Balance-corrective responses to unexpected perturbations at the arms during treadmill walking

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Forero J, Misiaszek JE. Balance-corrective responses to unexpected perturbations at the arms during treadmill walking. J Neurophysiol 112: 1790–1800, 2014. First published July 16, 2014; doi:10.1152/jn.00719.2013.—The arms have been shown to be involved in the regulation of balance during walking. The use of a walking aid enhances balance by increasing the base of support and reducing the load on the legs by partly transferring it to the arms. However, when actively engaged during a balance task, perturbations to the arms can destabilize balance. Previous studies have investigated postural adjustments associated with focal arm movements during standing and walking. However, balance-corrective reactions to unexpected perturbations to the arms during walking have not been well studied. In the present study, subjects walked on a treadmill while grasping a pair of handles when sudden perturbations were delivered by displacing the handles in the forward or backward direction. Instructing subjects to oppose the displacement of the handles resulted in strong responses in the arms that were accompanied by activation of muscles in the legs, comparable to those observed in other balance disturbance studies. Conversely, when subjects were instructed to allow the handles to move when displaced, no responses were observed in the arms. However, similar responses were observed in the legs whether subjects opposed the displacement of the handles or not when perturbations were applied at heel strike. The results from this study show that balance reactions can be elicited in the legs in response to perturbations applied at the arms, and that the expression of these responses is affected by the task engaged in by the arms.

balance; gait; perturbation; arms; human

PERTURBATIONS TO BALANCE delivered during walking evoke complex responses involving activation of muscles in the legs, trunk, and arms. Corrective reactions to perturbations delivered during walking have been studied for slips (Marigold et al. 2003), trips (Eng et al. 1994), translation perturbations of the support surface (Berger et al. 1984; Dietz et al. 1987; Tang et al. 1998), and also perturbations delivered at the waist (Misiaszek et al. 2000). Independently from the locus of the perturbation, the responses to balance disturbances involve activation of muscles of the legs that are accompanied by activation of muscles of the arms. In general, corrective reactions to balance perturbations during walking trigger whole-body responses (Marigold and Misiaszek 2009).

Mobility aids involving the use of the arms are largely used to improve balance control. Standing balance is achieved by maintaining the center of mass within the base of support. The use of a mobility aid increases the base of support (Joyce et al. 1991; Tagawa et al. 2000), hence allowing a greater range of motion for the center of mass without loss of balance. However, walking aids can also destabilize balance. For instance, Bateni and Maki (2005) reviewed the advantages and possible disadvantages associated with the use of mobility aids. Although they found strong clinical evidence about the effectiveness of the use of walkers and canes to improve balance in adults, they also found that there is an increase in the risk of falling when using these devices. The increase in risk was mostly associated with changes in attentional demand that could result from the use of the walking aid. For instance, a strategy commonly used to avert a fall results from targeting the arms to reach for nearby safety handrails (Maki and McIlroy 2006; McIlroy and Maki 1995). However, in another study Bateni et al. (2004) demonstrated that subjects holding a “cane” would not release it to reach for available handrails in order to recover balance upon delivery of a postural perturbation even if the “cane” was unable to stabilize balance (i.e., falling backward) or any value at all (i.e., the top of the cane). The authors concluded that the nervous system prioritizes the ongoing task of holding the object despite sacrificing balance performance and possibly falling. These results show that balance can be enhanced with the use of walking aids but the task of holding an object in the hands can compromise balance performance.

