RESEARCH ARTICLE

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Integration of the hand in postural reactions to sustained sideways force at the pelvis

Abstract In order to investigate the potential hand contribution to sideways balance, sideways pushes to the right, which subjects resisted using either the lower limbs ("*hip only*") or the lower limbs assisted by the right upper limb ("*hand and hip*"), were delivered to the pelvis. Analysis of force and electromyogram recordings from the legs, arm and hand in the *hand-and-hip* condition showed a close co-ordination of upper and lower limbs in terms of mean latencies and amplitudes. However, trial to trial fluctuations of forces generated by the hand and leg did not correlate, suggesting parallel pathways under central co-ordinative control.

Key words Human balance · Lateral perturbation · Posture · Muscle synergy · Interlimb co-ordination

Introduction

A perturbation to balance generates a stereotyped, coordinated response in muscles across a number of body segments in a spatiotemporal pattern contextually appropriate to restore equilibrium (Nashner 1977; Diener et al. 1988). A predominant component of the response occurs at a latency of 80–120 ms, consistent with involvement of supraspinal pathways (Matthews 1991) and suggesting possible central organisation of the response. In some cases, postural responses exhibit shorter latency components. Recently, Nardone and colleagues (Schiepatti et al. 1995a; Nardone et al. 1996) suggested that of these, medium-latency leg postural responses are mediated by polysynaptic spinal pathways. However, others (Diener and Dichgans 1986; Diener et al. 1991)

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consider such early postural responses in the leg muscles to have little functional significance in maintaining equilibrium. Indeed, these authors have advocated discarding these early contributions of less than 100 ms in analysing postural responses. However, this approach may be criticised for prejudging the duration of the effective response, and a safer position would be to evaluate all muscle contributions in parallel with the forces to which they contribute.

The majority of studies of postural control have focused on responses in the lower limbs and trunk; however, there is evidence that the upper limb can be recruited as part of a postural response. Marsden et al. (1981) and Cordo and Nashner (1982) have demonstrated that the proximal upper-limb muscles are activated in response to a perturbation of balance in a standing subject when holding a stable support. The latency of the upper-limb muscle activation was similar to that of the distal leg muscles.

Coordination between upper- and lower limbs is suggested by the observations of Cordo and Nashner (1982) and Schiepatti et al. (1995b), who reported that recruitment of the upper-limb muscles as part of a postural response leads to a reduction in the lower limb muscle activity in response to a platform translation. Also, McIllroy and Maki (1995) have shown that both upper- and lower-limb muscle responses increase in amplitude as the size of the perturbation increases. Such co-ordination suggests a common central organisation of activation of muscles of the upper and lower limb in response to balance perturbation.

This paper extends the study of upper-limb function in reactive postural responses by focusing on the role played by the hand and by documenting the forces generated by the upper limb. It aims to determine what rules exist for the co-ordination of upper and lower limbs into an integrated reactive postural response. This involves examination of the relative timing and magnitude of upper- and lower-limb contributions in terms of both muscle activity and forces. We ask whether the responses of upper- and lower limb occur, on average, at similar times after the perturbation and whether trial to trial variation

is similar and, so, positively correlated. Similar timing of this kind would suggest that the response to perturbation is mediated by means of a common pathway. By systematic manipulation of the size of perturbation, we examine whether scaling of the upper- and lower-limb responses is similar, further supporting the idea of a common path underlying co-ordination.

Previous research on upper- and lower-limb co-ordination in anticipatory postural responses to self-generated perturbations has demonstrated reliable positive correlations between anticipatory postural adjustments at the hand and leg (Wing et al. 1997). Subjects used precision grip to hold an instrumented manipulandum between thumb and index finger. They were required to push or pull the manipulandum while standing on a force plate [measuring ground reaction forces (GRFs)]. In pushing or pulling the object, anticipatory increase in grip force (normal to the grip surface) was observed, which generated frictional force tangential to the grip surfaces. This resisted the tendency of the hand to slip off the manipulandum due to the load force generated during pushing or pulling with the arm.

In addition to early rise in grip force, Wing et al. (1997) observed changes in GRF reliably preceded push or pull. These changes were identified as anticipatory postural adjustments serving to stabilise the body against effects of the self-induced perturbation to balance (Bouisset and Zattara 1981; Friedli et al. 1984, 1988). Reliable positive correlations were found between force lead times and rates of increase even after partialling out a common dependence on the hand load force (HLF) creating the perturbation. It seems reasonable to identify the common dependence on load force with variability in the self-selected nature of the perturbation to grasp and postural stability. By contrast, the residual positive correlation might reflect variability in a common process or pathway involved in any adjustment to grasp and posture. A reliable positive correlation might therefore also be expected between upper- and lower-limb forces generated in the reactive postural response to an external perturbation when both limbs are involved in the task of maintaining equilibrium.

