leg movements, to different perturbations.

Pitch plane rotations

Figures 4 and 7 show that the largest responses in tibialis muscles over all directions were obtained between 120 and 220 ms when the support surface was tilted toes-up. Quadriceps also produced the largest burst of activity over this time period for the same directions (see Fig. 10). At the same time soleus showed a small amount of balance-correcting activity (see Figs. 4, 8) for this direction. Presumably this coactivated activity in the leg muscles is largely responsible for bringing the lower-legs forward and braking the rearward motion of the upper legs depicted schematically in Fig. 2. Interestingly, although the largest angular velocity of the trunk was observed for 180° pitch rotations of the support surface (the average velocity of the trunk between 240 and 300 ms equalled 19°/s in the pitch direction, see Fig. 2), the paraspinal activity was smaller than that obtained for roll perturbations that caused trunk motion towards the paraspinals recording side (e.g. left paraspinals unloaded by right roll support-surface motion).

In response to toes-down perturbations, soleus produced the largest balance-correcting responses of all muscles we recorded from. As with toe-up perturbations in tibialis anterior, responses in soleus were similar between eyes-open and -closed conditions, although responses were larger on average for eyes closed. Presum-

Fig. 8 Polar plots for soleus EMG activity (eyes open) during four distinct time intervals representative of stretch, balance-correcting, secondary balance-correcting and stabilizing reactions. For details refer to the legend of Fig. 7



ably, soleus activity was recruited to oppose the continuing forward motion of the lower leg (see Figs. 1, 2). After motion of the support surface ceased at 150 ms, this forward motion of the lower leg led to a dorsiflexion of the ankle joint which peaked with a velocity of $35^\circ/\text{s}$ at 200 ms (Fig. 5). Quadriceps activity during the balance-correcting period acted to decelerate backward motion of the upper leg (see Fig. 2). Thereby knee flexion peaked at 200 ms and came to rest at ca. 350 ms. Minimal balance-correcting activity for tibialis anterior and paraspinal muscles was observed during toe-down perturbations (Figs. 6, 9). We assume that muscles such as the abdominals, from which we did not record, were responsible for the double-peaked profile of trunk pitch angular velocity seen in response to toe-down support-surface rotations (see Fig. 5).

Roll plane rotations

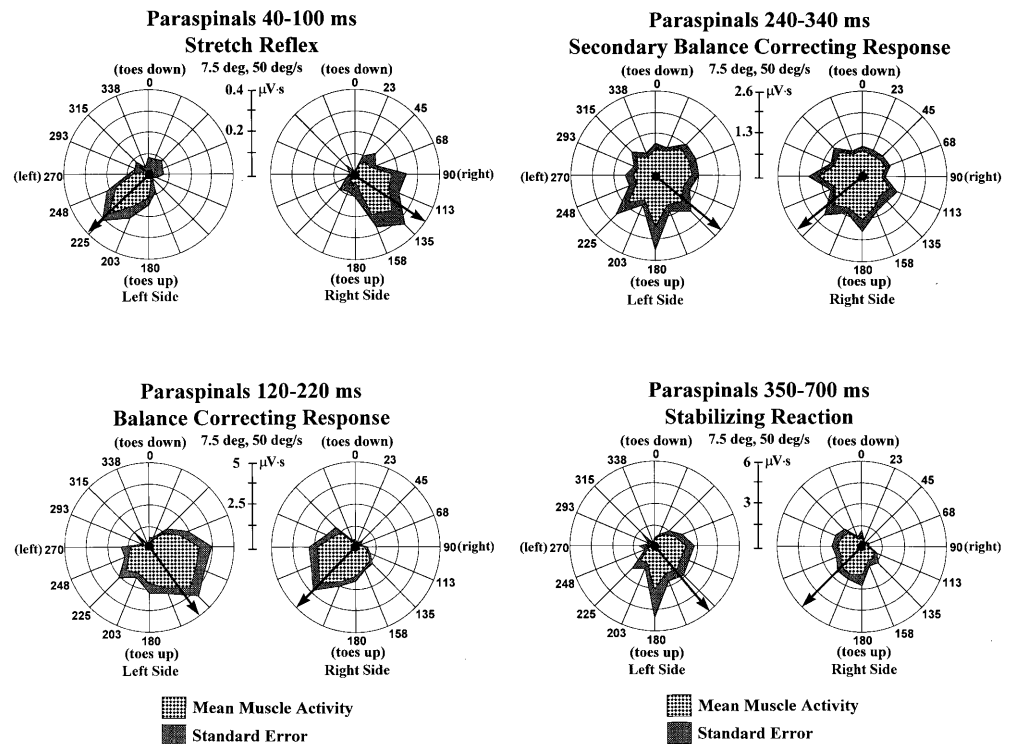
The automatic balance-correcting responses in left and right muscles during the pure roll conditions were not symmetrical. The asymmetries were similar under eyes-open and eyes-closed test conditions. An asymmetrical balance-correcting response is unavoidable given that the trunk tilts in the direction opposite the support-surface movement and the uphill leg is flexed at the knee and the downhill leg is extended into a knee-locked position (see Fig. 2). Thus, in response to right down support-surface movements shown in Fig. 6, balance-correcting activity in right tibialis anterior, quadriceps and soleus was involved in stabilizing the right ankle and knee joint to

maintain a straightened position and resist the initial rightward rotation of the legs. The larger tibialis anterior and smaller soleus activity in the left leg (see lower left in Figs. 6, 8) preceded flexion of the knee and ankle which commenced at approximately 160 ms (see Fig. 3). Simultaneously, the knee was pulled slightly to the left, reflected by increased knee roll velocity which peaked at 190 ms. Following the initial stretch reflex of the right and unloading reflex of the left paraspinal muscles, large balance-correcting responses in the left paraspinals were observed accompanied by a weak contraction in the right paraspinal muscles (Fig. 6). This activity presumably was required to counteract ensuing trunk roll in the rightward direction. Average right roll velocities of the trunk to right down support-surface movements were thereby limited to $2.4^\circ/\text{s}$ during the measurement period of 240–340 ms (Figs. 2, 3, 5).