When the arms are actively engaged during a balance task they can become the source of a balance disturbance. For instance, if the arms are engaged in additional tasks, such as carrying a load, then perturbations to the arms or the load can disrupt balance. Cordo and Nashner (1982) found that when standing subjects voluntarily pushed or pulled against a set of handles the focal actions of the arms were preceded by anticipatory postural adjustments in the legs. Moreover, when the handles were unexpectedly displaced rapid corrective responses were evoked in the leg muscles that were similar to corrective responses that followed perturbations of the support surface. These authors proposed that postural adjustments associated with focal arm movements, unexpected displacement of the arms, or unexpected displacement of the support surface were organized by a common balance mechanism, at least during standing. However, balance adjustments during walking must be integrated within the ongoing step cycle. If perturbations are applied at the arms, then a reasonable solution would be to make use of the arms to correct for the disturbance, thereby allowing the legs to proceed with the task of walking. Indeed, balance adjustments at the legs in response to pulls at the waist during walking are eliminated if subjects hold a stable support (Misiaszek et al. 2000). But what of
disturbances that originate at the arms themselves during walking? Voluntary movements of the arms during walking lead to anticipatory adjustments of leg muscle activity that vary depending upon when in the step cycle the arm movements occur (Hirschfeld and Forssberg 1991; Nashner and Forssberg 1986). However, these were voluntary movements of the arms involving anticipatory postural adjustments associated with the voluntary arm actions (Massion 1992). To date, only one study has investigated responses to unexpected arm pulls during walking in two subjects (Nashner and Forssberg 1986). Therefore, balance-corrective reactions to unexpected disturbances of the arms during walking are not well characterized.

Walking is associated with phasic modulation of the role of sensory feedback. For example, stimulation of the superficial peroneal nerve during early swing leads to a coordinated response to elevate the swing foot as part of an obstacle avoidance strategy, whereas the same stimulus during late swing leads to a foot lowering strategy (Van Wezel et al. 1997). These responses are further modulated if the subjects walk in an environment where obstacles are frequently encountered (Haridas et al. 2006). The changing role of sensory feedback during walking presumably reflects the changing mechanical demands of the task, as well as the changing states of the task (Misiaszek 2006). Similar task-dependent and phase-dependent modulations of balance reactions have been demonstrated in response to perturbations applied at the waist during treadmill walking (Misiaszek 2003; Misiaszek et al. 2000). Therefore, balance-corrective reactions evoked with perturbations applied at the arms during standing cannot be directly translated to walking balance control. The purpose of the present study is to characterize arm and leg reactions to unexpected perturbations delivered through the arms during walking. For this purpose, perturbations are delivered at random points across the step cycle in one of two directions (i.e., backward, forward). We hypothesize that unexpected perturbations delivered to the arms will induce rapid-onset balance-corrective reactions in the muscles of the legs. Responses in the arms to unexpected pulls resulted in responses with latencies shorter than the voluntary reaction times when subjects were anticipating the perturbation (Cordo and Nashner 1982). Thus two different conditions involving the “need” to respond (i.e., oppose or comply to the perturbations) are defined for the present study. We hypothesized that balance reactions induced by perturbations applied through the arms depend upon the task condition at the time of perturbation.

MATERIALS AND METHODS

To evaluate the responses associated with perturbations at the arms during locomotion, a total of nine subjects (three men and six women) were included in the experiment. Ages, heights, and weights ranged from 26 to 31 yr (mean ± SD, 27.7 ± 1.80 yr), from 158 to 175 cm (165.4 ± 5.48 cm), and from 50 to 76 kg (58.2 ± 9.24 kg), respectively. Subjects provided written consent for their participation. The procedures were approved by the University of Alberta Research Ethics Board.

Protocol. During the experiment subjects were asked to walk on a motorized treadmill. Each subject selected a comfortable walking speed (0.8 ± 1.2 m/s), which was maintained for the remainder of the experiment. Subjects were instructed to grasp two handles located in front of them and not to release them upon their displacement. The handles were adjusted for each subject so that each hand was aligned laterally with the corresponding shoulder, and the height was set so that the elbows would be held at 90° while the forearms were held horizontally. The handles were secured to a car mounted on a rail track that only allowed fore-aft displacements. The two handles moved together. A drum, located behind the subjects and connected to the car through a series of pulleys, was used to displace the handles in either the forward or backward direction by pushing or pulling the handle attached to it (Fig. 1). A few sample perturbations were delivered before the experiment began to familiarize the subjects with the protocol. Perturbations were delivered by displacing the handles in either the forward or backward direction. The handles were free to move along the track when perturbations were not being delivered.