In this paper, an investigation of upper-limb function in a postural task is described, in which the contribution made by the upper limb in responding to a temporally unpredictable lateral perturbation (a sustained sideways force), whilst standing and holding onto a stable support, was examined. Two conditions were studied, one in which use of the upper limb in response to the perturbation was permitted and the other a control condition in which the same stance configuration was maintained, but the hand was not actively used to assist balance. The relationship between upper- and lower-limb function in the postural task was studied in terms of electromyogram (EMG) responses and resulting force patterns in the first experiment. In the second experiment, the effect of changing the postural demands of the task on the upper- and lower-limb components of the response was examined by systematically increasing the force of perturbation.
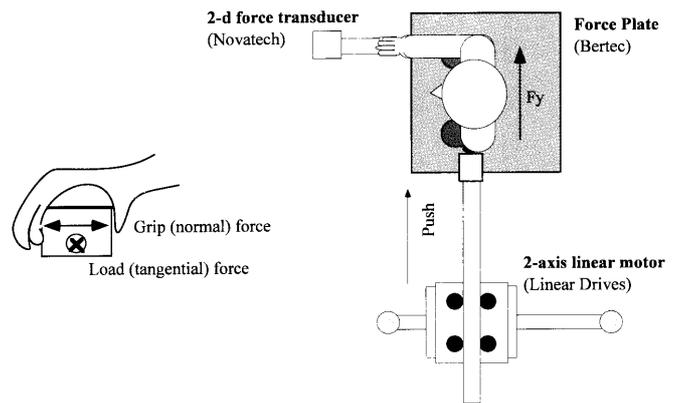

Fig. 1 Apparatus used to deliver right push to the standing subject with detail of hand force measurement

Methods

Fourteen right-handed subjects were studied (age range 22–50 years; 7 female) with local ethics committee approval and informed consent. Subjects stood with their feet slightly apart so that the lateral borders spanned 28 cm on a force plate (Bertec Corporation, Model 4060H), which was used to register the lateral component of the GRF. They used a right-hand precision grip to hold a force transducer (Novatech Ltd., Model F233) between the pads of the thumb and the first two fingers. The hand was positioned approximately 30 cm in front of and at the same height as the iliac crest (Fig. 1). The force transducer was firmly secured and so was capable of providing stable support. It was used to measure the hand grip force (HGF) normal to the transducer surface and HLF tangential to the surface.

A waist-high two-axis linear motor (Linear Technology Ltd, Model LDU25/HD/01) operating in the horizontal plane was coupled through a 6-df force/torque sensor (Assurance Technologies) to a semi-rigid belt around the pelvis. Each axis of the motor was driven under force servo control with a set point of zero (no resistance to motion) or a force directed to the right (right push) and set at 4, 5 or 6% of body weight.

Surface EMGs were recorded from muscles of the right (R) and left (L) lower limbs and R upper limb; R and L gluteus medius (GM), R and L gastrocnemius (GAS), R soleus (SOL), R first dorsal interosseous (FDI), R triceps (TRI) and R deltoid (DEL) using surface Ag/AgCl electrodes following skin preparation. The signals were amplified (gain 3400) by means of battery-powered amplifiers near the electrodes and passed through a unit gain isolating amplifier. A MACIIfx (Apple Corp.) computer with analogue interface (National Instruments NB-MIOI6X) sampled the eight channels of EMG and eight channels of force and position data at 1 kHz.

At the beginning of each trial, the subject lightly gripped the force transducer. After a random delay of between 1 s and 2.5 s, a push to the right was delivered by the linear motor. The subject was instructed to resist the push and maintain upright posture, by using either upper and lower limbs ("*hand and hip*") or just the lower limbs ("*hip only*") with the hand continuing to maintain light hold. After 2–3 s, the force returned to zero. A block of trials consisted of 20 pushes to the right. In experiment 1, the push force was set at 4% body weight throughout. A subset of seven subjects who had participated in experiment 1 took part on a separate occasion in experiment 2, for which push force was set at 4, 5 and 6% body weight in separate blocks of trials.

Data processing

The EMG data were conditioned by digital filtering (Butterworth 4-pass without phase shift, high-pass 10 Hz, low-pass 500 Hz;

bandstop 48–52 Hz) and rectification, and force data were filtered (low pass 15 Hz). Both single trial and averaged data were used to measure latencies of muscle activity onset, onset and peak latencies and amplitude of forces (GRF, HGF, HLF) generated and extent of lateral displacement of the pelvis from the starting position. The amount of muscle activity in each of the two conditions was compared in terms of the change in integrated EMG (iEMG) during a 100-ms window at the start of the trial before perturbation and during windows of 50–100 ms, beginning 50 ms after perturbation. Force records were differentiated to allow maximum rate of change of force to be used as an early index of the size of the response to perturbation.