Off-pitch, off-roll rotations

As roll and pitch perturbations were combined, the balance-correcting responses associated with pure pitch and roll stimuli were superimposed to create unique directionally specific postural responses. Balance-correcting responses, like stretch reflexes described above, and subsequent stabilizing reactions described below, were influenced by perturbation direction. Tibialis anterior demonstrated balance responses through all backward directions with the majority of activity observed in directions greater than 135° and less than 225° and maximal responses oriented just off 180° at 177° and 186° for left

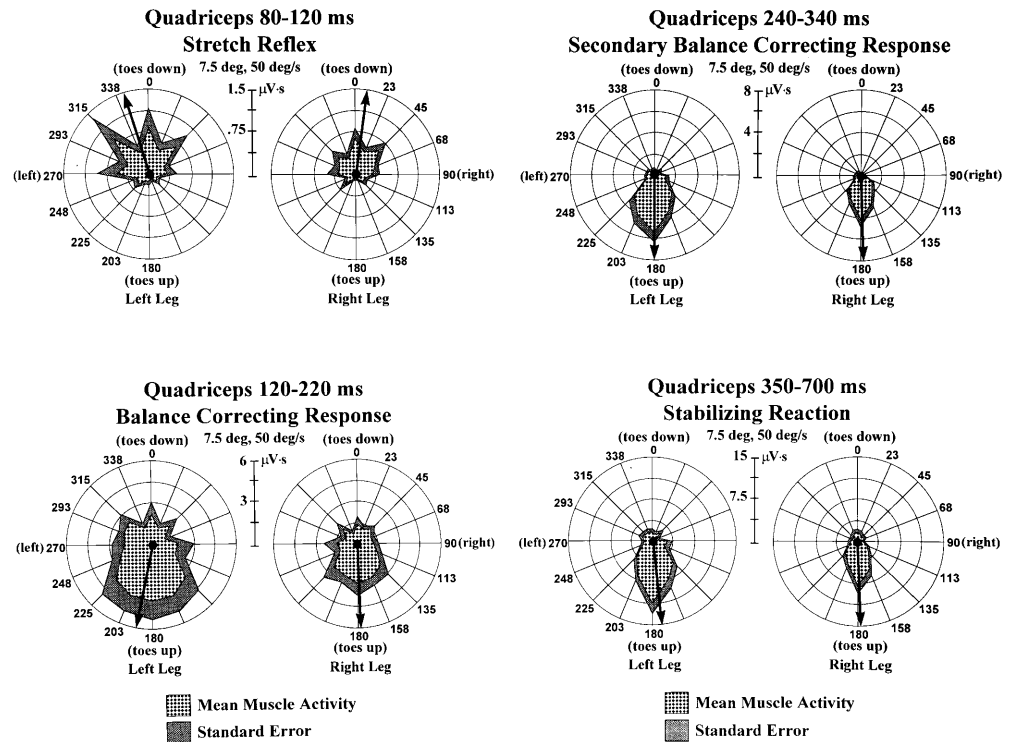
Fig. 9 Polar plots for paraspinal EMG activity (eyes open) over distinct response intervals. For details refer to the legend of Fig. 7. Note the off-pitch axis orientation of the maximum activity vectors



and right muscles, respectively (Figs. 4, 6, 7). Balance-correcting responses in soleus muscles were observed in all directions with maximum activity occurring in directions between 0° and 68° for the right and between 293° and 0° for the left muscle (Figs. 4, 6, 8). Smaller amplitude soleus activity was observed in directions between 90° and 270° corresponding to coactivation with tibialis anterior activity. Minimum activity was recorded for pure roll directions. These two zones of soleus activity caused maximal activity vectors for soleus to be oriented slightly off the pitch axis at 332° and 35° for the left and right leg, respectively (Fig. 8). Quadriceps followed the trend exhibited by tibialis anterior with maximum activity vectors aligned along the toe-up (180°) direction, except that some activation was observed for roll and the toe-down directions. Quadriceps demonstrated larger mean values for the left than the right leg. Though this difference is unlikely to approach significance because large standard errors were associated with these means (see Fig. 10, lower right), the difference in means is nonetheless surprising given the precautions we took to avoid a left/right bias. This was the only muscle for which such differences were observed and could be associated with the fact that most subjects were right-footed. As observed in Fig. 9, from both the directions of maximum activity vectors and the range of activity, paraspinals responded best to roll backwards, consistent with the combined roll and pitch effect of the stimulus on the trunk (see Figs. 3, 12). Maximal activity vectors for paraspinals were directed towards 142° and 225° for the left and right muscles with activation ranges between 90° and 225° and between 135° and 270° , respectively.

For all leg muscles we recorded from (tibialis anterior, quadriceps and soleus), maximum activity vectors for balance-correcting responses were oriented along the pitch axis. Even for the lateral quadriceps muscle this finding is consistent with the action of leg muscles, being restricted by ankle and knee joint motion to the pitch plane. The stretch responses in leg muscles were oriented approx. 180° from the balance-correcting response in the same muscle (compare polar plots in the left half of Figs. 7, 8, 10). Paraspinal muscles, however, demonstrated maximum stretch reflex activity in directions oriented 90° from the same muscle's maximum balance-correcting response (see left half of Fig. 9). This evidence, suggesting an underlying neurophysiological difference between the mechanisms responsible for eliciting stretch and subsequent balance-correcting responses, can also be observed in Figs. 4 and 6. Directions which elicited strong stretch reflexes in a particular muscle were followed by proportionally smaller balance-correcting responses. In addition, the inhibition or unloading reflex observed in left paraspinals during trunk motion caused by right roll perturbations, and likewise for right paraspinals during left roll perturbations, were succeeded by very prominent balance-correcting responses. Maximum activity for the unloading reflexes was observed at 57° and 310° , for the left and right trunk muscles respectively. Maximum unloading reflex activity was oriented 90° from the maximal balance-correcting response and 180° to maximal stretch reflexes in the same muscle. Thus in the trunk muscles the primary direction of the stretch reflex is not opposite that of the balance-correcting response, but phase shifted.

