RESEARCH ARTICLE

The effect of voluntary arm abduction on balance recovery following multidirectional stance perturbations

Laura Grin · J. Frank · John H. J. Allum

Abstract The goal of this study was to investigate how voluntarily abducting one arm, 90° at onset of a rotational perturbation of the support surface, influences the recovery of upright stance. Young adults were tested under four stance conditions: abducting one arm to the horizontal only (AO); perturbation of stance using a support surface rotation only (PO); combined support surface rotation and abduction of the downhill arm, ipsilateral to tilt (IPS); and fourth abduction of the uphill, contralateral arm (CON). Simultaneous auditory and visual trigger cues were used for arm raising. Perturbations consisted of six directions of combined support surface roll and pitch rotation (7.5° and 60°/s). Outcome measures were whole body centre of mass (COM) movements and body segment angular displacements recorded with a motion analysis system, as well as leg, trunk, and arm EMG responses. Arm raises contralateral and ipsilateral to the direction of support surface roll were more rapid than in the AO condition and significantly reduced or increased, respectively, COM lateral displacements relative to the PO condition. The changes in COM displacements and velocities during combined CON arm raise and perturbation were greater than expected from the sum of displacements for AO and PO conditions alone, but less for the IPS condition. Arm raising increased trunk roll in a direction opposite arm raising was more than for the AO and PO conditions. Robust effects were also observed for hip abduction but not for leg flexion. Early balance correcting activity was enhanced on the side opposite arm raising and later stabilising activity reduced bilaterally in lower trunk muscles compared to summed activity for the AO and PO conditions. Similar effects were observed in gluteus medius muscles but effects were weak in ankle muscles. EMG onsets in muscles of the raised arm were earlier than in the AO conditions. We conclude that triggered arm abduction, contralateral to the direction of support surface rotation, had significant stabilization benefits for young adults and ipsilateral arm movements had destabilizing effects. The arm raises could be simultaneously executed with balance corrections. These results provide insights into the integration of balance corrections and voluntary commands into one automatic reaction that may be useful in training fall avoidance.

Keywords Balance control · Arm movements · Trunk muscles

Introduction

Early studies of balance control and recovery of upright stance following a postural perturbation focused on leg and not on arm responses. It was noted, however, that sudden movements of the support surface resulted in automatic compensatory arm movements (McIlroy and Maki 1995). Increased perturbation magnitudes reduced arm muscle response latencies, and increased amplitudes. Responses persisted, unlike for startle reactions. These arm muscle

L. Grin · J. H. J. Allum (✉)
Department of ORL, University Hospital,
Petersgraben 4, 4031 Basel, Switzerland
e-mail: jallum@uhbs.ch

L. Grin · J. Frank
Department of Kinesiology,
University of Waterloo, Waterloo, Canada

responses demonstrated a directional sensitivity and were considered part of the automatic balance correcting response because onsets at approximately 90 ms occurred before any voluntary adjustments could be made, and prior to responses in ankle muscles (McIlroy and Maki 1995; Allum et al. 2002).

The function of such arm responses during balance corrections remains unclear. The responses might serve to increase the base of support following large perturbations by facilitating grasping nearby objects such as handrails (Maki and McIlroy 1997). However, arm responses do not always result in a grasping action, especially for the uphill arm (Allum et al. 2002), and often occur when handrails are well out of reach (McIlroy and Maki 1995). Alternative suggestions are that arm responses aid centre of mass (COM) stabilization over the base of support and/or act as a protective "cushioning" mechanism in the event of an impending fall (Maki and McIlroy 1997; Allum et al. 2002).

Arm movements appear to be very frequent in the elderly, presumably as an attempt to avoid a fall. For example, surveillance studies in geriatric facilities found that some 70% of loss-of-balance incidents result in some form of compensatory arm movement (Maki and McIlroy 1997). The elderly also make greater use of arm movements when evoked by sudden unexpected movements of the support surface during quiet standing or when walking in place (Maki et al. 2000). Moreover, due partially to the initial motion of the trunk, the elderly display early automatic arm movements that are in the opposite direction to those of young and middle-aged (Allum et al. 2002). Young individuals displayed trunk and arm roll movements in the opposite direction of support surface rotation, whereas elderly individuals showed arm roll movements in the same direction of support surface rotation, that is, in the direction of an impending fall (Allum et al. 2002) presumably as a result of increased trunk stiffness (Grüneberg et al. 2004). Thus these automatic arm response patterns in the elderly even though small in amplitude (less than 3°, see Allum et al. 2002) may result in greater instability and be significant contributors to the larger incidence of lateral falls in the elderly (Parkkari et al. 1999). For fall avoidance, it appears important to learn which types of triggered arm movements may enhance balance recovery in the elderly.

A number of investigations have examined the effects of triggered voluntary arm movements on stability during quiet stance. When such movements are performed in the saggital plane, neural command centres anticipate instability, activating leg and trunk muscles prior to the arm movements with so-called anticipatory postural activity (APA). APA provides counteracting stabiliza-

tion maintaining upright posture and reducing net displacement of the body's COM (Cordo and Nashner 1982; Friedli et al. 1984; Eng et al. 1992; Vernazza-Martin et al. 1999; Teyssèdre et al. 2000). Patla et al. (2002) suggested however that postural control counteracting voluntary arm flexion during quiet stance was passive for the first 200 ms. Active control of whole body COM, by alterations in muscle activity and joint moments, began much later (Patla et al. 2002). For voluntary arm abduction APAs appear to be restricted to trunk and upper leg muscles (Aruin et al. 2001; Krishnamoorthy et al. 2003). This would be in accordance with the concept that balance corrections in the pitch and roll planes are programmed separately because, in the roll plane, balance corrections are strongest in trunk and weak in lower leg muscles and vice-versa for the pitch plane (Grüneberg et al. 2005). Such a concept would have a stronger empirical basis if it could be shown that roll directed balance corrections in trunk muscles and postural activity occurring in the same muscles during arm abduction are executed using the muscle synergy.

The purpose of the current study was to examine the effects of triggered voluntary abduction of one arm on balance recovery following a sudden unexpected rotational perturbation of the support surface. Although we chose to have subjects generate much larger movements than those of balance corrections, these larger arm movements might mimic, to an exaggerated extent, natural arm responses during balance corrections and therefore could provide insights into the workings of neural command centres generating automatic balance corrections, which include arm movements. We surmised that these command centres might unify the commands by either delaying the balance correction or by making the voluntary abductions more automatic with timing characteristics similar to those of balance corrections. If the effect was an improved stability, study of the effects of such arm movements could also provide a basis for teaching an appropriate recovery strategy in the elderly. The question also arose concerning time point when triggered arm movement altered COM movements as these exaggerated arm movements would provide information on when arm movements of normal balance corrections aid or impair stability.

In accordance with previous work by Eng et al. (1992), Vernazza-Martin et al. (1999), and Patla et al. (2002), it was expected that voluntary arm abduction performed on an unperturbed surface would result in a COM displacement towards the direction of arm abduction. Support surface rotations were expected to result in whole-body COM displacement towards the direction of rotation. It was therefore hypothesized that raising the contralateral arm following support

surface rotation to one side (e.g. the uphill left arm for rightwards perturbations) would assist in stabilization by reducing the deviation of the COM. In contrast, raising the ipsilateral arm (e.g. the right downhill arm for rightwards perturbations) would result in further destabilization by increasing the deviation of the body's COM. In order to test whether this effect for a simple one arm abduction could be generalised to different unpredictable directions of perturbations, we randomly presented six directions of tilt to subjects.

Methods

Twelve male and 12 female healthy subjects, aged 18–33 years, who had not previously been involved in balance testing participated in this study. All participants gave witnessed informed and written consent to participate. Ethical committee approval for the study was obtained from the University Hospital of Basel.

Stimulus protocol

Each participant was examined under the following four conditions: (1) Arm abduction during quiet standing (Arms only, AO). (2) Perturbation of the support surface without voluntary arm raises (Perturbation only, PO). (3) Arm raises opposite to the direction of platform roll (Contralateral, CON). (4) Arm raises in the same direction as platform roll (Ipsilateral, IPS). The AO condition was further divided into an arm raise ipsilateral (AOI) and an arm raise contralateral (AOC) to the triggering stimulus.

In the AO, CON and IPS conditions simultaneous visual and auditory triggers prompted the participants to raise one arm in a spatially dependent fashion in the frontal plane to the horizontal. For instance, a green light stimulus appeared in the right visual field and a speaker to the right of the participant sounded with a pure tone of 70 dB SPL when the participant was expected to raise their right arm. The trigger cues were turned off by the arm crossing a light barrier when abducted 80°. Trigger lights were located at eye level, approximately 4 m in front of the participants. Loudspeakers for sound triggers were located to the left and right at arms' length and shoulder height, 45 cm anterior to the pitch axis of the rotating platform. Visual and auditory cues and servo-commands for support surface rotation occurred simultaneously for the IPS and CON conditions. Participants were asked to raise the appropriate arm as quickly as possible. Trials in which the incorrect arm was raised were excluded from analysis (12, 15, and 20% of the trials on average for the AO,

CON, and IPS conditions, respectively). Incorrect trials were significantly higher than for the IPS condition compared to the AO condition ($P < 0.05$).

Six platform perturbation directions were utilized (45°, 113°, 158°, 203°, 248° and 315°) where 0° is defined as a pure-pitch perturbation with toes down, 90° as pure right tilt, 180° a pure-pitch toe-up perturbation (see Fig. 1). Six directions were used to avoid subjects predicting the stimulus direction. Each perturbation had an amplitude of 7.5°, a constant velocity of 60°/s and was preceded by a random 5–20 s delay. A greater proportion of posterior directed perturbations (113°, 158°, 203°, 248°) were used as previous work has also shown that backwards perturbations are more destabilizing and challenging to the nervous system than forwards perturbations (Carpenter et al. 1999, 2001). During the CON condition the subjects were prompted to raise the right (uphill) arm when the platform tilted left, directions 203°, 248° and 315°, and to raise the left (uphill) arm when the platform tilted right (45°, 113°, and 158°). During the IPS condition the subjects were prompted to raise the right (downhill) arm as the platform tilted right and the left (downhill) arm as the platform tilted left. When results were pooled for equal pitch amplitude these were termed anterior lateral (AL) for directions 45° and 315°, lateral posterior (LP) for 113° and 248°, and posterior lateral (PL) for 158° and 203° (see Fig. 1).