Analyses of variance (ANOVA) and paired and unpaired *t*-tests were used to compare means in the single trial data from each subject and the mean data from all subjects. Pearson correlation tests were carried out on both the single trial (within subjects) and means (between subjects) data.

Results

Experiment 1

All subjects successfully resisted the pushes to the right without the need to take a step. The average lateral displacement of the pelvis was 3 cm. First, we present the EMG results and then turn to the resulting forces.

Muscle activity patterns

Average EMG traces for one subject in the *hand-and-hip* and *hip-only* conditions are shown in Fig. 2. Following the rise in sideways push force, there are clear increases in the activity of all of the muscles recorded. A small early response at 30 ms in LGM (a stretch reflex produced by the sharp rise in force applied through the overlying belt) is followed at 70 ms by an increase in RGM and, in the *hand-and-hip* condition, an increase in the right upper-limb muscles. Relatively small increases in the right calf muscles with a decrease in activity of LGAS at 100 ms are followed by larger responses in these muscles at 120 ms along with rise in LGM activity. At this point, differentiation between leg muscle activity in *hip-only* and *hand-and-hip* conditions is increasingly evident. This differentiation may also be seen in the iEMG traces at the bottom of the figure.

The group mean onset latencies of all the muscles plus the times of decrease in activity in LGM and LGAS for the two conditions are summarised in Table 1. In general, it will be observed that activation of RGM and decrease of activity in LGM occurred earliest, and these were followed some 10–20 ms later by RDEL. Although the group average shows that RFDI onset occurred some 10 ms later than RDEL, there were appreciable individual differences. In some cases, RFDI onset was markedly delayed – occurring even after the grip force onset. This suggests that, for these subjects, another muscle was the prime mover for the index finger's role in developing grip force.

The differences between the two conditions were not generally statistically significant on group analysis, with
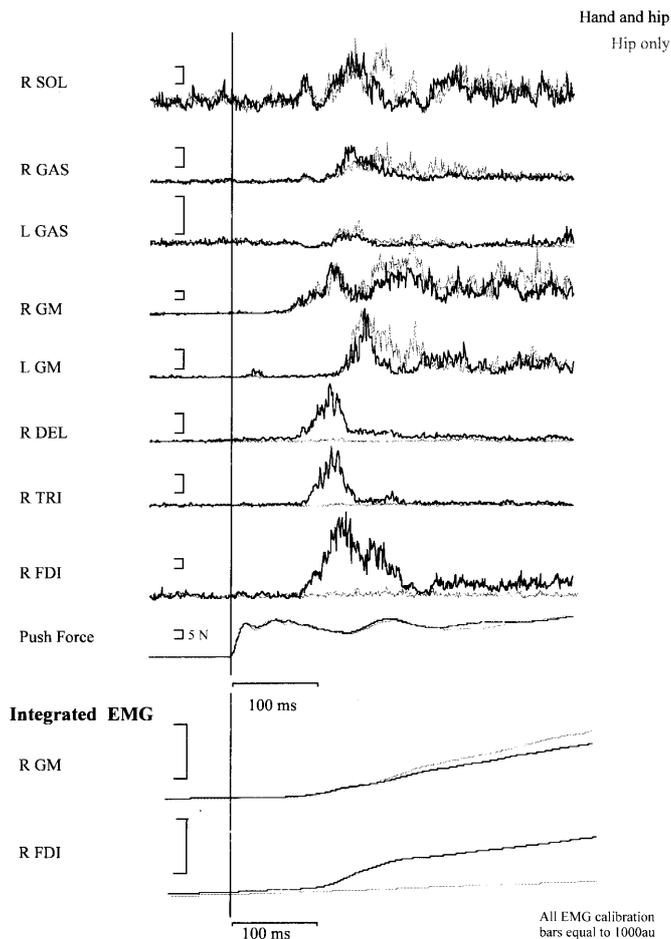

Fig. 2 Means data for the electromyogram (*EMG*) activity recorded in one subject (AW) with integrated EMGs of right gluteus medius (*RGM*) and right first dorsal interosseous (*RFDI*)

the exception of the onsets of R- and LGM, which occurred reliably earlier in the *hip-only* condition. However, although there was a significant group effect, only 2 of 14 subjects showed a significant difference in RGM onset latency between the two conditions on individual subject statistical analysis. Analysis of the iEMG measures (Table 2) revealed reliable changes in both RGM and RFDI within 100 ms of the perturbation during the 50-ms to 100-ms window. There was also a trend for an increase in RDEL, which achieved statistical significance (along with RTRI) when the time period was enlarged to a 100-ms window, 50–150 ms after the push onset.