Fig. 10 Polar plots for quadriceps EMG response activity (eyes open) over distinct time intervals. For details refer to the legend of Fig. 7



Joint torques

Our findings with respect to the A-P directionality of leg muscle maximum activity vectors was replicated in ankle muscle torques. This was done by examining the directionality of torque muscle responses during the period 160–260 ms, that is, in the period influenced by balance-correcting responses acting over the time frame of 120–220 ms. The upper part of Fig. 11 shows the amplitudes of A-P and M-L ankle torque change calculated from the strain gauge measurements over 160–260 ms. Notice that the difference in the scales for the A-P and M-L torques in Fig. 11 signifies that the ankle torque is dominated by the A-P torque. As with the lower-leg muscle responses, eyes-closed A-P torques were slightly larger than those obtained under eyes-open test conditions. The centre plot of the three polar plots in the upper part of Fig. 11 shows the direction of the movement forces for the right ankle torque vector, that is, the direction in which the body would move (viewed from above) if it could be modelled as an inverted pendulum rotating at the ankle joints. These directions are almost exclusively aligned along the slightly off-pitch direction of the tibialis anterior and soleus maximum activity vectors for the right foot for all perturbation directions. The alignment of the torque vectors was not different for eyes-open and -closed conditions (only eyes-closed torque directions are shown in Fig. 11).

Likewise our findings of a different directional sensitivity for trunk muscles could be confirmed by examining the directionality of average trunk velocity responses over the period 160–220 ms. This time frame encom-

passes the peak pitch velocity of the trunk backwards for all forward and roll support-surface rotations (see Fig. 5), the peak roll velocity of the trunk (see Figs. 3, 5), and would presumably reflect the action of ankle and hip torques between 160 and 260 ms. The upper part of Fig. 12 shows how the amplitude of the average pitch and roll trunk velocity over 160–220 ms varies with perturbation direction. The centre plot of the three upper polar plots indicates that the direction of trunk motion is highly directionally tuned and symmetrical. That is, the trunk motion is always opposite the direction of support-surface perturbation. Differences between this directional sensitivity of trunk motion under eyes-open and eyes-closed conditions were not observed.

Secondary balance-correcting responses

A somewhat unexpected finding was an extension of the burst of balance-correcting activity for backwards perturbations compared to forwards and/or roll perturbations. It is possible that this additional activity is due to the greater instability of the body during backward compared to forward falls. This extension of activity leads to a distinct burst of muscle activity at a latency of 220–240 ms in tibialis anterior, specifically for toe-up (180°) directions (see Fig. 4). The mean latency of this burst has been shown to be 226 ms in previous studies (Allum and Pfaltz 1985; Fig. 1). Furthermore the secondary balance correction in tibialis anterior is larger than normal in vestibular-loss subjects, whereas the primary balance correction is smaller (Allum and Honegger

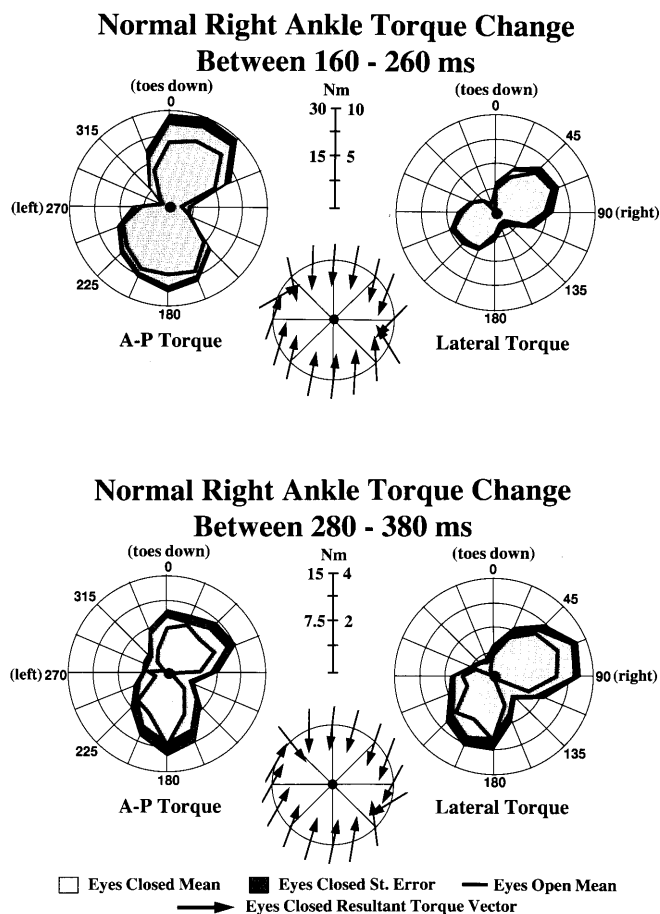


Fig. 11 Polar plots of the calculated change in right ankle torque between 160 and 260 ms (*upper plots*) and between 280 and 380 ms (*lower plots*) under eyes-open and eyes-closed conditions. Each radial line or spoke represents the direction of platform rotation. The magnitude of the mean change (*pattern*) and mean standard error (*shaded*) in anterior-posterior (A-P) and lateral torque of all subjects are plotted for each direction on the left and right graphs respectively. Concentric circles indicate the amplitude of the torque change as shown by the vertical scale between the left and right pair of polar plots. Black arrows in the centre graphs illustrate the direction of the resultant vector calculated from A-P and lateral torque for each perturbation direction with which the body would move assuming the body was simply an inverted pendulum. Note the similar constant direction of torque for all directions of perturbation with a changeover from rearward- to forward-directed torque at 112.5° and 292.5° .