For each subject, 26 AO trials were presented first, in order for the arm movements to become well learned. A small (approximately 0.1°), just perceptible, pure roll perturbation (see Beule and Allum 2006) was presented with the auditory and visual arm raising prompts in order to have a somatosensory stimulus
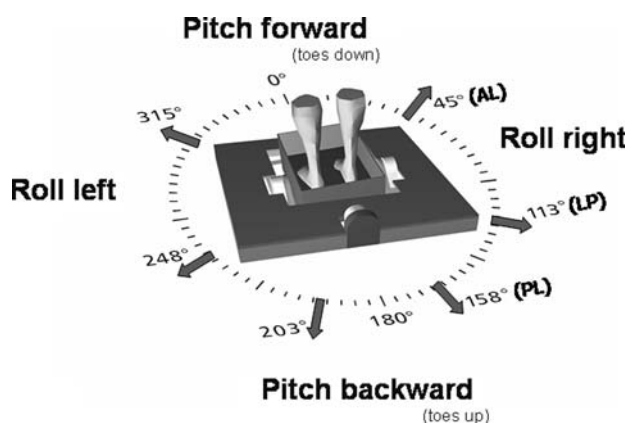
Fig. 1 Schematic diagram of perturbation directions. The angular notation indicates the direction of the stimulus. The abbreviations used for the directions in the text are shown (45 and 315 anterior lateral, *AL*; 113 and 248 lateral posterior, *LP*; −158 and 203 posterior lateral, *PL*). The schematic also shows how the gimbled axis of rotation were raised above the surface of the platform on which the subjects stood

present without perturbing balance. The 26 AO trials were divided into two sets. One set of 13 trials was performed raising the arm ipsilateral (AOI) to the small perturbation and the other was performed raising the contralateral arm (AOC). Six small perturbations to the left and six to the right were presented in a randomized order within each set. A single adaptation trial was presented at the beginning of each set and the direction of perturbation was randomized between sets. These adaptation trials were excluded from analysis. The order of AOI and AOC presentations was randomized across participants.

The PO, CON, and IPS conditions were then presented in a randomized order. Each of these conditions included a total of 43 trials. Seven trials per six perturbation directions were presented in a different randomized order (controlling for any directional anticipation). A single adaptation trial was presented at the beginning of each condition (and excluded off-line from analysis) and the direction of perturbation was randomized across conditions.

Experimental equipment

Subject's feet were lightly strapped into heel guides fixed to the top surface of the dual-axis rotating platform. Thus only in-place balance corrections were possible. The height of the gimbaled platform axes of rotation above the top surface of the platform was equal to the average height of the centre of rotation of the ankle joints in adults above the soles of the feet (8.5 cm). The guides were adjusted in the anterior–posterior (AP) direction to ensure that the ankle joint axis was aligned with the pitch axis of the rotating platform. The roll axis passed between the feet at the same height as the pitch axis. Just prior to beginning the experiment, subjects were asked to stand quietly in their "preferred/comfortable" standing posture with their arms hanging at their side. The AP and medial lateral (ML) ankle torques associated with this stance position was then treated as the reference value for the remainder of the experiment (AP and ML ankle torque were calculated from the outputs of strain gauges imbedded in the platform and mounted underneath a plate supporting each foot.). During the delay period before each perturbation, subjects were asked to monitor two rows of LED's mounted at right angles to one another in the form of a cross that provided the subjects with feedback about their AP and ML ankle torque. Using this visual feedback the participants were required to adjust their stance in order to maintain AP and ML ankle torques within a range of ± 6 Nm from their preferred stance. A 5–20 s inter-stimulus delay was initiated automatically once the platform had returned to its original pre-stimulus position and the subject had regained and maintained his or her preferred stance position. With onset of the perturbation the feedback was switched off during data collection.

The experiment was conducted without handrails to allow adequate space for the voluntary arm raises. Therefore, two spotters were present at all times (one behind and one to the side) 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 of 43 trials. A longer seated rest period (5–6 min) was provided between the series of trials between each arm raising condition.

Whole body kinematics were obtained with an Optotrak™ motion analysis system (Northern Digital, Ontario, Canada) in order to calculate AP and ML whole body COM displacement, ankle angle, knee angle, hip angles, pelvis pitch and roll, trunk pitch and roll, and arm abduction angles.

Collection of whole body kinematics was achieved by placing infrared-emitting diodes (IREDs) on 18 anatomical landmarks (see Fig. 2) and sampling the IRED positions at 64/s. Three additional IREDs were placed on the platform (see Fig. 2) to monitor the pitch and roll movements of the support surface. These later movements were also monitored with potentiometer systems mounted on the axes of the platform, providing a check of the body segment angle calculations.

Electromyographic (EMG) signals were recorded using pairs of silver–silver chloride electrodes placed approximately 3 cm apart along the muscle bellies of left tibialis anterior (TA), left peroneous longus, and bilaterally for gluteus medius, paraspinals at the L1–L2 level of the spine, the abdominal muscle, oblique externus, and medial deltoid muscles. EMG pre-amplifier band-pass filtering was over 0.7 Hz to 2.5 KHz with a gain of 2,000. Pairs of electrodes and lead lengths assigned to individual muscles were not changed between subjects throughout the experiments. The latter value was channel dependent. EMG recordings were band-pass analog filtered between 60 and 600 Hz, full wave rectified, and low pass filtered at 100 Hz and amplified 5–10 times prior to sampling at 1 KHz. A verification of this filtering technique for tracking EMG response onsets and area calculations can be found in Gottlieb and Agarwal (1970, 1979).

All measurements were initiated 100 ms prior to the onset of the electronic command signal for the platform movements and had a sampling duration of 1 s for each trial. Stimulus onset was set 4 ms later than the electronic command signal, when the first inflexion in platform velocity occurred.

LED Locations
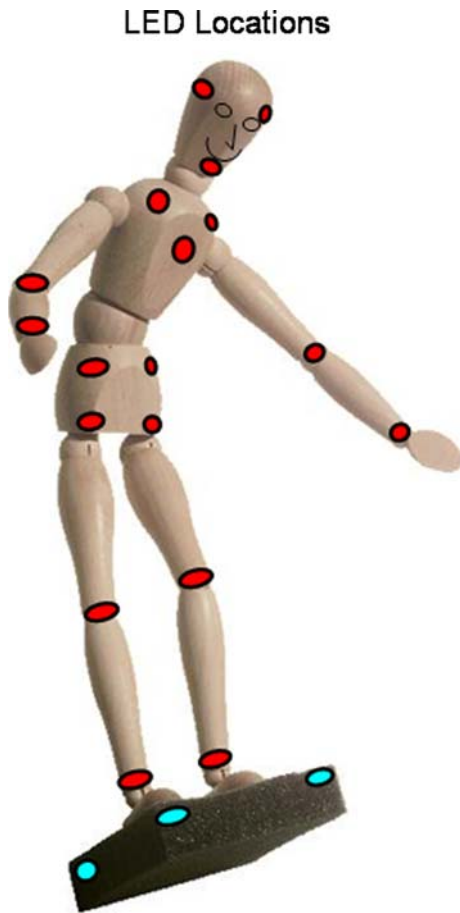
Fig. 2 Schematic showing the location of the IRED markers on the subject and the platform

Data analysis

Individual subject trial data was averaged by perturbation direction except for AO condition, which was pooled according to side. Participants means were used for all analyses. Subject means were then pooled to generate sample population plots as shown in the figures for single directions and the arm raising conditions (CON, IPS, AOC and AOI).

Using the location of the IREDs, joint angles (ankles, knees, hips, and shoulders) as well as pitch and roll movements of the pelvis and trunk were calculated for each subject. As described by Bakker et al. (2006) ankle angles were calculated using the knee to ankle line segment relative to the platform (using the knee, ankle and three platform markers). The unidirectional knee joint angles were calculated as the angle spanned by the 2-unit vectors pointing away from the joint (using the ankle, knee and greater trochanter markers). The ball joint hip and shoulder angles were calculated as polar angles of the line segment relative to the plane of the pelvis and trunk segments, respectively. A

zero angle for hip and shoulder abduction meant that the extremity was parallel to the plane (pointing vertically downwards) of the reference segment. A positive angle meant that the extremity was moving away from the reference segment (abduction). A zero angle for hip flexion meant that the extremity was pointing vertically downwards whereas a positive angle meant that the extremity was flexed. Pelvis and trunk rotations were calculated based on gimbal rotations using the greater trochanter and anterior superior iliac spine markers for the pelvis and the shoulders and sternum for the trunk. Angular changes from pre-stimulus values were calculated for statistical analyses.