The baseline levels of iEMG were the same for all conditions except for RGM which was larger in the *hip-only* condition. Since it was not matched by an elevated LGM, this may indicate an anticipation of the upcoming right push. Greater activity was also observed in the RGM in the *hip-only* condition than in the *hand-and-hip* condition, during the window after the push; ANOVA showed this to be a significant effect of condition and not just a result of different baseline levels with a reliable interaction ($F(1,13)=8.5$, $P<0.05$) between the con-

Table 1 Group mean (n=14) latencies of right (R) and left (L), upper- and lower-limb muscle onsets in *hip-only* and *hand-and-hip* conditions. *SOL* soleus; *GAS* gastrocnemius; *GM* gluteus medius; *DEL* deltoid; *TRI* triceps; *FDI* first dorsal interosseous. Mean±SD shown with results of paired t-tests (in terms of probability that the mean difference observed could have occurred under the null hypothesis

	RSOL	RGAS	RGM	LGM	LGM decreased activity	LGAS	LGAS decreased activity	RDEL	RTRI	RFDI
	(s)	(s)	(s)	(s)	(s)	(s)	(s)	(s)	(s)	(s)
Hand-and-hip (mean±SD)	0.104±0.033	0.106±0.026	0.077±0.013	0.156±0.045	0.068±0.006	0.217±0.111	0.090±0.008	0.087±0.024	0.098±0.024	0.099±0.019
Hip-only (mean±SD)	0.095±0.032	0.106±0.034	0.066±0.008	0.117±0.027	0.066±0.009	0.212±0.098	0.105±0.030	0.088±0.018	0.098±0.020	0.109±0.041
Paired t-test	0.604	0.74	0.011	0.03			0.327	0.757	0.861	a

[a]RFDI was not consistently activated in the *hip-only* condition and, therefore, a paired t-test between *hand-and-hip* and *hip-only* results could not be performed. LGM decreased activity and LGAS excitation were also not consistently seen in each subject in each condition

Table 2 Group mean (n=14) integrated electromyogram (iEMG) values for all the muscles studied under the two conditions. Mean±SD shown with result of paired t-test between means of the 14 subjects for each time period in *hip-only* and *hand-and-hip* conditions . *SOL* soleus; *GAS* gastrocnemius; *GM* gluteus medius; *DEL* deltoid; *TRI* triceps; *FDI* first dorsal interosseous

iEMG period	Condition	RSOL	RGAS	RGM	LGM	LGAS	RDEL	RTRI	RFDI
Background	Hand-and-hip	33.0±29.3	17.2±8.6	14.0±8.6	27.7±30.5	25.1±18.6	68.0±83.7	20.5±15.8	54.9±39.8
-	Hip-only	29.9±27.5	16.0±7.0	27.8±22.2	25.8±21.9	30.3±35.8	62.3±68.0	19.2±9.5	44.6±40.1
-	Paired t-test	0.106	0.227	0.013	0.618	0.560	0.445	0.749	0.180
50–100 ms post push	Hand-and-hip	18.8±15.5	15.3±15.9	40.4±28.4	9.5±7.3	9.8±6.4	48.6±42.6	17.1±13.5	40.5±26.6
-	Hip-only	16.9±14.2	15.1±16.6	61.0±48.5	11.6±10.8	12.1±12.8	39.5±42.9	11.9±6.9	25.7±24.1
-	Paired t-test	0.148	0.853	0.013	0.396	0.490	0.087	0.161	0.006
50–150 ms post push	Hand-and-hip	46.3±44.7	59.5±78.3	122.3±60.5	25.0±23.6	17.1±9.0	124.8±87.4	62.1±40.0	170.0±99.0
-	Hip-only	40.3±37.1	56.0±82.3	166.0±94.0	29.3±21.0	20.3±13.6	76.3±58.2	27.0±12.8	59.9±45.2
-	Paired t-test	0.141	0.493	0.006	0.279	0.369	0.007	0.004	<0.001