1998; Figs. 2, 6, 7). These population differences in the pitch plane responses and observations of corresponding changes in time-parsed (160–260, 280–380 ms) ankle torque responses in all planes (M.G. Carpenter, J.H.J. Allum, F. Honegger 1999, unpublished) provide a rationale for considering the muscle synergy of the secondary balance corrections as a distinct response. This secondary balance-correcting activity following the decline of the initial automatic balance-correcting response was generally absent for roll perturbations and much smaller for forwards perturbations. A comparison of the amplitudes of primary and secondary balance corrections in Figs. 7 and 8 shows that soleus secondary balance cor-

rections were some 40% of the main balance-correcting activity whereas that of tibialis anterior was of equal amplitude. Activity was also apparent in soleus and paraspinal muscles for toes-down rotations during the period we designated as secondary balance-correcting activity (240–340 ms), but did not have the same burst-like profile as seen with the toe-up rotation (cf. Figs. 4, 6). As observed in Figs. 7 and 10, secondary balance-correcting activity in both tibialis anterior and quadriceps was oriented in the same directions as earlier automatic balance-correcting responses (between 113° and 248°) and shares similar maximum activity directions at 180° . As shown in Fig. 9, paraspinal activity during this period is observed over a diverse range of directions; however, the direction of maximum activity vector remained unchanged.

A-P directionality was also a feature of ankle torques associated with secondary balance corrections. The lower part of Fig. 11 shows the magnitude of the torque change generated for the right foot over the period 280–380 ms as the A-P torque approaches a minimum (Fig. 3). The torque change during this period was approximately one-third of that during the previous balance-correcting period (160–260 ms, see upper part of Fig. 11). The features noted for the earlier period were similar: resultant torque vectors were orientated just off the pitch axis, the changeover from forward- to backward-directed torque occurred slightly backward of right roll and slightly forward of left roll for the right foot, and lastly eyes-closed magnitudes were larger than those for eyes open.

Average trunk angular velocities computed during the period of the secondary balance correction displayed a strong pitch plane asymmetry and oppositely directed roll components to those observed during the main balance correction. The lower part of Fig. 12 illustrates both the amplitudes of the trunk pitch and roll velocities over the period 240–300 ms, and the direction of trunk motion. This measurement period includes the peak pitch velocity to toe-up (0°) displacement of the support surface, as well as the peak roll velocity opposite to that initially induced by the stimulus. It is apparent from the directional polar plot that the underlying torque profile at the trunk must have a stronger roll component than that at the ankle joint.

Stabilizing reactions

Muscle activity between 350 and 500 ms reflects stabilizing reactions which fall well within the bounds of possible voluntary control (Allum et al. 1996). This tonic low-level activity is required to maintain the new posture dictated by the biomechanical constraints of the new platform orientation and to control residual velocities of the trunk which are particularly prevalent in the pitch direction. Tibialis anterior and quadriceps had stabilizing activity which focused around 180° , reinforcing the automatic and secondary balance-correcting activity (Figs. 7, 10, lower right). Soleus activity was oriented to toes-

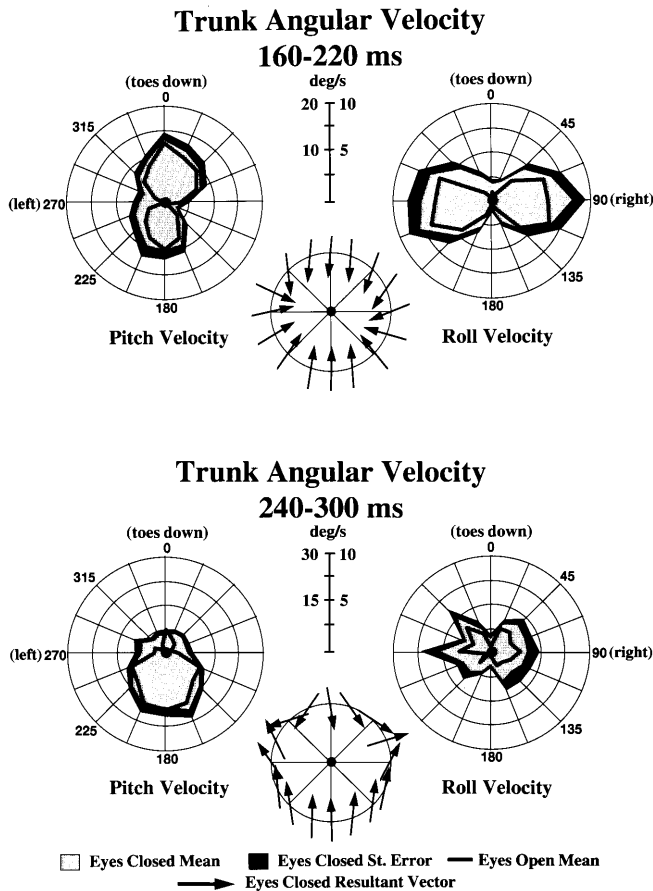


Fig. 12 Polar plots of the average amplitude of trunk angular velocity between 160 and 220 ms and between 240 and 300 ms under eyes-open and eyes-closed conditions. The form of the plot is similar to that of Fig. 11. The black arrows in the centre graphs illustrate the resultant direction of the trunk movement during the time periods as viewed from above the subject. Note the highly direction-specific motion of the trunk in contrast to the almost bidirectional nature of ankle torque vectors in Fig. 11

down directions lateral to the pitch plane with maximum activity directed between 23° and 45° for the right side, similar to that of the automatic balance-correcting response (cf. Fig. 8, lower-left and lower-right panels). As expected from ongoing trunk pitch, paraspinal activity is still relatively high during the stabilizing period with activity ranges and maximum activity vectors directed to 225° and 135° for right and left muscles (Fig. 9, lower right).