Perturbations were delivered by rapidly rotating the drum, which in turn pulled the handles forward or backward, producing the corresponding displacement. Rotations of the drum were manually generated through a rigid bar attached to it, so that pushing the bar would produce a forward displacement and pulling it a backward displacement. The maximum displacement of the handles never exceeded 15 cm in either direction; hence the arms were not extended beyond their maximum reach or flexed as to hit the subject. The duration of the displacement of the handles, measured from the displacement onset until the maximum displacement was reached, never exceeded 250 ± 50 ms. Before each perturbation, the handles were repositioned at the center of the rail track and the elbow position was verified to be at 90°. Perturbations were delivered while the subjects performed one of two tasks. In the first task, subjects were instructed to react as rapidly as possible to “not allow the handles to move” (OPPOSE). In the second

Fig. 1. Schematic diagram of the experimental setup. Subjects walked on a motorized treadmill while grasping a pair of handles. The handles were positioned so that the elbows would be held in a 90° position while the forearms were held horizontally when subjects were holding on to the handles. The handles were secured to a car mounted on a rail track that only allowed fore-aft displacements. A drum, located behind the subjects and connected through a series of pulleys to the car, was used to generate the perturbations in either the forward or backward direction. Perturbations were delivered at heel strike, midstance, toe-off, and midswing of the step cycle for both task conditions.

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task, subjects were asked to allow the handles to be displaced freely but not to release them (OPPOSE). All subjects performed the OPPOSE task first and were permitted to rest between tasks if needed. Perturbations were delivered in two directions [forward (FWD), backward (BWD)] and at four different points in the step cycle (heel strike (HS), midstance (MSt), toe-off (TO), midswing (MSw)).

To apply the perturbations at each point in the step cycle, the experimenter visually estimated the appropriate timing of the manual delivery of each perturbation. The actual timing of each perturbation was then screened post hoc using step cycle data and handle displacement data, as described in Data analysis. In total, 20 perturbations were delivered for each combination of direction (2) and step phase location (4), resulting in a grand total of 160 perturbations per task.

The order of delivery for the perturbations was randomized before the beginning of the experiment for each subject and each task. The experimenter repositioned the handles to the center of the rail after the subject regained stable walking and allowed the subject to take another three to five steps before delivering the next perturbation. The same experimenter delivered the perturbations throughout the study.

**Measurements.** A force transducer (Omega LCCA-500, Stamford, CT) located in series with the handles allowed for the recording of the pulling (positive values) or pushing (negative values) force progression through them, and a linear position sensor (Penny & Giles SLS320, Santa Monica, CA) connected to the car measured the horizontal displacement of the handles. Two force-sensitive sensors were located at the heel and the metatarso-phalangeal joint on the left foot to record foot contact with the ground (Interlink Electronics, Camarillo, CA). Kinematic data were recorded from the ankle, knee, and elbow joints with electrogoniometers (Biometrics, Newport, UK). Electromyographic (EMG) recordings were obtained from the tibialis anterior (TA), soleus (SOL), vastus lateralis (VL), and biceps femoris (BF) of the left leg and the anterior deltoid (AD), posterior deltoid (PD), biceps brachii (BB), and triceps brachii (TB) of the left arm. A pair of Ag-AgCl surface electrodes was placed over the bellies of each recorded muscle, 2 cm apart and aligned to the predicted direction of the muscle fibers. Two ground electrodes were placed over the left tibia and left clavicle. Raw EMG signals were preamplified and band-pass filtered (30 Hz–1 kHz) with Grass P511 preamplifiers (Astro-Med, West Warwick, RI). All signals were digitized online at a sampling rate of 1 kHz and stored directly to hard drive with a custom-written LabVIEW v8.20 data acquisition routine and a National Instruments data acquisition card (National Instruments PCI-MIO-16E-4, Austin, TX). Postprocessing of the signals was performed off-line: EMG signals were full-wave rectified and low-pass filtered at 50 Hz (zero-lag 4th-order Butterworth filter), and signals from the handle force transducer, goniometers, and handle position sensor were low-pass filtered at 10 Hz (zero-lag 2nd-order Butterworth filter). The acceleration of the handles was estimated from the handle position trace by first fitting a smooth spline function to the data points and then calculating the second derivative.