Fig. 3 Five representative single-trial force traces from one subject (AW) under the two different conditions
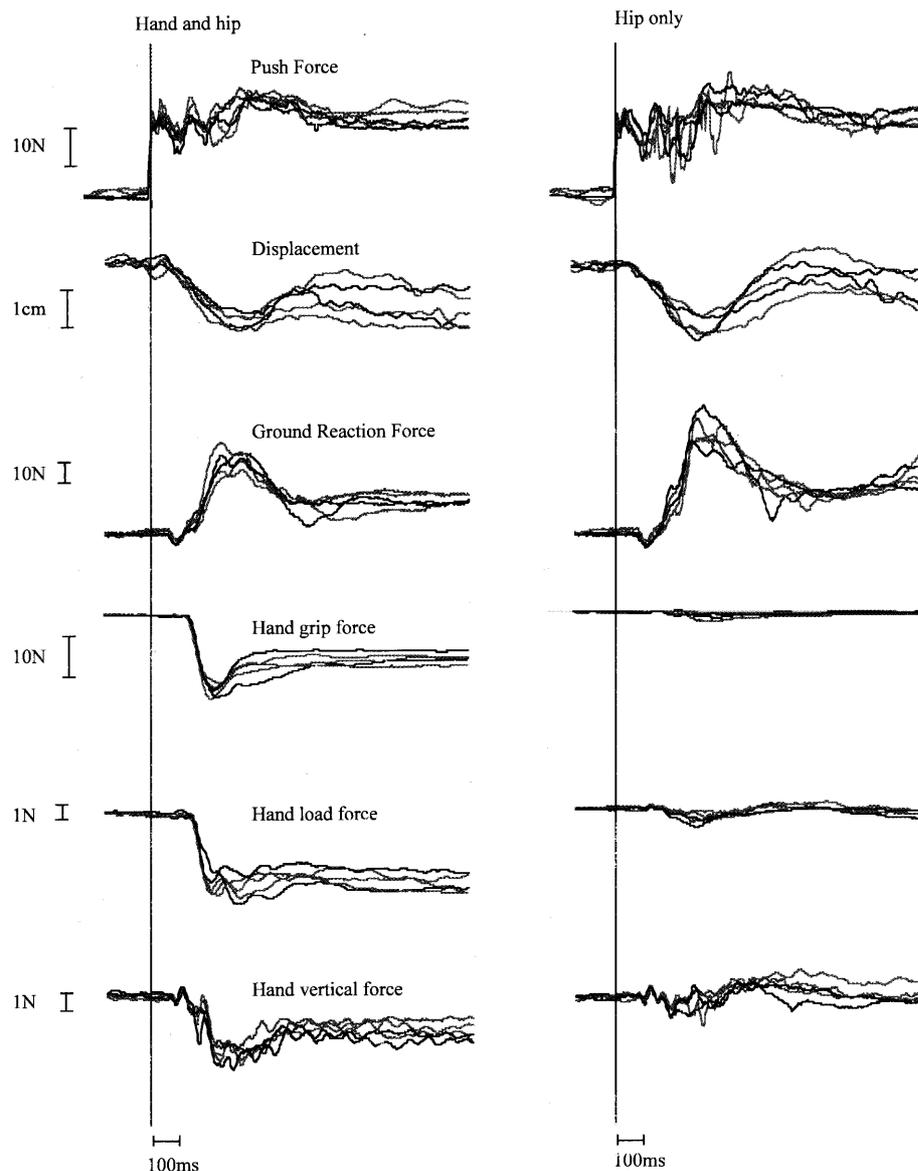
dition (*hand and hip*, *hip only*) and the period over which the EMG was integrated (before and after the push).

There appeared to be a depression from the background level as a result of the perturbation, as indicated by the decrease in iEMG in the early window relative to baseline in LGM and LGAS, although only LGAS showed a reliable difference in the ANOVA ($F(1,13)=8.08$, $P<0.05$).

Force data

Figure 3 shows illustrative force data from five separate trials for one subject. The abrupt application of the push force to the right (top trace) results, after a short delay, in lateral displacement of the pelvis, which continues for some 400 ms before returning some way towards the initial position. An initial negative deflection of the GRF (reflecting passive effects of rightward sway) is reversed at around 120 ms as a result of active muscle forces. The GRF attains a maximum value around 300 ms and then settles back to a steady level. Both maximum and steady level values of GRF are somewhat higher in the *hip-only* condition, indicating that hand use is functional in the *hand-and-hip* condition. In this *hand-and-hip* condition, the GRF changes are paralleled by sharp changes in HGFs and HLFs. Note that the rise in HGF before HLF permits an effective increase in HLF without a slip of the hand from the load cell. This pattern of hand forces would not have been expected if the increased grip was generated as a reflex response to a slip of the hand across the apparatus at the time of perturbation; in this case, HLF would change before HGF. In the *hip-only* condition, there are small departures from zero in the hand forces.

Table 3 Group mean (±SD; *n*=14) forces at the hand and ground in resisting sideways push. Group result refers to two-tailed *t*-test between paired results from *hip-only* and *hand-and-hip* conditions for the 14 subjects. The number of subjects showing a significant difference in the variable between the two conditions as measured using an unpaired two-tailed *t*-test on the single trial data is also stated

	Condition		*t*-Tests	
	Hand and hip	Hip only	Group *P* value	*N* (subjects) with significant difference
Displacement (cm)	3.0±0.8	3.0±0.9	0.93	2/14
Peak force				
Ground shear (N)	37.6±11.3	42.7±8.2	0.024	12/14
Hand load (N)	13.5±8.6	2.4±2.1	<0.01	14/14
Hand grip (N)	21.8±9.7	1.61±1.5	<0.01	14/14
Onset latency[a]				
Ground shear (ms)	130.5±16.0	124.6±15.6	0.01	3/14
Hand grip (ms)	126.9±21.1	129.4±39.0	0.82	7/14
Hand load (ms)	140.3±15.6	135.2±25.1	0.50	5/14