Center of mass displacement and velocity were calculated based on a 10-segment model adapted from Winter (1990). (The arms were considered as one rather than two segments and the trunk as two rather than three segments as shown in Fig. 2)

Measurement variables of joint angles were evaluated at 150 ms post-perturbation (prior to voluntary arm movement onset, see Fig. 3), 350 ms post-perturbation (following onset of voluntary arm movement, at approximately peak lateral COM velocity in the CON condition, see Fig. 4), and at 900 ms post perturbation (trial completion). Additional joint angle analyses were conducted on limb, pelvis and trunk kinematics at the time of maximal divergence of the joint angles between the IPS and CON conditions: hip abduction (550 ms), pelvis roll (550 ms), and trunk roll (650 ms).
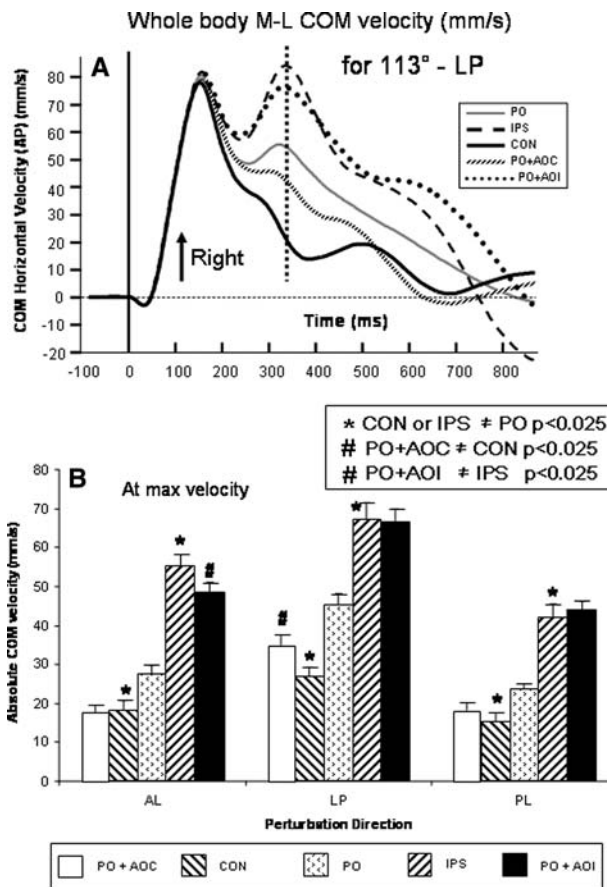
To ensure that no differences occurred between the right and left arm raises for the IPS and CON conditions, as a result of all subjects being right handed, two-way repeated measures ANOVAs (2 conditions × 6 directions) were conducted comparing measures of onset time (ms), peak velocity (deg/s) and time-to-peak velocity (ms) of arm abduction. An abduction velocity of 35°/s defined the onset of voluntary arm movement. This allowed for distinction between the 'automatic' arm responses to the PO and those due raising the arm. Maximum mean abduction velocity for the PO condition was 24.8 with a standard deviation (sd) of 6.4°/s (therefore the mean + 2 sd equaled 37.6°/s) for the 113° and 248° directions and less for other directions. Time-to-peak (ms) shoulder abduction velocity was determined by subtracting the onset time (ms) from the time of peak velocity (ms).

For all muscles, except TA and peroneus longus, muscle recordings were available bilaterally enabling consideration of effects on uphill and downhill muscles. EMG areas (that is, integrals) were calculated for a balance correcting and a later stabilizing interval. The latter was a fixed interval over 500–800 ms post stimulus onset. All areas were calculated using trapezoid

Shoulder abduction velocity for 113° (LP -Right)
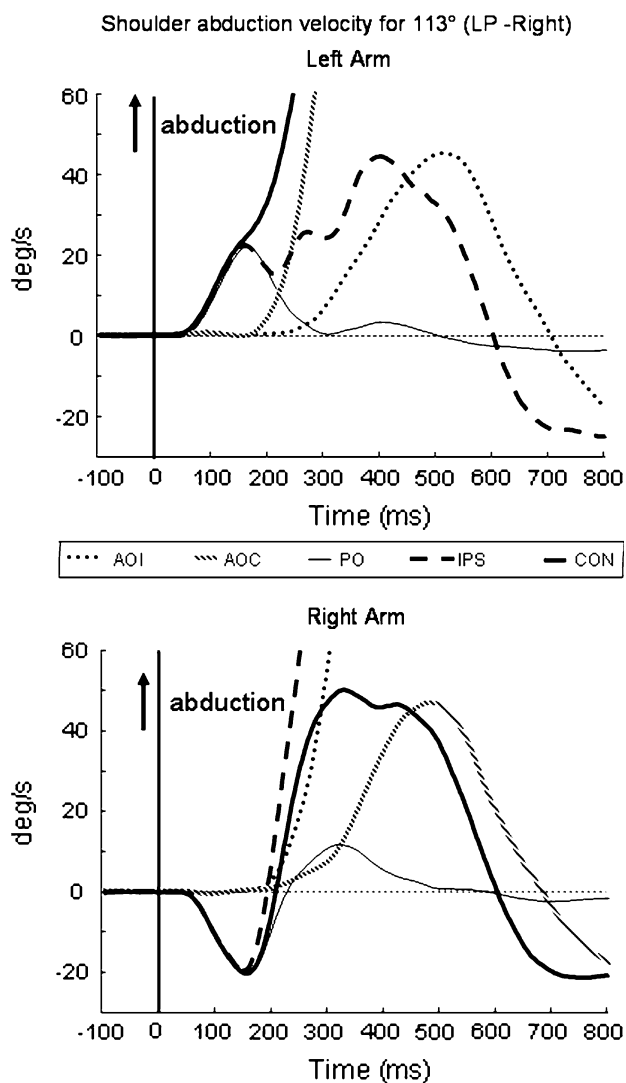
Left Arm

Right Arm

Fig. 3 Population traces of left and right arm abduction velocity under the 4 conditions (with two directions of arm raise only) for the stimulus 113° (an almost pure roll perturbation to the right). Each trace for the IPS, PO and CON conditions consists of the average of 7 responses from 24 subjects or an average of 168 responses per trace. Each trace of the AOI and AOC consists of the average of 12 arm raises from 24 subjects. The start of the support surface tilt and/or the cue for the arm raise, is indicated by the thick vertical line at 0 ms (defined by the first deviation of platform velocity). For the 113° tilt the contralateral arm is the left arm and the ipsilateral arm the right arm. For the PO condition, both arms first move in the same direction as the support surface with a maximum velocity ca. of 20°/s

Whole body M-L COM velocity (mm/s)

Fig. 4 Population traces of M–L COM velocity for stimulus 113° (**a**) and mean values (**b**) of the velocity at approximately 350 ms (when COM velocity for the IPS condition reached a maximum—see *vertical dotted line* on the traces). To show the different effects of condition, that is, the difference between CON and summed AOC plus PO conditions in the outcome measures, the traces for PO and AOC, and PO and AOI have been added together. The columns in the figure represent the population means and standard error for each condition or summed conditions, measured at approximately 350 ms from stimulus onset. Means were pooled for direction as follows AL (45° and 315°), LP (113° and 248°), and PL (158° and 203°). Standard errors of the means (*sem*) are indicated by *vertical bars* on the columns. *Asterisks* (*) on the columns indicates significant differences between the PO and CON or PO and IPS conditions, a gate symbol (#) indicates significant differences between the CON and (PO + AOC) or IPS and (PO + AOI) means

integration and were referred to baseline activity levels in the 100 ms prior to stimulus onset. Because we were interested in the condition effects during balance correcting activity we needed to modify our previously used interval of balance-correcting EMG activity (Carpenter et al. 1999; Bloem et al. 2000; Allum et al. 2002). In the current study, the interval for the balance correcting activity (120–250 ms) was calculated as follows:

1. For each muscle, the perturbation direction with the largest peak EMG activity (and its time) was sought for every subject over the interval 100–340 ms for the PO condition. The maximum response direction for each muscle was averaged out across subjects to yield one mean maximum direction per muscle.
2. On the response for this mean maximum direction we defined the duration of the difference effect AOI + PO − IPS or AOC + PO − CON for balance

correcting activity. To find the onset of the difference effect, the first EMG activity sample with an amplitude less than 10% of the maximum, prior to the peak difference response (AOS + PO − IPS or AOC + PO − CON) was sought. The search was ended at 70 ms. To find the end of the interval the first sample with an amplitude less than 15% of the maximum, after the peak response, was sought. Across the population the intervals between onset and end of the difference effect were averaged and the limits of the range of values was determined for all muscles. The resulting interval was 120–250 ms and similar to the interval used to measure balance-correcting activity in previous studies (Carpenter et al. 1999; Allum et al. 2002).

A one-way repeated measures ANOVA was conducted to evaluate the percentage of trials excluded due to errors in voluntary arm raising comparing the AO, CON and IPS conditions. Arm raises were deemed to be errors when the participants raised the arm in the opposite direction of the visual and auditory cues (left arm when cues presented on the right), raised both arms, or raised the incorrect arm followed by the correct arm.

Our main ANOVA's consisted of three pre-planned analyses. First, three-way repeated measures ANOVAs [side: right vs. left × condition: CON vs. IPS vs. PO × direction: AL (45° and 315°) vs. LP (113° and 248°) vs. PL (158° and 203°)] were conducted on all dependent measures using a significance level of 0.05. Having determined that side did not influence the results our analysis of EMG results was restricted to a two-way ANOVA of condition × direction. Then similar three way ANOVA's compared the differences between combined and summed responses, that is for IPS versus PO + AOI and CON versus PO + AOC. Significant difference effects between arm raising were evaluated within each pooled perturbation direction using Bonferroni ($P < 0.025$) post-hoc tests.

Results

Kinematics

Automatic and triggered voluntary arm abduction responses

Arm abduction responses resulting from the different experimental conditions are illustrated in Fig. 3 for the left and right arms, following a tilt of the support surface to the right. For such a right tilt without additional

arm raising (that is PO), the left (uphill arm) abducted with an onset of 44 ms (± 7.5 ms), reached a peak velocity of 24.2°/s (± 5.5°/s) and remained abducted. The right downhill arm adducted with an onset of 42 ms (± 8.2 ms), reached a peak velocity of 21.3°/s (± 4.7°/s), then abducted to return to the pre-stimulus position. The tendency of the uphill arm to have a higher peak velocity was consistent across all perturbation directions; however, the peak abduction velocities decreased with a decreasing roll component to the perturbation. Onsets of arm abduction/adduction based on exceeding 2 sd of pre-stimulus (practically zero) abduction velocities did not change with perturbation direction under the PO condition.