**Data analysis.** The data stream from each task was divided into sweeps, each sweep starting 300 ms before heel strike, as determined by the foot sensor signal, and lasting for 2,000 ms. A perturbed sweep was defined as a sweep within which a perturbation was delivered, and the sweep preceding it was used to define the corresponding control sweep. Control step durations were defined for each control sweep as the time between heel strikes within that sweep. The average control step duration was calculated as the mean of the control step durations. The onset of the handle displacement was manually determined by the researcher from the handle position trace as the first visible deflection in the trace. The handle displacement delay was defined on every perturbed sweep as the time elapsed between left heel strike and the onset of the handle displacement, expressed as a percentage of the average control step duration (%ASD). Perturbation sweeps were categorized according to the delay and direction of the handle displacement (BWD, FWD). Four different bins, spanning 10%ASD, were defined, representing the four different points in the step cycle to be analyzed: heel strike, 0 ± 5%ASD; midstance, 30 ± 5%ASD; toe-off, 60 ± 5%ASD; midswing, 80 ± 5%ASD (Fig. 1). Perturbations that could not be classified in any of the bins were removed from any further analysis. This sorting process resulted in 8–18 sweeps (of 20) being analyzed for each combination of direction and bin for each task from each subject.

Perturbed and control data traces were captured for each subject accordingly from the perturbed and control sweeps and grouped for each combination of direction, bin, and task. Perturbed traces for each data grouping were aligned to the handle displacement onset and then averaged. Each average perturbed trace was then truncated to 500-ms duration starting 100 ms before the onset of the handle displacement. Control traces were aligned to heel strike and then normalized in time to the average control step duration with a linear time-normalization method to make their length equal to the average control step duration. From the time-normalized control traces, averaged control traces and their 95% confidence bands were calculated. For each group, averaged control traces and their confidence bands were truncated to 500 ms starting 100 ms before the average handle displacement delay for that data grouping. Subtracted traces were then calculated by subtracting the averaged control traces from the corresponding averaged perturbed traces. Analysis of EMG and joint angle data was performed with the subtracted traces.

The average control sweep duration before time normalization was used as a measure of the average step duration. Within a subject, a response to a perturbation was considered to be significant in any given muscle if the subtracted trace fell outside the 95% confidence band for >25 consecutive milliseconds. The onset of the response was defined as the point after the onset of the perturbation at which the subtracted trace deviated from zero, and the response onset latency was measured as the time from the onset of the handle displacement until the onset of the response. Muscle response amplitudes were calculated for both tasks as the average amplitude of the subtracted trace for the first 200 ms following the onset latency. It was often found that during the COMPLY task the displacement of the handles did not evoke discernible responses. Therefore, latencies could not be estimated for these instances. Consequently, the latency of the response onset identified in the OPPOSE condition was also used in the COMPLY condition so as to provide a comparable window for analysis.

Muscle background activity was calculated as the mean amplitude over a 50-ms window centered at the onset latency of the perturbation to assess muscle activity levels at the time when the perturbation was delivered. EMG amplitudes were normalized to the peak EMG amplitude for each muscle measured from the control steps. Similarly, ankle and knee joint angles were calculated as the mean amplitude over a 50-ms window centered at the onset latency of the perturbation.

**Statistics.** Response onset latencies were only estimated if the evoked response in the subtracted EMG trace exceeded the 95% confidence band for that muscle. Discernible responses were not detected in every instance. Consequently, comparisons of onset latencies were made with a combination of Student t-tests or one-way ANOVAs, depending upon the extent of the data set available. Additional details of the tests employed are provided in RESULTS as appropriate.

As described above, we used the average onset latency during OPPOSE for a given muscle to define a window of analysis for estimating the response amplitude in a muscle across all TASKs and PHASEs. In this way, an estimate of response amplitude was obtained for every condition, muscle, and subject, assuming that some responses might have occurred that were subliminal for our criteria. The amplitude of the responses evoked in each muscle was compared across TASK and PHASE with separate two-factor repeated-measures ANOVAs for each muscle. Separate ANOVAs were used for each direction of perturbation given the clear direction-specific responses that were evoked (see Fig. 2). When significant TASK × PHASE
interactions were detected by the ANOVAs, Tukey’s honestly significant difference test was used to identify the specific differences.

Step cycle duration of the control steps was compared between tasks with a paired \( t \)-test. Background EMG and joint angles at each of the points in the step cycle used for analysis were estimated from the control steps and compared across TASK and PHASE with two-factor repeated-measures ANOVAs.