Discussion

Until recently, almost all hypotheses about the sensory mechanisms underlying human reactive postural control have been based on observations derived from unidirectional perturbations to equilibrium, specifically in the pitch plane (Nashner and McCollum 1985; Dietz et al. 1992; Forssberg and Hirschfeld 1994). These theories have mainly converged to describe human postural reac-

tions as highly stereotyped patterns of muscle activity which are activated in an ascending distal-to-proximal order (Horak and Nashner 1986) in leg and trunk muscles after being triggered by ankle inputs (Horak et al. 1990; Inglis et al. 1994). Leg-muscle balance-correcting activity, as we have demonstrated here, is almost exclusively pitch-plane directed. However, from the standpoint of external validity it is unreasonable to assume that under conditions of daily living a postural perturbation will be experienced along a purely pitch plane. As our findings demonstrate, the trunk moves readily in the roll plane even if leg movements are restricted by joint motion to the pitch plane.

Rushmer et al. (1983) and Allum et al. (1990) have shown that appropriate balance-correcting responses are elicited within a single trial following directional change from forward to backward translations or rotations of the support surface. This finding highlighted the possible sensitivity of balance corrections to the pitch plane characteristics of the perturbation. Out of the pitch plane, COP displacements even for quiet stance in the A-P and M-L directions are controlled through different mechanisms (Winter et al. 1996). A-P displacements are achieved through dorsi- and plantarflexion ankle torques, whereas M-L corrections are achieved through loading/unloading hip torques. Therefore, it might well be expected that multidirectional perturbations would provide insights on the CNS control of muscle coordination between ipsilateral and contralateral postural muscles to achieve appropriate directionally specific ankle, knee and hip torques to prevent a fall. The main purpose of the present study was to increase the understanding of postural control mechanisms through examination of muscular and biomechanical responses to postural perturbations in multiple planes. The focus of our investigation centered specifically upon three distinct characteristics of automatic postural responses. The first issue related to identifying the origin of directionally specific triggering information responsible for the initiation of muscle responses generating appropriate timing patterns for ankle and hip torques. Secondly, to understand how proprioceptive, vestibular and visual information could modulate triggered balance-correcting responses relative to the direction of the perturbations. Thirdly, to gain insights into the action of central pattern generators in executing appropriate ankle and hip torque movement strategies.

Possible triggering mechanisms

Moore et al. (1988) were the first to examine how changes in perturbation direction would influence variations in human muscle response patterns. Observation of discrete muscle responses corresponding to specific perturbation directions led to the conclusion that automatic postural responses were not components of a relatively small number of postural synergies (Nashner and McCollum 1985; Horak and Nashner 1986), but a complex process in

which perturbation direction was a significant variable. Systematic variation of muscle responses to perturbation direction has also been observed in cats responding to multidirectional translations (Rushmer et al. 1988; Macpherson 1988b). However, the findings of these multidirectional studies must be weighed against the limitations of their design. To generate multidirectional perturbations, Moore et al. (1988) employed a uniplanar platform upon which the subject was turned to produce translations in 16 different directions relative to the subject. Therefore, unlike in the present study, the participant was capable of deducing that the upcoming perturbation would be directed in either the positive or negative direction of a given plane, based on their orientation relative to the platform's constant translational plane. Previous studies have shown that prior knowledge of the direction or magnitude of an upcoming perturbation may influence the prestimulus posture of a subject, reflected by anticipatory changes in the mean position of the centre of pressure (COP) in healthy normals (Maki and Whitelaw 1993) and patient populations (Diener et al. 1991). Anticipatory postural leaning, supported through changes in the mean position of COP, significantly influences postural responses to unexpected surface translations (Nashner and McCollum 1985; Horak and Moore 1993) and rotations (Diener et al. 1983; Allum and Pfaltz 1985; Schieppati et al. 1995). The second limitation of the study by Moore et al. (1988) and Henry et al. (1998) was the restriction of muscle recordings to unilateral muscles, preventing any comparisons between bilateral muscle activity and asymmetries related to loading/unloading responses to perturbations with lateral components. Henry et al. (1998) attempted to improve upon the shortcomings of Moore et al. (1988) by investigating postural reactions under narrow and wide stance width to unexpected random translations of the support surface through both A-P and M-L planes. Their findings also supported different EMG synergies specific to the biomechanical constraints imposed by direction of the perturbation. Mechanical constraints were found to be imposed at the very initiation of the perturbation in the present study. As has been argued previously (Allum et al. 1993; Allum and Honegger 1998), the number of links the body is forced into by the perturbation plays a significant role in determining the subsequent movement strategy underlying the balance correction (see Figs. 1, 2). We could demonstrate essentially three types of movement strategy and combinations thereof depending on whether the support surface moved toe-down, toe-up or into roll (see Figs. 2, 3, 5). Interestingly, these movement strategies appeared to be generated by two types of muscle synergistic timing patterns that were simply modulated appropriately for the direction of perturbation. We termed these two types of activation pattern the primary and secondary balance-correcting activity (see Figs. 7, 8, 9, 10). Given that two types of timing patterns are generated for all directions, with some predominance of the secondary correction for backwards perturbations, it would seem appropriate that a restricted number of trigger signals with directional information would initiate these pattern types.