As illustrated in Fig. 3, raising an arm with the platform tilt induced an earlier onset of some 60 ms in abduction velocity (with respect to the 35°/s threshold) compared to the arm raising only (AOI and AOC) conditions but caused no significant change in the peak velocity of approximately 300°/s and time to peak velocity of approximately 300 ms.

Thus for the right tilt shown in Fig. 3, the left arm abduction velocity first exceeded 35°/s at 228 ms (± 48 ms) under CON arm raising condition and the right arm onset measured in this manner for the IPS arm raising condition was 235 ms (± 37 ms), values which were both 57 ms (± 9.5 ms) earlier ($P < 0.001$) than under the arm raising conditions alone.

These similarities in peak velocities and differences in onset times were consistent across direction and identical for the left and right arms. We therefore concluded that the right-handiness of the test subjects did not influence arm raising in the current experiments. Even if we compared an arm abduction onset (crossing 35°/s) for an arm first adducted by the perturbation tilt (for example the right arm under the IPS condition in Fig. 3), onsets were still earlier (53 ± 12 ms, $P < 0.001$) than for the arms only conditions. It may be noted in Fig. 3 that raising an arm under the CON and IPS conditions induced an abduction in the contralateral arm with peak velocities of approximately 50°/s that were significantly greater than for the PO condition ($P < 0.05$).

COM displacements

There was no significant effect of voluntary arm raises on A–P COM measures. Therefore we report only on lateral COM movements. These had amplitude on average some 20% larger than posterior COM measures (see also Bakker et al. 2006). During the first 150 ms post stimulus no effect of arm raising on COM M–L velocity was observed (Fig. 4). COM velocity first

peaked in the tilt direction at about 150 ms with a secondary peak in the same direction at about 350 ms. Significant differences in the second peak in M–L COM velocity became evident between the arm raising conditions across all perturbations directions. Figure 4 displays the differences in the whole body M–L COM velocity profiles for a LP perturbation (113° direction).

Differences in M–L COM velocity were examined at the time of second peak of velocity for the IPS condition (350 ms). A three-way ANOVA revealed a significant interaction of arm raising condition and direction of perturbation ($F(2, 87) = 3.6$, $P < 0.01$) between the PO, CON and IPS conditions as well as a main condition effect ($F(2, 44) = 55.4$, $P < 0.001$). Main and interaction effects were also seen between summed and combined effects [PO + AOC vs. CON and PO + AOI vs. IPS ($P < 0.01$)].

Post-hoc tests within each perturbation direction revealed that raising the contralateral (uphill) arm significantly reduced whole body M–L COM velocity while raising the ipsilateral (downhill) arm resulted in an increase in whole body M–L COM velocity in the direction of tilt for all directions (see Fig. 4b). COM remained driven rightwards in rightwards perturbations for all arm raising conditions and leftwards in leftwards perturbations for all arm raising conditions. Figure 5a shows an example of this for the 113 direction of perturbation (to the right).

An examination of differences between summed AO and PO effects compared to the CON and IPS conditions revealed that there was no difference between COM velocity at approximately 350 ms for the IPS and summed AOI and PO conditions, except for anterior directed perturbations (AL) for which the IPS effect was greater (Fig. 4b). However for the CON condition, the peak ML COM velocity at 350 ms was always significant less the expected from the AOC and PO summed effect for all perturbation directions (Fig. 4b).

Analysis of COM displacement (Fig. 5) revealed that raising the contralateral arm was associated with reduced final deviations at 900 ms while raising the ipsilateral arm resulted in increased final COM deviations ($F(2,89) = 77.3$, $P < 0.001$). The three-way ANOVA demonstrated that M–L final COM displacement was dependent on both perturbation direction and arm raising condition as evidenced by a significant interaction effect ($F(2, 87) = 7.8$, $P < 0.001$). No significant effect of side (right vs. left) or interaction of arm raising condition and side was found. Comparisons of the CON and PO + AOC and IPS and PO + AOI conditions revealed significant effects of condition ($F(2,22) = 7.6$, $P = 0.01$ and $F(2,22) = 11.5$, $P = 0.003$).
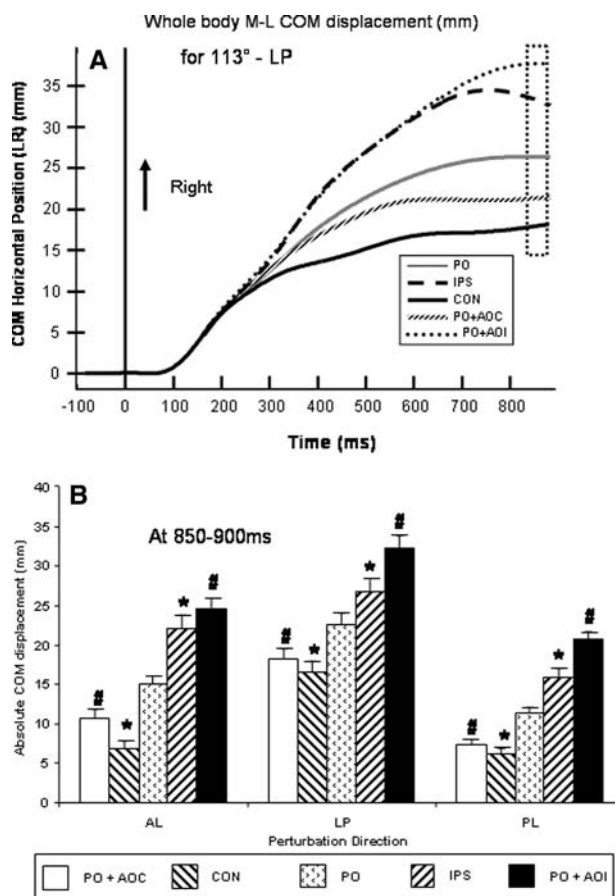
Fig. 5 Population traces of M–L COM displacement (**a**) and mean values of COM displacement over 850–900 ms from stimulus onset (**b**). The population traces are for a displacement in the 113° direction (as in Fig. 1). The columns in the figure represent the population means for each condition or summed condition over 850–900 ms form stimulus onset. For other details of the figure refer to the legends of Figs. 3 and 4

There was a weak interaction effect for the IPS and PO + AOI comparison ($P = 0.035$).

Mean final M–L displacements (as measured at 850–900 ms, see Fig. 5b) for the AL (−45° and 315°), LP (−113° and 248°), and PL (−158° and 203°) perturbation directions in the CON conditions were 7.0, 16.6, and 6.2 mm, respectively. These displacements were less than the sum of PO and AOC conditions (10.8, 18.2, and 7.3 mm, $P < 0.025$) and also less than that for the PO condition (15.0, 22.6, and 11.5 mm). The displacements for the IPS conditions (22.1, 26.8, and 15.9 mm, respectively) were less than the summed PO and AOI conditions (24.5, 32.3, and 20.7 mm) but greater than those of the PO conditions ($P < 0.025$, see Fig. 3).

Trunk roll and pitch

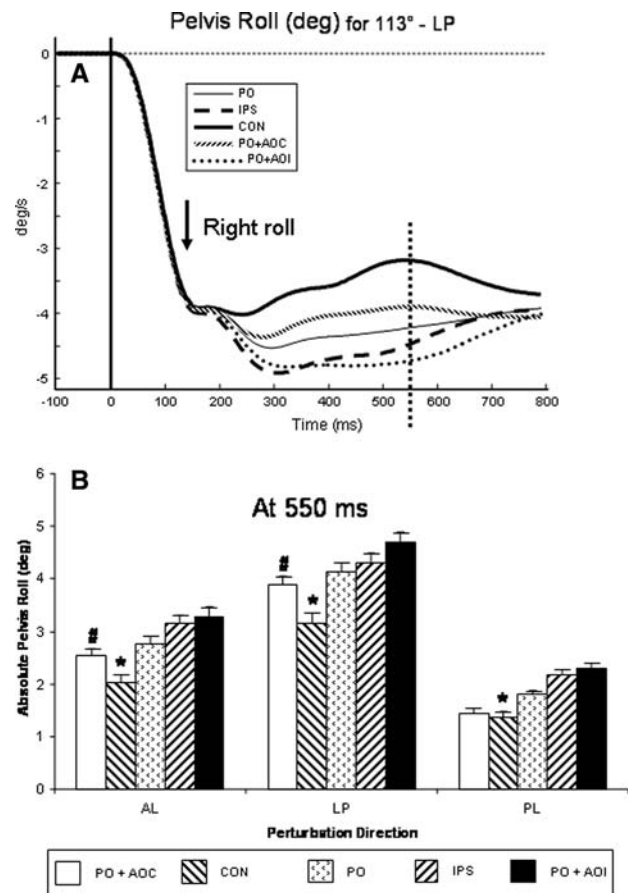Figure 6 shows that raising the IPS caused trunk roll in the same direction as that for the PO condition (opposite
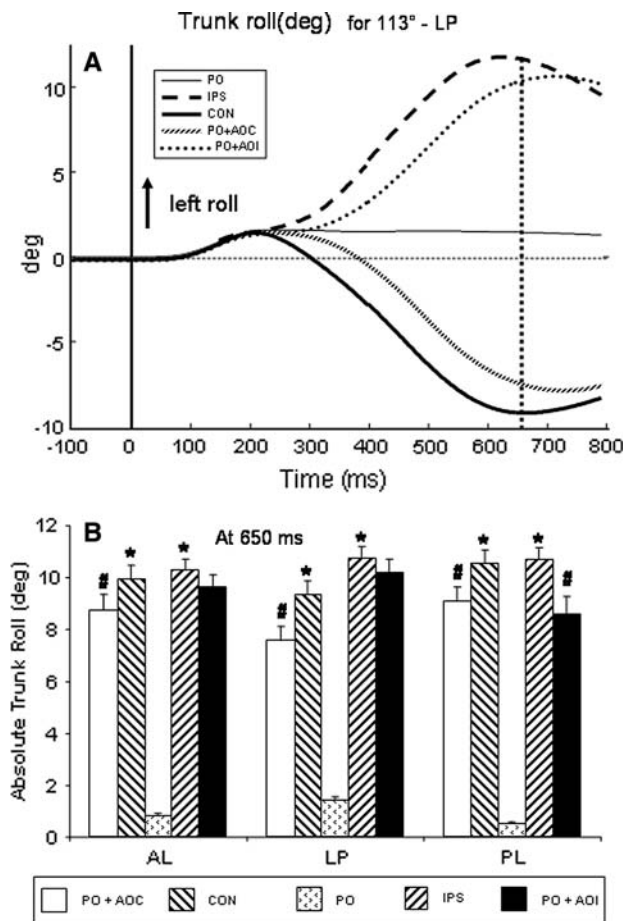
Fig. 6 Population traces of trunk roll across conditions for stimulus 113° (**a**) and mean values of absolute trunk roll across directions and conditions (**b**) measured at 650 ms when trunk roll displacement plateaued (see *vertical dotted line* on the traces). For details of the figure refer to the legends of Figs. 3 and 4

Fig. 7 Traces of pelvis roll for the 113° stimulus (**a**) and mean values of absolute pelvis roll (**b**) measured at 550 ms when pelvis roll diverged maximally across conditions (see *vertical dotted line* in the traces). For details legends of Figs. 3 and 4

that of the support-surface) but to a much greater extent (9–11° more) whereas raising the CON caused the trunk to roll in the opposite direction (9–11° less).