All comparisons were performed with a significance level of 0.05. All measures are presented as means ± SE.

RESULTS

Perturbations applied at the arms during walking produced corrective reactions that involved activation of arm and leg muscles. However, the expression of the reactions depended upon whether the subjects were asked to OPPOSE the displacement of the handles or COMPLY and allow the handles to move. As can be seen in Fig. 2, displacement of the handles at heel strike during the OPPOSE task resulted in clear responses in the muscles of both the arms and legs. In contrast, the frequency of occurrence of the muscles of the arms and only modest responses in the muscles of the legs. The general characteristics of the evoked responses emphasizing the muscles activated and their onset latencies are reported in General characteristics of evoked responses, providing a context in which to allow comparisons of response amplitudes in greater detail. Modulation of evoked responses by TASK and PHASE describes the influence of the task conditions on the amplitude of the evoked responses across the step cycle. Finally, the influence of task instructions on parameters of the undisturbed control steps is presented along with an analysis of the parameters of the applied perturbation to support the discussion of the proposed explanations of the findings.

General characteristics of evoked responses. The largest and most consistent responses were evoked at heel strike for both the OPPOSE and COMPLY tasks. Discernible responses were evoked in all four of the arm muscles tested after forward and backward displacements in all nine subjects at all points in the step cycle during the OPPOSE task, but responses were never seen in the arm muscles during the COMPLY task. In contrast, the frequency of occurrence of

Fig. 2. A: sample data from 1 subject showing average EMG and electrogoniometer traces for perturbed (thick traces) and the corresponding unperturbed (thin traces) steps for perturbations delivered during the OPPOSE task. The vertical dashed line in each column is aligned to the onset of the perturbation. Upward deflections in the kinematic traces indicate extension for the elbow and knee and dorsiflexion for the ankle. B: the data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the average perturbed traces. The subtracted traces are shown as thick lines. The 2 thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical dashed line in each column is aligned to the onset of the perturbation. The shaded areas indicate the time window in which the amplitude of the response was analyzed. BWD, backward; FWD, forward; AD, anterior deltoid; PD, posterior deltoid; BB, biceps brachii; TB, triceps brachii; TA, tibialis anterior; SOL, soleus; VL, vastus lateralis; BF, biceps femoris.
discernible responses in the leg muscles varied with the direction of the perturbation, the task being performed, and the point in the step cycle. A summary of the frequency of discernible responses in the leg muscles across subjects is provided in Fig. 4. As can be seen, discernible responses were not evoked ubiquitously across tasks, phases, or subjects. Therefore, estimates of response onset latencies could only be calculated from the discernible responses.

Displacement of the handles at heel strike during the OPPOSE task evoked responses in all four recorded muscles of the arms, regardless of the direction of the displacement (Fig. 2). However, backward perturbations resulted in responses that were dominated by activation of AD and BB, and forward perturbations resulted in responses that were dominated by activation of PD and TB. The average onset latency across subjects for the responses in AD and BB to backward perturbations was $61 \pm 3.5$ ms and $48 \pm 3.6$ ms, respectively. The average onset latency for the responses in PD and TB to forward perturbations was $82 \pm 2.2$ ms and $54 \pm 3.0$ ms, respectively. The responses in the arm muscles shown in Fig. 2 for perturbations applied at heel strike were typical of the responses that were evoked at other points in the step cycle during OPPOSE, with backward perturbations evoking prominent activation of AD and BB and forward perturbations evoking prominent activation of PD and TB. The onset latencies of the responses in the arm muscles did not vary across the step cycle. One-way ANOVAs comparing onset latency across the step cycle for each muscle, separately for each direction of perturbation, during OPPOSE revealed no main effects for step cycle, with all $F$ values <1.