The present findings support the notion proposed in previous work (Allum et al. 1995; Allum and Honegger 1998) that proprioceptors responsive to early stretch and release of paraspinals (and muscle spindles in other muscles acting at the pelvis) provide the primary trigger signal for balance corrections. We can now provide additional details concerning the directional specificity of this trigger signal. In a follow-up study we obtained even earlier stretch reflex responses in the lower hip muscles, gluteus medius, at 25 ms (Bloem et al. 1999b). These reflexes are also most active in roll directions. Such early proprioceptive reflexes in hip and pelvic muscles are different on each side of the body, providing an immediate indication of the lateral direction of the trunk motion. This indication appears as early as 25 ms in hip and trunk muscles (see Bloem et al. 1999b as well as results reported here) presumably because the trunk roll motion, when the balance perturbation has any roll component, occurs earlier than pitch motion (Figs. 3, 5). That is the trunk is more flexible in the roll direction. Such directionally specific information does not appear to be available in lower-leg muscles. For this reason it is surprising that Henry et al. (1998) still cling in their conclusions to an ankle-input triggered, distal-to-proximal activation of automatic postural responses in leg and trunk muscles, even though they observed early trunk flexor/extensor and tensor-fascia latae activity for perturbations in A-P and M-L directions, respectively, which consistently preceded lower leg muscle activation. Early proximal muscle activity could be triggered by muscle or joint proprioception underlying paraspinal stretch reflex activity with onset latencies equivalent to those observed in soleus muscles (Fig. 5) or by proprioceptive inputs underlying gluteus medius reflex activity at 25 ms (Bloem et al. 1999b). All three sets of reflex responses are within the range of 40–70 ms, which has been proposed as the latency limit for feedback information to facilitate an automatic postural response (Macpherson 1994). Likewise, Moore et al. (1988) observed abdominal bursts of balance-correcting activity in response to backward translations prior to activation of gastrocnemius, hamstring or paraspinal activity. Keshner et al. (1988) have reported balance-correcting activity in neck muscles prior to observed activity in ankle musculature, further challenging the theory of an ascending ankle-motion triggered synergy for postural reactions.

A growing body of evidence can be found which contradicts a proprioceptive trigger for postural reactions located at the ankle joint. Bloem et al. (1999a) have demonstrated normal onset latencies of balance corrections in patients with selective proprioceptive loss of ankle stretch receptors in response to unexpected dorsiflexion rotations of the support surface. Allum and Honegger (1998) found normal latencies for automatic postural reactions when plantarflexion rotations were combined with backward translations to null proprioceptive ankle input. Therefore, evidence of early activity in trunk muscles and tensor fascia latae muscles during multiple direction translations (Henry et al. 1998) and in paraspinal

muscles in response to multidirectional rotations, as observed in the present study, focuses on proprioceptive receptors at the level of the trunk or the hip as the most likely directionally specific triggering centres for automatic postural reactions. Interestingly, observation of trunk proprioceptive reflexes with the range of maximum activity along 45° axes highlights the necessity for off-pitch perturbations to accurately investigate trigger signals for balance corrections. The choice of a trigger signal aligned along the planes of the vertical semicircular canals would presumably offer some simplification in the central processing of appropriate balance corrections using vestibular inputs. Paraspinal stretch and unloading reflexes provide another advantage for central processing because in contrast to leg and neck muscles (Allum and Honegger 1998; Kanaya et al. 1995) these reflexes appear not to be modified by vestibular loss. That considerable central processing must occur in generating appropriate amplitudes for the bursts of muscle activity in the range of 90–120 ms has been emphasized by several authors (Horak and Nashner 1986; Dietz 1996; Forssberg and Hirschfeld 1994). Concerning the use of trunk proprioceptive reflexes, we can add the information that this processing may well include a vectorial transformation from the planes of maximum activity of stretch reflexes to those of balance corrections. For this reason it seems crucial to consider balance corrections as generated by different neurophysiological processes from those generating stretch reflexes.

Platform rotations will elicit stretch reflexes in lower-leg muscles antagonistic to those used in balance-correcting responses and act to further destabilize the body (Nashner 1976; Diener et al. 1983, 1984). Alternatively, translational perturbations will elicit stretch reflexes and balance-correcting responses in the same muscles (Allum et al. 1993). As observed in Fig. 4, the stretch reflex activity of the soleus muscle in response to toe-up perturbations does not subside until at least 80–90 ms following perturbation onset. Likewise, tibialis anterior stretch reflexes in response to toe-down perturbations begin at approximately 80 ms and diminish at 120 ms (Fig. 6). In the trunk muscles, balance-correcting activity to roll stimuli is asymmetrical, with the larger response preceded by an unloading response and the smaller response by a stretch reflex (Figs. 4, 6). Thus the time interval utilized by Moore et al. (1988) and Henry et al. (1999) to examine muscle responses must have included portions of both stretch reflex and balance-correcting responses and lead to an inability to separate stretch reflex and subsequent balance-correcting responses from one another. For example, Henry et al. (1999) used an interval which began at 70 ms after support surface movement and lasted 200 ms. Under these circumstances it is more difficult to reach conclusions about neurophysiological mechanisms underlying balance corrections. By examining stretch (or unloading) and balance-correcting responses separately, as in the present study, an interesting, muscle-specific, relationship between stretch and balance-correcting responses in the same muscle be-

comes apparent. As shown in Figs. 7 and 8, maximum activity vectors for stretch reflexes for both tibialis anterior and soleus muscles are oriented approximately 180° from those associated with the balance-correcting response in the respective muscle. Alternatively, paraspinal muscles demonstrated maximal balance-correcting responses in directions approximately 90° from initial stretch reflexes (Fig. 7). This trade-off between stretch and subsequent balance-correcting amplitude may at first glance suggest that automatic balance corrections may be based upon localized stretch responses in individual muscles. However, previous research has argued against such a local mechanism for postural control. Toe-upward rotation and backward translations of the support surface elicited similar ankle stretch; however, different timing patterns and response modulation of balance-correcting activity was required in several muscles to respond to rotation in contrast to activity required during translation (Allum et al. 1993). In addition, observations of early arm movements with latencies similar to corrective activity in lower leg muscles despite a lack of prior stretch in shoulder and elbow muscles led McIlroy and Maki (1995) to conclude that balance-correcting responses could not be related to simple localized reflexes.