ANOVA analyses revealed a main effect of arm raising on trunk roll at each of the measurement times considered; 350, 650 and 900 ms ($P < 0.001$ at each time). There was also a direction by condition effect. As Fig. 6 shows, the difference between trunk roll with and without arm raising was profound. The post-hoc analysis revealed that differences were significant for each direction of roll ($P < 0.017$). When however, differences between the CON and IPS arm raising conditions with respect to summed PO plus arm raising alone (AO) effects were considered, significant differences were revealed at 350 and 650 ms but not at 900 ms. The differences in the means at 650 ms are illustrated in Fig. 6b. In contrast to COM displacements, trunk roll for the CON condition was greater than that from the summed effect of PO and AOC

($P < 0.025$). There was no difference between trunk roll induced by the IPS condition and the summed effects of PO and AOI, except for the PL perturbations directions (158° and 203°).

As a roll perturbation of the support surface induces trunk pitch rotation (Carpenter et al. 1999), an effect on trunk pitch can be expected with arm raising. A main effect emerged from the ANOVA analyses ($P < 0.001$); however the effect was not different from the effect of AO and PO.

Pelvis roll and hip abduction

Figure 7 depicts the effect of arm raising on pelvis roll. Between 200 and 800 ms post stimulus, pelvis roll, and with it hip abduction, diverged from the pelvis roll for the PO condition. The effect of arm raising was strongest for CON raise and absent for the IPS raise.

At 350 and 550 ms, a main effect of arm raising condition was observed for pelvis roll ($F(2,45) = 58.4$ and 27.3, $P < 0.001$). Differences between the CON and PO

conditions were revealed by post-hoc analyses at 550 ms but not between IPS and PO conditions (see Fig. 5b). For the contralateral arm raise, the combined effect of raising the arm with the perturbation (CON) differed from the summed effect of PO and AOC. The PO condition was greater than the summed effect of PO and arm raising ($F(2,22) = 13.0$, $P = 0.0015$) but only for the deviations with larger roll components (AL, 45° and 315°; LP, 113° and 248°—see Fig. 7B). The differences in these cases followed the trend for COM displacements, the summed effect (PO + AOC) was greater than that of raising the contralateral arm with the perturbation (CON).

The effects of arm raising on uphill and downhill hip abduction were similar in both ANOVA and post-hoc analyses for the 350 and 550 ms time points. The differences of the CON and IPS conditions to the PO condition were not different from the summed effect of arm raising alone (AOC and AOI) and PO conditions.

Ankle, knee and hip angles

Some kinematic changes in lower limb joint angles were found as a result of arm raising conditions. Most of these effects were inconsistent except for ankle flexion. Thus at 600 ms both uphill and downhill ankle flexion was changed by the arm raising of the CON and IPS conditions ($F(2,46) = 6.9$ and 9.6, respectively; $P < 0.002$). Examination of comparisons with the effect of arm raising alone summed with the effect of PO indicated borderline differences ($P = 0.03$) with post-hoc analyses revealing no differences to the summed effects. As expected (see Carpenter et al. 1999; Grüneberg et al. 2005), direction only effects were seen in leg kinematics.

Muscle responses

Lower trunk muscles

Balance correcting activity in the lower trunk muscles was altered by arm raising conditions in a manner consistent with the effect described above for the trunk, that is, facilitating a roll displacement of the trunk in the direction opposite to that of the raised arm. It would be expected that increased activity should be observed in the lower trunk muscles contralateral to the arm raised, regardless whether the uphill or downhill am was raised. Figure 8a provides an example of the increase in the left (downhill) external oblique muscles when the contralateral (uphill), that is right arm was raised and Fig. 9a an example for the left (uphill) paraspinal muscles when

the arm ipsilateral (downhill) to the platform tilt is raised, that is, again the right arm. The periods used to provide statistical support for the observations described above are shown by boxes with dotted perimeters in Figs. 8 and 9.

ANOVA analysis for the period 125–250 ms when the effect of IPS and CON arm raising was strongest and for later stabilising period of 500–800 ms provided clear evidence for a condition effect of arm raising on lower trunk muscle activity. Uphill and downhill oblique and paraspinal muscles showed a condition effect over 125–250 ms ($F(2, 44) = 12.3$, 6.2, 20.4, 16.4, respectively; $P < 0.001$). Analyses of arm raising with perturbation (CON and IPS) in comparison to the separate effects of AO and PO revealed large changes which became evident in post-hoc analyses (Figs. 8b, 9b). Thus downhill oblique and paraspinal activity was always larger than the combined activity for the AO and PO conditions when the contralateral arm was raised ($P < 0.001$); likewise for the uphill muscles when the arm ipsilateral to the tilt direction was raised ($P < −0.001$). For the more lateral perturbations (LP: 113° and 248°), this larger activity occurred bilaterally (Figs. 8b, 9b). ANOVA analyses for the later period of activity (over 500–800 ms) also revealed effects of arm raising condition in the uphill and downhill oblique and paraspinal muscles ($F(2, 44) = 29.7$, 13.4, 12.9, 10.9, respectively; $P < 0.001$). Generally though, activity over this period for the CON and IPS conditions was less than or equal to that for the summed effects AO and PO effects (Figs. 8b, 9b).

Leg muscles

The effect of arm raising on gluteus medius muscle activity was weaker than for the lower trunk muscles. This was as expected from the size of the effect on pelvis roll for the CON condition and negligible effect for the IPS condition. Figure 10 shows the effect on gluteus medius for the CON condition. ANOVA analyses indicated an effect on both uphill and downhill gluteus medius for CON and IPS conditions ($F(2,46) = 17.5$ and 26.9, respectively, $P < 0.001$) however post-hoc effects were either absent or of borderline significance for the IPS conditions. A similar situation emerged for the later period of activity (500–800 ms). For this reason only CON arm raising effects are plotted in Fig. 10b.

In the lower leg muscles the only consistent effects observed were previously noted directional effects (Carpenter et al. 1999; Grüneberg et al. 2005). Some ANOVA analyses yielded arm raising condition effects in the peroneus longus and tibialis anterior muscles

A

B
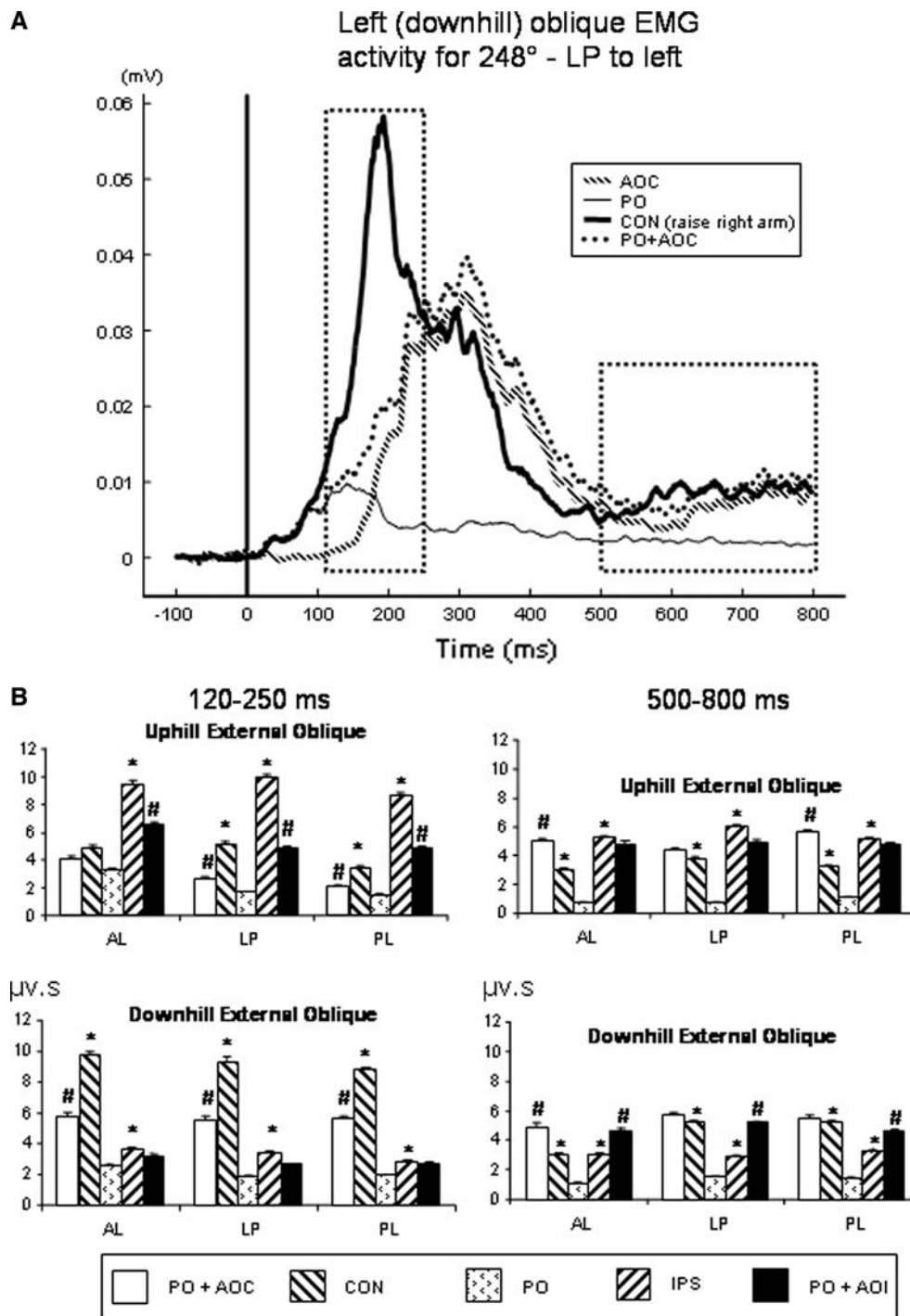
Fig. 8 Changes to external oblique muscle activity with arm raising conditions. The upper set of population traces in A shows the effect on EMG responses from the left oblique externus muscle for a 248° (*left*) directed roll, the direction with the largest response. The population responses traces in **a** show an enhancement for the CON condition with respect to PO + AOC in the first measurement interval (shown by the *dotted box* at 125–250 ms). A slight reduction is observed for in the second measurement interval (*dotted box* at 500–800 ms). Population means and standard error across these intervals are shown by column plots in **b**. Because external oblique muscles were recorded bilaterally, uphill and downhill muscle activity could be calculated across directions for all conditions shown