Backward displacements of the handles at heel strike during OPPOSE were also characterized by prominent early activation of TA and VL, with a modest initial activation of SOL. Unlike the responses in the arm muscles, the pattern of muscle activity in the legs was not consistent across the different points of the step cycle. For example, TA and VL were normally activated after backward perturbations applied at heel strike and midstance, but no discernible responses were evoked in these muscles to backward perturbations at toe-off or midswing (Fig. 4A). The onset latency of the responses in TA and VL was $55 \pm 1.3$ ms and $80 \pm 4.2$ ms at heel strike, respectively, and $62 \pm 4.3$ ms and $76.8 \pm 3.4$ ms at midstance. Student’s $t$-tests comparing the response latencies at these two points in the step cycle did not reveal a significant difference for either muscle ($t = 0.67$ for TA and $t = 0.59$ for VL). In general, responses in the leg muscles to backward perturbations during OPPOSE

![Fig. 3. A: sample data from 1 subject showing average EMG and electrogoniometer traces for perturbed (thick traces) and the corresponding unperturbed (thin traces) steps for perturbations delivered during the COMPLY task. The vertical dashed line in each column is aligned to the onset of the perturbation. Upward deflections in the kinematic traces indicate extension for the elbow and knee and dorsiflexion for the ankle. B: the data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the average perturbed traces. The subtracted traces are shown as thick lines. The 2 thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical dashed line in each column is aligned to the onset of the perturbation. The shaded areas indicate the time window in which the amplitude of the response was analyzed.](http://jn.physiology.org/)

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### Table 1: Summary of the Frequency of Discernible Responses in the Leg Muscles across Subjects

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<tr>
<th>Muscle</th>
<th>BWD</th>
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<td>VL</td>
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<td>BF</td>
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**Notes:**
- BWD: Backward
- FWD: Forward
- Values are % of responses observed.
are characterized by early activation of TA and VL, with a
distal to proximal sequence. Forward perturbations at heel
strike during OPPOSE were characterized by prominent early
activation of SOL and BF, with a modest initial activation of
TA (Fig. 2) in most subjects (Fig. 4A). The onset latency of the
activation was 62 ± 1.5 ms in SOL, 91 ± 2.7 in BF, and 71 ±
2.5 ms in TA. BF and TA continued to respond with increased
activity after forward perturbations at midstance, with onset
latencies of 94 ± 2.5 ms and 73 ± 3.3 ms, respectively. The
onset latency was not different between heel strike and mid-
stance for responses in these two muscles (BF, t = 0.82; TA,
t = 0.48). However, the response in SOL at midstance was no
longer an early activation but rather an early inhibition with an
onset latency of 96 ± 4.2 ms. The inhibition of SOL activity at
midstance had a significantly later onset than the excitation of
SOL observed at heel strike (t = 7.62, P < 0.001). Responses
in the leg muscles to forward perturbations were expressed
infrequently at other points in the step cycle (Fig. 4A).

Typical responses evoked after displacement of the handles
at heel strike during COMPLY are depicted in Fig. 3 for one

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<tr>
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<th>Step cycle position (bin)</th>
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<td></td>
<td>HS MSt TO MSw</td>
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<td><strong>TA</strong></td>
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<td><strong>SOL</strong></td>
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<td><strong>BF</strong></td>
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Fig. 4. Frequency of occurrence of a response in each
muscle of the leg to perturbations delivered during
OPPOSE (A) and COMPLY (B) for each bin as indicated
by the subtracted traces. HS, heel strike; MSt, midstance;
TO, toe-off; MSw, midswing.
subject. As can be seen, no discernible responses were observed in the arm muscles for either forward or backward displacements of the handles. However, responses were typically evoked at heel strike in the leg muscles of most subjects (Fig. 4B). For the subject’s data depicted in Fig. 3, backward perturbations resulted in an early modest activation of TA and VL, with an inhibition of activity in SOL. The average onset latencies across subjects were 65 ± 12.3 ms, 97 ± 12.2 ms, and 88 ± 14.9 ms for TA, VL, and SOL, respectively. In contrast, forward perturbations at heel strike resulted in an early inhibition of SOL and activation of BF. The inhibition in SOL had an average onset latency of 102 ± 21.2 ms, while the activation of BF had an average onset latency of 76 ± 15.3 ms. During COMPLY, discernible responses were not observed in the leg muscles with perturbations at any other points in the step cycle (Fig. 4B).