[a] Onset latencies of forces defined as the time after perturbation onset at which a pre-perturbation baseline is exceeded

Group averages for the displacement, maximum forces and force onset latencies calculated from single-subject means obtained by single-trial analysis are shown in Table 3 along with an indication of the statistical reliability of the results. The table shows clear differences in GRF, HLF and HGF as a function of the condition. Maximum GRF was smaller, and HLF and HGF were much greater in the *hand-and-hip* condition than in the *hip-only* condition, whereas the maximum displacement in the two conditions was identical (note that the difference between GRF values in the two conditions did not exactly match the difference in HLF because the body was not in static equilibrium – for example, there was continuing pelvis displacement – at the time of the respective maxima). The latency of onset of GRF and HGF were both in the region of 130 ms in the *hand-and-hip* condition with HLF occurring some 10 ms later. In the *hip-only* condition, GRF onset occurred 6 ms earlier, a small, but statistically reliable difference in the group analysis. Note that the method used to determine time of onset of forces (see footnote, Table 3), although providing a reliable and consistent measure of GRF increase, overestimated GRF onset latency compared with HGF and HLF onset latencies. This is because the negative shear force produced passively as the mass of the body accelerates following perturbation has to be opposed and exceeded by leg and trunk muscle activity before the pre-perturbation baseline is reached. The over-estimation of GRF onset latency explains the apparently longer time interval observed between leg muscle activity and GRF onset compared with that observed between RFDI muscle activity and HGF onset.

Force rate correlations

Positive correlation between performance measures is commonly taken as an index of common central drive (Schmidt et al. 1979; Wing 1992; Wing et al. 1998). Moreover, in voluntary arm movements, positive correlations between HGF and GRF were taken to reflect the common processing underlying anticipatory adjustments of posture and grip (Wing et al. 1997). In the present case, similar latency measures are seen in upper- and lower limb in the *hand-and-hip* condition, suggesting the possibility of common drive. To test for this, correlations were computed on maximum rates of rise of GRF, HGF and HLF, reflecting operation of lower limb, upper-limb distal and upper-limb proximal muscles respectively.

Correlational analysis of hand forces showed moderate coupling between the distal and proximal upper-limb responses with a consistent positive correlation of 0.57±0.27 between the maximum rate of rise of HLF and HGF. No such link was observed between upper- and lower-limb function; the average correlation between GRF and HLF was –0.01±0.34 and between GRF and HGF 0.07±0.35. In contrast to the lack of correlation between response magnitudes in upper- and lower limbs, latencies of maximum force rates were positively correlated; an average correlation of 0.41±0.26 was observed between HLF and GRF, similar to the within-limb correlation of 0.66±0.20 seen between HGF and HLF.

Experiment 2

In experiment 1, only one level of push force was used. In experiment 2, subjects were exposed to three levels of push force in separate blocks of trials. Experiment 2 permitted an examination of the changes occurring in peak force and onset latency of forces generated both at the ground and at the hand in response to changes in perturbation strength.

Figure 4 shows the effect of increasing push force on upper- and lower-limb response measures. At higher levels of force, producing greater pelvis displacement, GRF, HLF and HGF all increased. For each type of force, the increase was in proportion to the force produced in the 4% condition. Group mean GRF, HLF and HGF magnitude all increased by a factor of 1.3 when the push force was increased from 4% to 6% body weight and ANOVA showed no significant difference in the ratios of increase of these three forces ($F(2,12)=0.03$, $P=0.972$). Force on-