which on closer post-hoc inspection failed to yield significant differences compared to the perturbation only condition. Thus overall, no consistent changes were observed in lower leg balance correcting muscle activity as a result of abducting the arms in the same or opposite direction roll to that of the platform.
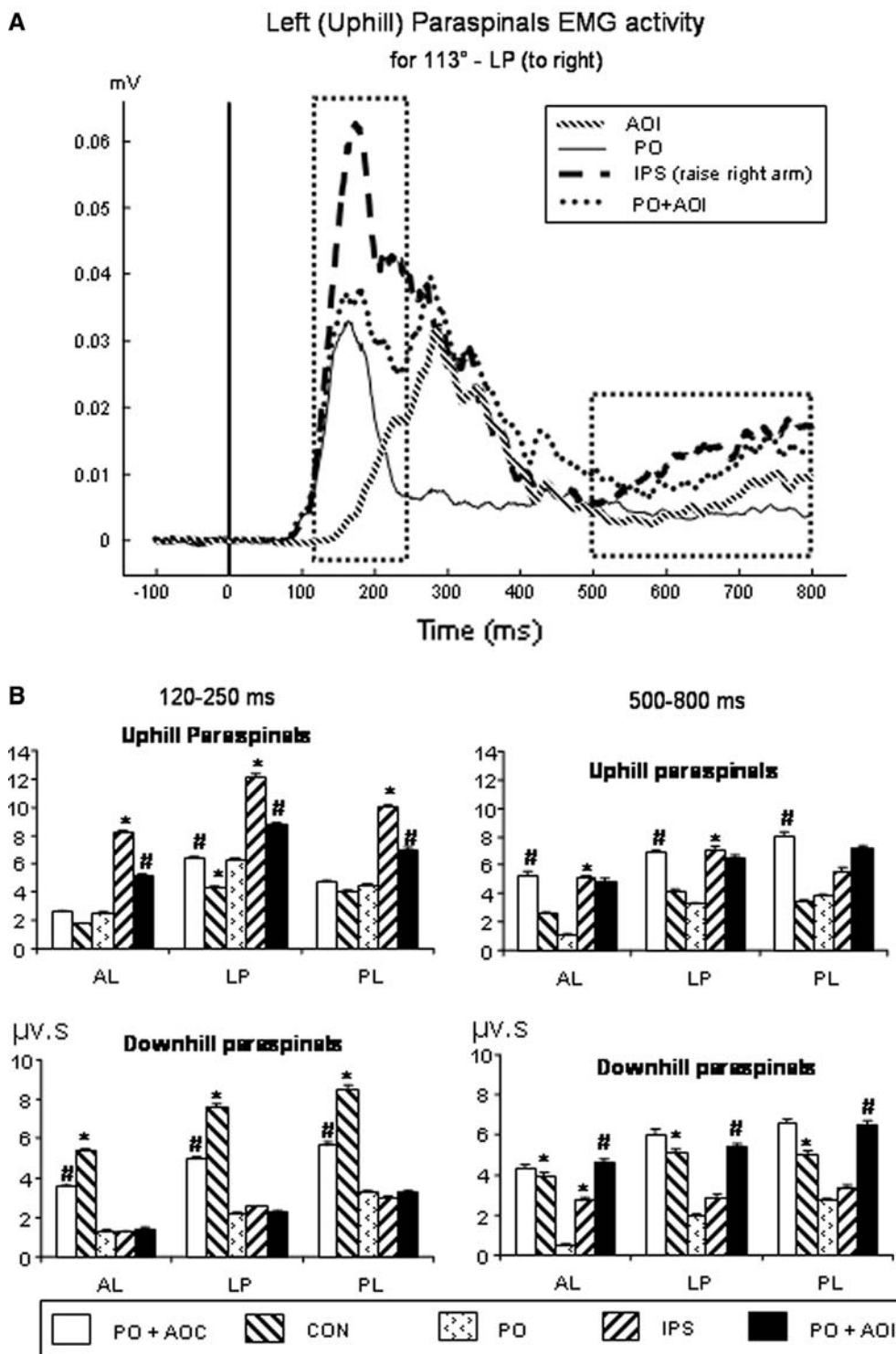
Fig. 9 Changes to paraspinal muscle activity with arm raising conditions. The layout of the figure is identical to that of Fig. 8

Arm muscles

It was not surprising that the deltoid muscle activity during the combined arm raising and perturbation conditions (CON and IPS) should be much larger than for the PO condition (see columns with an amplitude of approximately 60 μv.s in Fig. 11c). Raising the arm at the time of perturbation will lead to such increased activity. A more interesting question answered by our ANOVA analyses was whether activity in the non-raised arm was altered and if this activity could be predicted from the sum of arm raising and perturbation
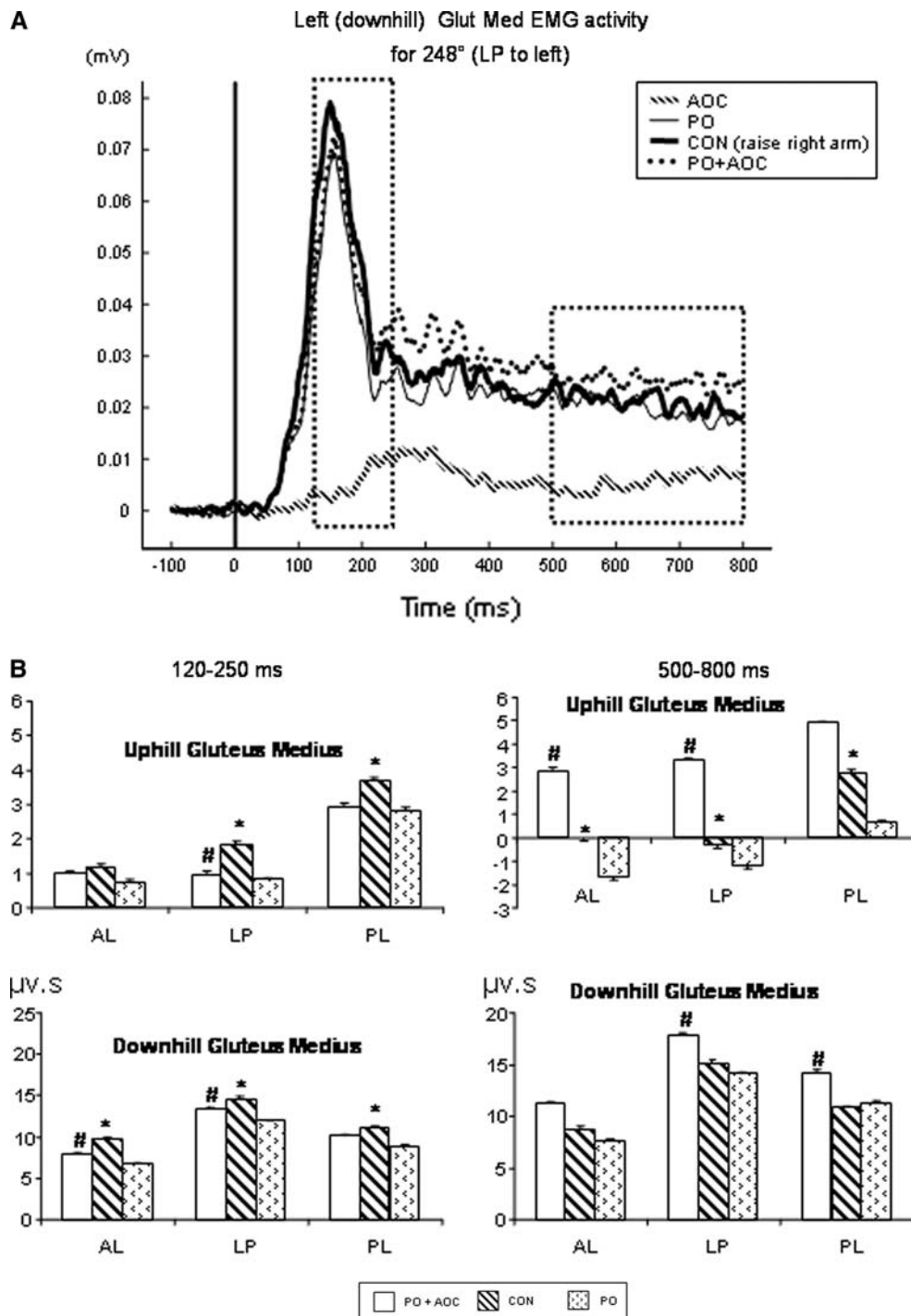
Fig. 10 Effect of arm raising conditions on EMG responses of the gluteus medius muscles

only activity (AO + PO). Activity in the non-raised arm showed such a condition effect. ($F(2,23) = 18.6$ in the downhill deltoid for the CON condition and $F(2,23) = 16.5$ in uphill deltoid for the IPS condition: $P < 0.001$). As the columns in Fig. 11c indicate, activity was always greater for the combined than for the summed activity of AO and PO conditions. No similar effect was seen over the later 500–800 ms measurement interval.