As opposed to backward roll perturbations, which elicit stretch reflex responses in paraspinal muscles at 63 ms, on average (Fig. 4, right paraspinal), forward roll perturbations are associated with unloading responses in the paraspinals, consistent with latencies at 39 ms, on average (Fig. 6, left paraspinal). Similar to paraspinal stretch responses, maximum activity vectors for unloading responses are oriented 90° to subsequent balance-correcting responses. Other researchers have also reported observations of unloading responses in trunk and neck muscles following unexpected postural perturbations. Hirschfeld and Forssberg (1994) observed postural reactions of lower leg and trunk muscles in seated infants following unexpected rotations and translations. Calculation of mean muscle activity (area) during the first 100 ms following both legs-up rotation and forward translation of the support surface revealed reduced EMG activity below background levels associated with inhibition of neck, leg and trunk extensor muscles. Likewise, Kanaya et al. (1995) observed inhibition of splenius/paraspinal muscles following unexpected pitch movements to seated healthy and labyrinthine-defective patients. The inhibitory activity was observed with latencies of 20 ms and preceded a short muscle burst characterized by Kanaya et al. as an unloading response. The latency of the inhibitory activity in splenius/paraspinal muscles following seated rotations is similar to the unloading of paraspinals observed in the present study (Fig. 3), and previously reported by Allum et al. (1995). Similar unloading responses have been reported in other skeletal muscles as well, including the hand (Marsden et al. 1983; Traub et al. 1980). In response to translations of the support surface at the 113° direction, Macpherson (1988b) observed significant decreases in muscle activity of hip, knee and ankle extensors in the unloaded limb of cats. Therefore, the unloading responses

we observed in released paraspinal muscles following forward and roll perturbations are not a unique phenomenon. One receptor mechanism through which such muscle unloading may be coded to trigger postural reactions may be through afferent information received from force-related Golgi tendon organs of the lower trunk and pelvic muscles. The abundance of Golgi tendon organs in the muscle-tendon junction of most muscles (approximately 1:2 ratio to stretch receptors) and low-sensitivity threshold of approximately 0.1 g (Rothwell 1994) makes these receptors plausible candidates for postural triggering mechanisms. Usually considered to have an inhibitory role, feedback from Golgi tendon afferents via spinal interneurons has demonstrated a capability to modulate its reflex output, producing both inhibitory and excitatory signals during different phases of locomotion (Yang and Stein 1990; Pearson 1995). Based on the observation of compensatory EMG responses to platform translations and rotations of the support surface in vertical and supine orientations, Dietz et al. (1992; Dietz 1996) concluded that loading information, detected by Golgi tendon organs in extensor muscles, was responsible for activating postural reflexes. Therefore, based on recent evidence, it is very conceivable that unloading reflexes of paraspinal and other trunk and hip muscles may provide directionally sensitive triggering information in parallel with muscle stretch information.

Attaching a high importance to early stretch and unloading responses in paraspinals focuses attention on the very early roll responses observed in the trunk segment. As demonstrated in Figs. 4 and 6, trunk roll occurs approximately 20 ms following perturbation onset and almost 40 ms prior to any pitching movements of the trunk. However, we cannot exclude other possible mechanisms through which early trunk movements, particularly in the roll direction, could be detected and integrated as a directionally sensitive triggering signal. Forssberg and Hirschfeld (1994) observed rotations of the pelvis as early as 10 ms following sudden rotations of the support surface beneath seated adults. They concluded that rotation of the pelvis may trigger a primary level of a central pattern generator (CPG) responsible for initial spatial and temporal activation of appropriate postural muscles. Following initial triggering of the postural response, a secondary system is required to modulate the magnitude of the response to correspond with the demands of the perturbation. As movements of the hip joint have been postulated to entrain the CPG for stepping during locomotion, it is possible that a similar CPG could tune postural responses to platform perturbations using similar directionally specific information for angular hip motion (Macpherson 1988b). Besides muscle spindle and Golgi tendon organs detecting stretch and unloading of paraspinal and hip muscles, other receptors at the level of the hip and trunk have been previously hypothesized as possible triggering mechanisms, such as joint receptors of the vertebral column (Gurfinkel et al. 1979; Horstmann and Dietz 1990; Forssberg and Hirschfeld 1994) and changes in abdominal pressure (Mittelstaedt 1992; Do et al. 1988).

Vestibular signals may also be considered as a possible triggering mechanism for postural reactions. Directionally sensitive vertical accelerations were observed for pitch perturbations with latencies of 15 ms (Figs. 4, 6); these could provide early stimulation to otolith receptors. During roll perturbations, semicircular canal afferents would transmit angular roll acceleration information with latencies as early as 40 ms to the CNS (Figs. 3, 5). Forssberg and Hirschfeld (1994) also reported early (10 ms) vertical accelerations of the head in seated adults following up- and downward pitch plane rotations. By changing the location of the pitch axis relative to the hip joint, these authors were able to induce vertical vestibular accelerations in different directions while maintaining constant rotation of the pelvis. Observations of no significant change in the activation patterns of postural muscle responses in leg and trunk muscles provided contradictory evidence against a vestibular trigger. Allum et al. (1994) and Horak et al. (1990) observed normal response latencies in patients with bilateral vestibular loss even under eyes-closed conditions following unexpected toe-up rotations and backward translations, supporting the notion of both a non-vestibular and non-visual origin for a triggering mechanism of postural reactions. Furthermore, the magnitude of postural leg balance-correcting responses was significantly influenced by vestibular loss, suggesting a modulatory role for the vestibular system.

Direction-specific modulation of balance-correcting responses

A directionally specific modulatory role for the vestibular system has been further supported by recent studies in which unexpected translations and rotations were experienced by patients suffering from total body somatosensory loss (Horak et al. 1996; Bloem et al. 1999b). Although bursts of muscle activity in postural leg and neck muscles were delayed with respect to normal response latencies, the muscle activity was observed to be sensitive to the direction of the perturbation. These findings seem to converge with the two hypotheses we have developed above: the triggering mechanism for automatic balance-correcting responses between 120 and 220 ms is tied to a trunk proprioceptive origin, and the directional sensitivity of postural responses must be modulated by vestibular information.