58

Fig. 4 Effect of push force magnitude on (**A**) peak force and (**B**) onset latency from time of push of the forces generated at the ground and at the hand in the *hand-and-hip* condition. Group means±S.E. (*n*=7)
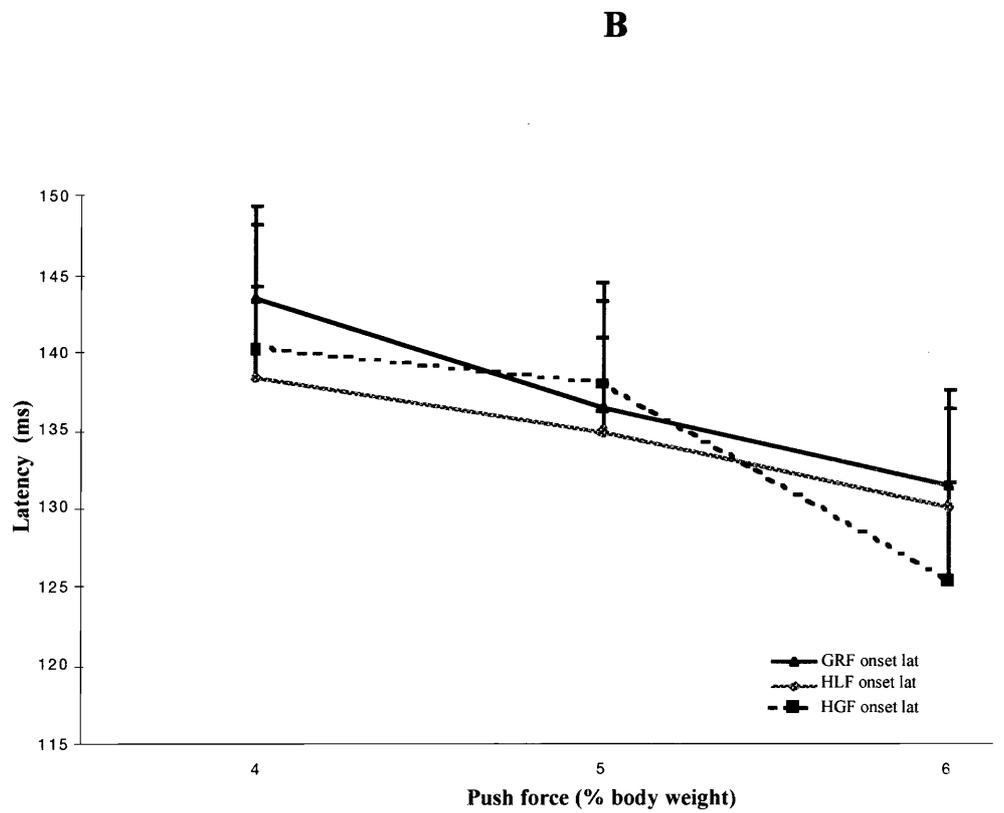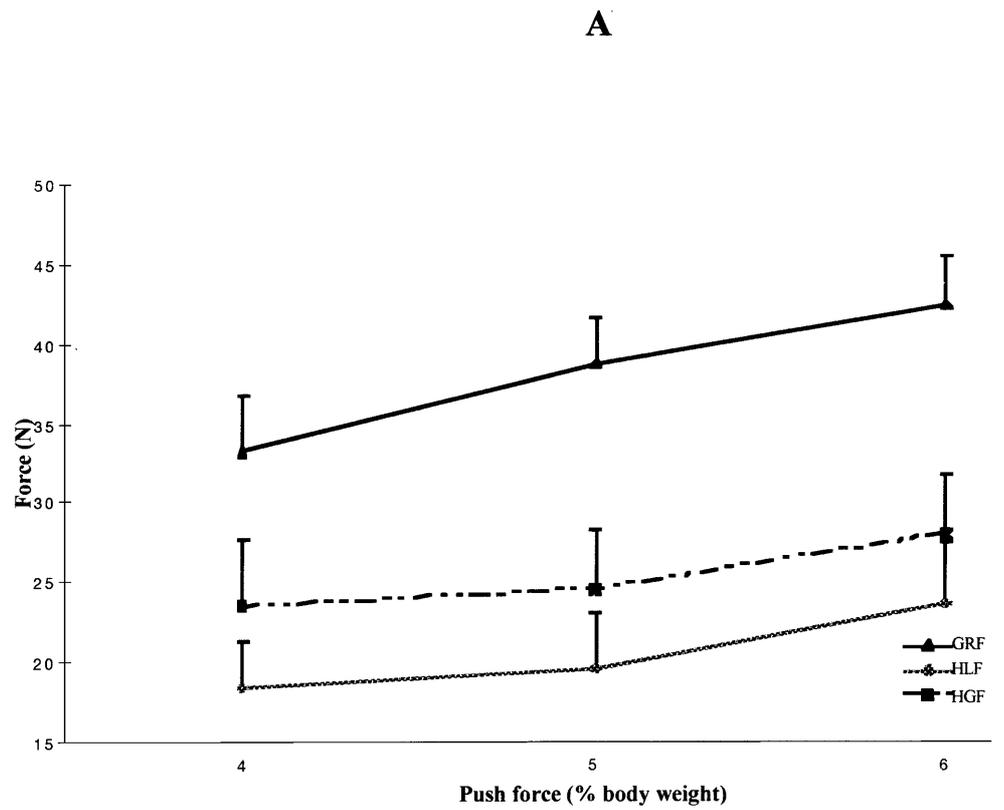
set latencies all showed reliable decreases at higher push forces confirmed by ANOVA.