The example traces in Fig. 11a and b illustrate bilaterally increased arm muscle activity in the deltoid muscles when one arm is raised. Activity initially follows
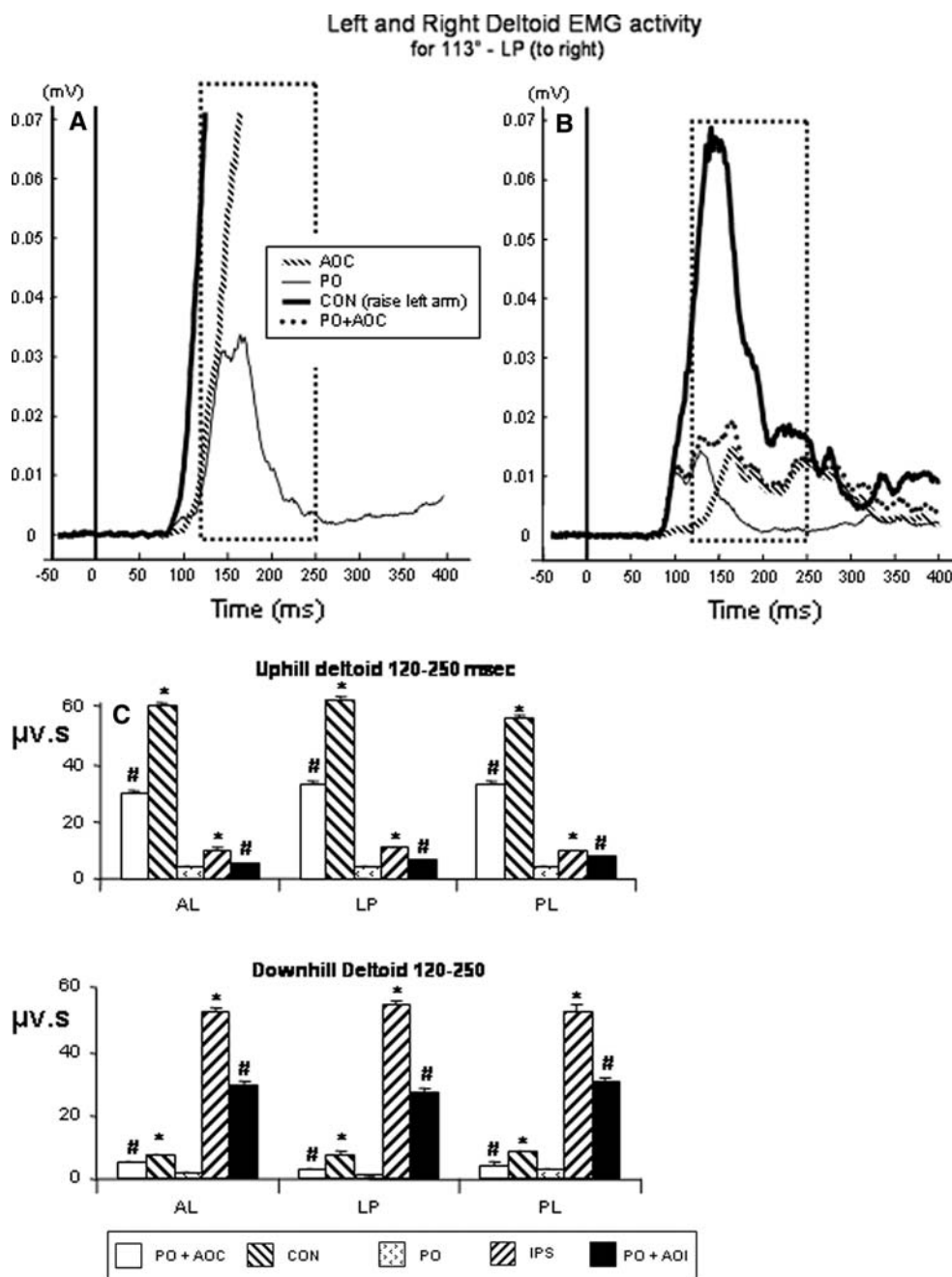
Fig. 11 Changes to deltoid muscle activity with arm raising conditions. **a** and **b** show the activity in the left and right deltoid muscles when the left arm is raised. In **b** the activity has been truncated at 0.07 mv in order to have the same scale as in **a**. Means across the balance correcting interval of 120–250 ms are shown in **c**. The layout of the figure is identical to that of Fig. 8

the same time course as the PO activity, that is, onset of the increased activity for CON and IPS conditions was indistinguishable from onsets for the PO activity. Average onsets of deltoid across all directions for the PO condition were at 106 ms, as expected from Allum et al. (2002). As shown in Fig. 11a and b, the onsets of deltoid activity for the AO condition were later than for the PO and CON conditions. For the direction of tilt shown in Fig. 11, the mean onsets were 97.5 and 111 ms for the CON and AOC conditions, respectively, in the raised arm and, 93 and 136 ms, respectively in the non-raised arm, differences of AOC onsets of 13.5, respectively 43 ms, with respect to the CON condition ($P < 0.05$).

Discussion

Triggered arm responses

When required to raise either the arm ipsilateral or contralateral to the directions of support-surface tilt, subjects activated their arm muscles just as rapidly as when subjects were suddenly tilted in one direction. However arm movements (with respect to a threshold of 35°/s, which is greater than the velocity observed for tilt alone) and onsets of the underlying EMG responses were earlier than those of triggered arm velocity raises without a simultaneous balance perturbation.

Previous work has shown that, in humans, movements of the support surface result in arm muscle EMG responses comparable in timing to or even earlier than the early "automatic" ankle muscle responses (McIlroy and Maki 1995; Allum et al. 2002). Posterior deltoid mean onsets of 88 ms were found for high-magnitude forwards translations of the support surface (McIlroy and Maki 1995) and Allum et al. (2002) reported slightly later deltoid mean onsets of 109 ms in response to backward tilt support surface rotations. Here we reported similar latencies (106 ms), which were not altered by requiring a simultaneous arm raise, but were considerably earlier than onsets for arm raising alone. Thus it appears from EMG onsets in arm muscles that arm raises triggered by a balance perturbation became more "automatic" than voluntary raises triggered by light and sound cues. Similar results were noted for arm movement kinematics.

As noted previously, arm movements for a tilt alone (the PO condition) were directed 'uphill' (Allum et al. 2002). The results presented here also showed early onset arm movements that were initially directed 'uphill' in young adults (Fig. 3). It is evident in Fig. 3 that these arm responses (mean onset of 41 ms) occur well before the triggered voluntary arm raises (mean onset of approximately 230 ms). However these early onsets of 41 ms are a stimulus induced biomechanical response to perturbation of the support surface. However when a 35°/s threshold was used to separate the early biomechanical effect of the perturbation from the effect of triggered arm raising, onsets of arm movements (as determined by shoulder abduction) were some 60 ms earlier when triggered with the support-surface tilt compared to triggered by auditory and visual cues in the AO condition. Thus arm kinematic analysis also indicated that arm raises become more automatic when triggered by a balance perturbation.

Voluntary arm raises and stability

According to the results of this study, voluntary arm raises in the frontal plane, which are triggered by the tilt perturbation, cause response onsets in arm muscles to be marginally earlier than the onset of arm movements muscle activity for tilt alone (106 ms). The effects of the voluntary arm raises emerged more strongly in EMG response amplitudes.. Influences on body and COM kinematics appeared after 150 ms. Thus, the influences of arm raising on balance corrections do not appear to be anticipatory in nature. Anterior–posterior COM was unaffected by voluntary arm raises even for perturbations with a considerable pitch component. This can probably be attributed to the fact that participants were directed to raise their arms in the frontal plane regardless of the exact direction of the perturbation.

The effects of arm raising were clearly observed in a peak of lateral COM velocity at approximately 350 ms. Raising the ipsilateral arm clearly increased this peak observed in the PO condition, whereas raising the contralateral arm caused a temporary trough in lateral COM velocity (Fig. 4). From these observations it may be deduced that arm movements influence lateral COM velocity primarily at this time point. Raising the contralateral arm this caused a beneficial reduction in the final displacement of whole body ML COM (39% across directions) as well as significant reductions in peak ML COM velocity (87% across directions). In contrast, destabilizing effects of raising the ipsilateral (downhill) arm were demonstrated through a significant increase in final whole body ML COM displacement (32% across directions) as well as increases in peak ML COM velocity (73% across directions). Thus specifically requested the subjects to abduct the uphill or downhill arm regardless of the exact direction of tilt caused a general improvement or worsening of stability, respectively. Figure 12 provides a summary of our observations. It is an open question whether a general improvement in AP stability would be obtained by bilateral arm raises in the saggital plane and whether these could be integrated into balance corrections as well as the unilateral abductions were in this study.