While there are obvious advantages to the concept that the early vertical linear accelerations and roll angular accelerations of the head may be coded as directionally specific vestibular information which was used to modulate the magnitude of the balance-correcting response, there are also disadvantages. Certainly the finding from the present study provides evidence of early vestibular directionally specific stimulation. As observed in Figs. 4 and 6 (top panels), vertical and angular roll accelerations provide very early (15 and 40 ms) directionally specific stimuli to both the otolith and the vertical semicircular canal systems. Furthermore, muscle activity

associated with automatic balance corrections is modulated with respect to the direction of the perturbation. Although this evidence alone does not confirm a vestibular modulation of postural control, it does collaborate with the findings of previous studies which make similar conclusions (Forssberg and Hirschfeld 1994). The disadvantage of this concept is the permanent disability that results from loss of peripheral vestibular function. For example, Allum et al. (1994, 1998; Allum and Pfaltz 1985) observed similar latency, but changed amplitudes of EMG activity in tibialis anterior, soleus, and paraspinal muscles in response to unexpected rotations in the pitch plane measured from bilateral vestibular loss patients compared to healthy controls.

Ankle and hip torque strategies

The modulation of muscle activity with the direction of perturbation has been shown to markedly influence both ankle torque generation and trunk angular velocities. As shown in Fig. 11, vectorial orientation of the resultant ankle torque was along one of two directions, similar to the "force constraint strategy" suggested by Macpherson (1988a, 1988b). An exception to this strategy was observed at the changeover points from forward- to backward-directed ankle torque close to the pure-roll perturbation direction (see Fig. 11). In contrast, Henry et al. (1998) reported that orientation of ground reaction forces was dependent upon the direction of translational perturbations. This result may, however, be fortuitous, because these authors only perturbed in two sets of opposite directions, A-P and M-L, i.e. close to the roll changeover points we observed. An interesting difference to our two-legged force constraint strategy at the ankle joint and that of Macpherson (1988a, 1994) appeared. Cats generated ground reaction forces along one of two directions along the 45° plane, with a 90° shift of symmetry between paws for all perturbation directions. Only the amplitude of the force was changed as a function of direction as in our study. Differences between the directional orientation of the ankle torques we noted and those of the "force constraint" strategy demonstrated by cats (Macpherson 1994) may be explained by differences in the biomechanical constraints inherent in quadrupedal stance compared with bipedal stance. Macpherson et al. (1989) have shown that humans do demonstrate similar postural responses and torque profiles to cats when assuming a quadrupedal posture. These findings emphasize the need to take into account differences in the postural constraints between humans and animal models before attempting to parallel observations between the two. The interesting similarity between the results of the present study and those of Macpherson (1988a, 1994) is the consistent orientation of ankle vectors slightly off-pitch for pure dorsiflexion and plantarflexion rotations. Possible explanations include the biomechanical constraints associated with anatomical configuration of the foot, line of action of ankle dorsiflexor and plantarflexor muscles and

point of calcaneal insertion which may act independently or in concert to fix ankle torques to an off-pitch plane (Nichols et al. 1993; Bonasera and Nichols 1996). Certainly the off-pitch-axis orientation of ankle torques is not unexpected in our results considering that maximum activity vectors of all leg muscles we recorded from favoured this orientation (see Figs. 7, 8, 10).

It is an open question whether the ankle force-constraint strategy is also applicable to the hip joint; we suspect that this is not the case for two reasons. Firstly paraspinal, and presumably other trunk, muscle maximum activity vectors are not oriented along the pitch direction. Secondly, the flexibility of the trunk in the roll direction and the large roll velocities we observed in our study necessitates early roll torques prior to those in the pitch direction. Furthermore, we expect that from polar plots of trunk velocities (Fig. 12) and previous modelling studies (Allum and Honegger 1992), in contrast to ankle torques, hip torques will be oriented in a highly directional fashion and will be triphasic in the roll direction, and biphasic in the pitch direction. All of these factors suggest that hip torques will be multidirectional in contrast to ankle torques. However, to answer the question definitively, two-dimensional calculations of hip torques similar to those already performed in the pitch dimension (Allum and Honegger 1992) are required. We assume that the results of these calculations will add more evidence for an at least three-stage vectorial transformation of sensory signals by the CNS to provide the appropriate modulation of joint torques via muscle activity to correct a postural disturbance from any direction. At one stage the appropriate hip-torque strategy is computed. At a second stage the "constrained" ankle torque is computed with an intermediate calculation of knee torques depending on whether this joint is forced into the locked position by the perturbation and at a third stage the stabilizing neck torques are worked out. This proximal to distal separation of torque strategies, coupled with the differences in sensitivity to roll and pitch of lower-leg, trunk and neck muscle responses, indicates that balance corrections must be triggered and organized in other than a distal-proximal pattern.

In summary, we have established that stretch reflex, automatic balance-correcting, and subsequent balance and stabilizing reactions in trunk and leg muscles have different sensitivities to the direction of external perturbation. The observation of very early paraspinal stretch reflexes and unloading reflexes, coupled with early roll velocities of the trunk, brings into question previously established theories regarding ankle-based triggering mechanisms. Perturbations containing roll characteristics are necessary to elicit maximal muscle responses, particularly in paraspinal muscles. In light of previous reports of enhanced sensitivity of otolith afferents, vestibular neurons, and neck and vestibular reflexes to roll movements (Tomko et al. 1981; Schor et al. 1984; Wilson et al. 1986), it seems that multidirectional perturbations may prove to be a sensitive tool for assessing the contributions of vestibulospinal inputs to balance corrections.

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