Discussion

A number of previous studies (Marsden et al. 1981; Cordo and Nashner 1982; Schiepatti et al. 1995b; McIlroy and Maki 1995) have shown that the upper limb can contribute to the postural response to perturbed balance. Our work extends the earlier research in documenting the precise involvement of the hand, in characterising forces as well as muscle activity patterns, and in examining the covariation between the upper- and lower-limb responses.

The main finding of the present study is that the hand and arm are used with the leg in responding to a temporally unpredictable perturbation of balance. Application of a sustained sideways push to the pelvis while the hand grasped a stable support resulted in increases in muscle activity in the upper limb, which occurred at a similar latency (87 ms for RDEL) to that in the lower limb (77 ms for RGM) if the subject had previously been instructed to use the hand to resist the push. The muscle activity patterns led to force being developed at the hand in parallel with force developed at the feet and, together, these forces preserved equilibrium and minimised resulting body sway. In contrast, when subjects were instructed not to use the hand for support, no upper-limb contribution was seen. When instructed to use the hand and the perturbing force was increased in amplitude, scaling of the postural response was seen in terms of the EMG and forces at both the hand and the feet.

Central conduction-time measures predict activation of upper-limb muscles 10–15 ms prior to activation of lower-limb muscles in a voluntary reaction time task (Cordo and Nashner 1982). As part of the postural response to lateral perturbation, we observed activation of proximal lower-limb muscles occurring slightly earlier than proximal upper-limb muscles, which may appear paradoxical. However, others have also reported a discrepancy between upper- and lower-limb onset latencies in a postural response compared with central conduction time predictions; in subjects standing upright with their arms by their sides, McIlroy and Maki (1995) found proximal upper limb muscles to be activated only 2 ms prior to distal lower limb muscles in response to a platform translation. These latency observations may reflect the operation of two separate pathways involved in the activation of upper- and lower-limb contributions to the postural response.

Previous work (Wing et al. 1997) has suggested a common process that co-ordinates the upper- and lower-limb contributions in an anticipatory response to voluntary arm movement. Voluntary arm movements resulting in perturbations of balance are associated with anticipatory postural responses, which are reflected in the GRFs (Bouisset et al. 1981). These are thought to serve the role of stabilising the body against the inertial forces generated in moving the arm (Friedli et al. 1988). Changes in grip force used to hold an object in the hand are seen prior to arm movement (Flanagan and Wing 1997) and these serve to stabilise the object against inertial forces due to arm acceleration and deceleration. Simultaneous recordings of HGF and GRF during voluntary arm actions, which included both moving an inertial load and pushing against a static load, have shown the rates of change of force at the hand and ground to be positively correlated (Wing et al. 1997). This was taken to suggest a common process of predicting the effect of voluntary arm movement.

The results presented here suggest relative independence of control of upper- and lower limb in the reactive postural response to an unpredictably timed lateral push. Independence is supported by the lack of correlation on a trial-by-trial basis of the rate of rise of forces generated at the hand and at the ground. A positive correlation would have been expected if both upper- and lower-limb components had been subject to noise from a common pathway. Independence is also indicated by the finding that the variance of latency of the RGM is unaffected by the addition of the hand into the postural response as confirmed by t-test analysis on the variances from the two conditions ($p=0.194$), suggesting a lack of interference of hand use on leg use.

Although these findings suggest independence of control of the upper and lower limb components of the reactive postural response to lateral perturbation, there is also evidence for a common influence acting on the arm and leg responses. The results showed that there was a similarity in timing of the upper and lower limb, and there was a systematic effect of changing push force on onset latency. Also, as the magnitude of perturbation to balance was increased, joint scaling of upper and lower limb forces was observed. However, this close systematic dependence could be explained purely on the basis of the common trigger for the postural response, with a more rapid processing of the peripheral stimulus with greater perturbing force.

Although the lack of correlation suggests independent pathways, an effect of central set (Horak et al. 1989) associated with the verbal instruction to use the upper limb in the *hand-and-hip* condition on the lower-limb response suggests some common central input to upper- and lower-limb control. A statistically significant decrease in RGM iEMG during the early window after the push is observed in the *hand-and-hip* condition compared with the *hip-only* condition, which is too early to be as a result of peripheral feedback effects of hand-use alone. Parallel pathways for upper- and lower-limb involvement under the influence of central co-ordinative control and receiving common peripheral inputs are therefore proposed.

The latency of responses observed and the ability of voluntary command to override upper-limb inclusion makes the involvement of supraspinal, perhaps cortical, pathways a possibility. Reflex responses in the hand musculature observed when a hand-held object unexpectedly slips have been postulated to involve a transcortical route

(Johansson et al. 1994). Such a route may also be exploited in the hand response to a postural challenge, albeit with the stimulus arising physically remote from the hand. The influence of the sensorimotor cortex on the upper- and lower-limb contributions to standing balance in a reactive postural response is currently being explored using transcranial magnetic stimulation techniques.

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