Figure 12 shows schematically that lateral arm raises in the AO condition resulted in COM deviations towards the direction of arm movement (mean ± 1 std displacement of 7 ± 3 mm). Rotations of the support surface without voluntary arm raises resulted in COM displacements to the right for rightwards perturbations and to the left for leftwards perturbations by an amount dependent on the roll amplitude (Fig. 5b). When the support surface was rotated to the right and the participants were directed to raise the right arm (IPS condition), the COM was displaced to the right by an amount greater than the PO condition but less than the summed PO + AOI conditions (Fig. 5b). When the

Summary biomechanical and EMG results
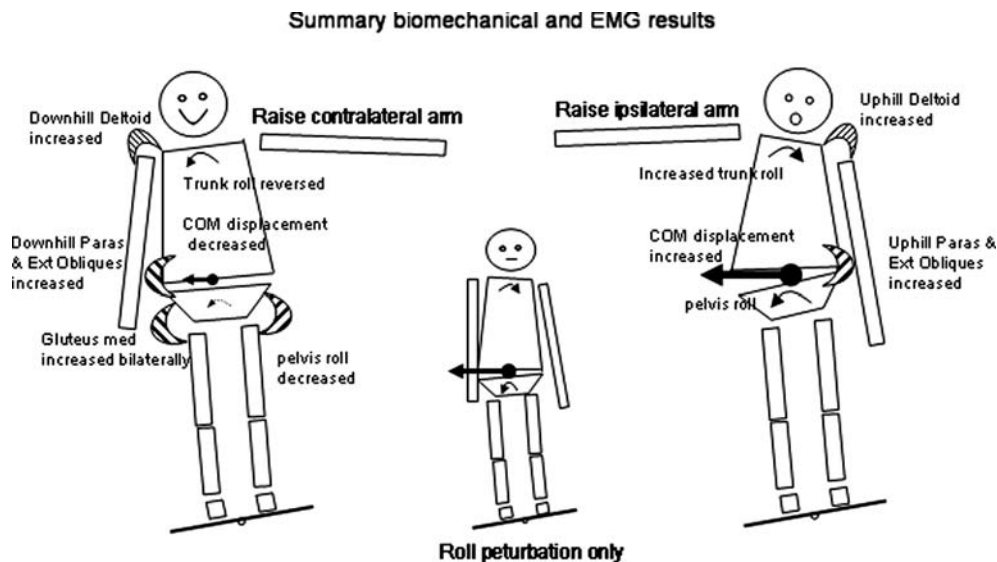
Fig. 12 Schematic Summary of biomechanical and EMG activity changes with arm raising conditions. For details refer to text in the discussion

support surface was rotated rightwards and the participants raised the left arm (CON condition), the net rightwards COM displacement was reduced due to the opposing shift in arm COM. For this direction of arm raise, the reduction in COM displacement compared to that of the PO condition was greater than the sum of the PO and AO conditions (Fig. 5b). Thus contralateral arm raises aid COM stability more than ipsilateral raises interfere with COM stability, and the sum of the PO and AO provides only a lower bound for predicting the amount of improvement when the contralateral arm is raised.

Allum et al. (2002) demonstrated that the trunk segment rolls (1°–2° after 300 ms) in an 'uphill' direction in healthy young individuals when the support-surface is tilted some 8°. Comparable values were found in the present study for trunk roll in the PO condition (Fig. 6). Voluntarily raising the arm caused a divergence of trunk roll after 300 ms. Specifically raising the contralateral arm resulted in a 'downhill' trunk roll. This result may appear somewhat paradoxical in that raising the contralateral arm resulted in a reduced whole body COM displacement, while the trunk rolled approximately 10° in the direction of an impending fall. In order to reduce the net whole-body COM displacement segments other than the arm may have contributed to the more stable COM displacement. A compensatory change was found in reduced pelvis roll (Fig. 7).

Thus the changes in trunk and pelvis roll, in the arm raising conditions as compared to the perturbation only condition, appear to be due to stabilizing reactive moments counteracting the moments created at the

shoulder joint due to voluntary arm raises. The primary role of these opposing stabilizing moments is to maintain upright posture. Although joint moments were not calculated in this study, the resultant changes in trunk and pelvis roll support the presence of stabilizing moments, in agreement with the results from Eng et al. (1992). Furthermore the presence of initially larger EMG amplitudes in comparison to the PO and AO conditions supports this notion. Interestingly as the later (500–800 ms interval) responses are smaller, especially for the CON condition, this indicates that the CON condition is statically more stable and requires less muscular energy.

For example see Fig. 12 left, when the left arm was raised in combination with a rightwards perturbation (CON condition), the trunk rolled initially leftwards, due to the support surface rotation, and then rolled to the right. Similarly, the pelvis rolled initially rightwards due to the support surface rotation and the roll was then reduced (still rightwards but less so). The reduction in pelvis roll in combination with the shift in COM due to arm raise to the left, reduced the whole body COM displacement as compared to the PO condition.

In contrast, when the right arm was raised in the AO condition, the trunk rolled to the left and the pelvis rolled slightly to the right, indicating a compensating stabilizing moment at the hip on the left side of the body. In the condition where raising the right arm was added to a rightwards perturbation (IPS condition—see Fig. 12 right), the trunk rolled to the left, initially due to the support surface rotation, and then much further to the left due to stabilizing reactive moment counteracting the arm raising moment. Similarly, the

pelvis rolled initially to the right due to the support surface rotation and then slightly further to the right. The summing of the moments generated by the support surface rotation and the stabilizing moments necessary following the arm raise caused the whole body COM to shift further in the direction of an impending fall.

General conclusions

In healthy young adults, voluntary arm raises triggered at the time of support surface rotation significantly alter measures of stability as well as the patterns of balance recovery in body segments. Arm raises contralateral to the support surface roll direction provide considerable benefits to stability through reduced ML COM velocity and displacement as compared to perturbations that are not followed by lateral voluntary arm raises. Conversely, arm raises ipsilateral to the direction of support surface roll result in greater instability. Moreover, the effects of such voluntary arm raises following perturbation appear to be primarily limited to the pelvis and trunk segments and muscles acting at these segments and are well integrated into balance correcting commands.

References

Allum JHJ, Carpenter MG, Honegger F, Adkin AL, Bloem BR (2002) Age-dependent variations in the directional sensitivity of balance corrections and compensatory arm movements in man. J Physiol 15:643–663

Aruin AS, Ota T, Latash ML (2001) Anticipatory postural adjustments associated with lateral rotational perturbations during standing. J Electromyogr Kinesiol 11:39–51

Bakker M, Allum JHJ, Visser JE, Grüneberg C et al (2006) Postural responses to multidirectional stance perturbations in cerebellar ataxia. Exp Neurol (in press)

Beule AG, Allum JHJ (2006) Otolith function assessed with the subjective postural horizontal and standardized stance and gait tasks. Audiol Neurootol II:172–182

Bloem BR, Allum JHJ, Carpenter MG, Honegger F (2000) Is lower leg proprioception essential for triggering human automatic postural responses? Exp Brain Res 130:375–391

Carpenter MG, Allum JHJ, Honegger F (1999) Directional sensitivity of stretch reflexes and balance corrections for normal subjects in the roll and pitch planes. Exp Brain Res 129:93–113

Carpenter MG, Allum JHJ, Honegger F (2001) Vestibular influences on postural control in combination of pitch and roll planes reveal differences in spatio-temporal processing. Exp Brain Res 140:95–111

Cordo PJ, Nashner LM (1982) Properties of postural adjustments associated with rapid arm movements. J Neurophysiol 47(2):287–302

Eng JJ, Winter DA, MacKinnon CD, Patla AE (1992) Interactions of the reactive moments and center of mass displacement for postural control during voluntary arm movement. Neurosci Res Commun 11:73–80

Friedli WG, Hallet M, Simon SR (1984) Postural adjustments associated with rapid voluntary arm movements 1. Electromyographic data. J Neurol Neurosurg Psychiatr 47:611–622

Gottlieb GL, Agarwal GC (1970) Filtering of electromyographic signals. Am J Phys Med 40:142–146

Gottlieb GL, Agarwal GC (1979) Response to sudden torques about ankle in man: myotatic reflex. J Neurophysiol 42:91–106

Grüneberg C, Duysens J, Honegger F, Allum JHJ (2005) Spatio-temporal separation of roll and pitch balance-correcting commands in humans. J Neurophysiol 94:3143–3158

Grüneberg C, Allum JHJ, Honegger F, Bloem BR (2004) The influence of artificially increased hip and trunk stiffness on balance control in the pitch and roll planes. Exp Brain Res 157:472–485

Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky (2003) Muscle synergies during shifts of the centre of pressure by standing persons. Exp Brain Res 152:281–292

Maki BE, McIlroy WE (1997) The role of limb movements in maintaining upright stance: the change in support strategy. Phys Ther 77:488–507

Maki BE, Edmondstone MA, McIlroy WE (2000) Age-related differences in laterally directed compensatory stepping behavior. J Gerontol Med Sci 55A:M270–M277

McIlroy WE, Maki BE (1995) Early activation of arm muscles follows external perturbation of upright stance. Neurosci Lett 184:177–180

Patla A, Ishac M, Winter D (2002) Anticipatory control of mass and joint stability during voluntary arm movement from a standing posture: interplay between active and passive control. Exp Brain Res 143:318–327

Parkkari J, Kannus P, Palvanan M et al (1999) Majority of hip fractions occur as a result of a fall and impact on the greater trochanter of the femur: a prospective controlled hip fracture study with 206 consecutive patients. Calcif Tissue Int 65:183–187

Teyssèdre C, Lino F, Zattara M, Bouisset S (2000) Anticipatory EMG patterns associated with preferred and non-preferred arm pointing movements. Exp Brain Res 134:435–440

Vernazza-Martin S, Martin N, Cinera M, Pedotti A, Massion J (1999) Arm raising in humans under loaded vs. unloaded and bipedal vs. unipedal conditions. Brain Res 846:12–22

Winter D (1990) Biomechanics and motor control of human movement, 2nd edn. Wiley, New York