Modulation of evoked responses by TASK and PHASE. To draw comparisons of response amplitudes between tasks and across the step cycle, we measured response amplitudes over a 200-ms period beginning at the average response onset latency observed during OPPOSE for each muscle for each subject. Responses to forward and backward perturbations were compared separately, given the clear direction-specific responses that were evoked (Fig. 2).

Figure 5A depicts average response amplitudes following backward perturbations in both the OPPOSE and COMPLY conditions, across the step cycle. As shown in Fig. 2, the response to backward perturbations was dominated by evoked activation of AD, BB, TA, and VL. Therefore, we focused the analysis to the responses in these muscles. As can be seen, responses in AD and BB were of much larger amplitude during the OPPOSE task than during the COMPLY task, given that no discernible responses were observed in the arm muscles during the COMPLY task (Fig. 3). Consequently, two-way ANOVAs identified a significant main effect of TASK for response amplitudes in both AD (F = 40.89, P < 0.0001) and BB (F = 18.10, P < 0.0001). However, neither the responses in AD (F = 1.23, P = 0.31) nor the responses in BB (F = 0.31, P = 0.82) revealed a significant main effect of PHASE. Similar to the responses in the arm muscles, the responses in TA and VL were typically of larger amplitude during the OPPOSE task than during the COMPLY task. However, the ANOVAs revealed a significant TASK × PHASE interaction for both TA (F = 14.64, P < 0.0001) and VL (F = 7.64, P = 0.003). The significant (P < 0.05) simple effects identified by Tukey’s post hoc comparisons are identified by the asterisks in Fig. 5A. Generally, the largest responses in both TA and VL occurred at heel strike during the OPPOSE task and were of smaller amplitude elsewhere in the step cycle.

Figure 5B depicts average response amplitudes following forward perturbations. As shown in Fig. 2, the response to forward perturbations was dominated by evoked activation of PD, TB, SOL, and BF. Therefore, we focused the analysis on the responses in these muscles. As can be seen, responses in PD and TB were of much larger amplitude during the OPPOSE task than during the COMPLY task. This difference was revealed as a significant main effect of TASK by two-way ANOVAs for each of PD (F = 28.14, P < 0.0001) and TB (F = 25.60, P < 0.0001). Visually, responses in both PD and TB appear to demonstrate some modulation of amplitude over the step cycle; however, neither PD (F = 0.70, P = 0.56) nor TB (F = 1.10, P = 0.36) showed a significant main effect of PHASE. Responses in SOL and BF were also typically larger during the OPPOSE task than the COMPLY task. Responses in BF revealed a significant main effect of both TASK (F = 10.82, P < 0.0001) and PHASE (F = 4.66, P = 0.006), with the largest-amplitude responses occurring at heel strike and the smallest responses occurring at toe-off. Responses in SOL also varied in amplitude according to the point in the step cycle at which the perturbation was applied; however, the ANOVA revealed a significant TASK × PHASE interaction (F = 30.92, P < 0.0001). The significant (P < 0.05) simple effects identified by Tukey’s post hoc comparisons are identified by the asterisks in Fig. 5B for SOL. Generally, the largest responses in SOL occurred at heel strike during the OPPOSE task. Note that at midstance FWD perturbations typically resulted in a suppression of the activity of SOL during the OPPOSE task.

Effect of task instruction on step cycle duration. During this study the participants were asked to either OPPOSE the randomly applied displacement of the handles or permit the handles to be displaced in the COMPLY task. Average control step cycle durations during COMPLY (1.395 ± 11.0 ms) were marginally longer than during OPPOSE (1.346 ± 10.1 ms). However, a paired t-test revealed that this difference was significant (t = 2.68, P = 0.03), indicating that it was a consistent finding across subjects.

Two-way ANOVAs compared the amplitude of the background EMG activity and joint angle between tasks and across the phases of the step cycle for all of the muscles and joints recorded. No differences were detected in any of the muscles or joints, with all F values being <1.

Features of applied displacements. Figure 6 depicts the average traces for the displacement and acceleration of the handles, along with the horizontal force applied to the handles, during FWD and BWD perturbations delivered at heel strike for a single subject. As can be seen, during the COMPLY task (solid lines in Fig. 6) the perturbation leads to a displacement of the handles that is sustained for several hundred milliseconds. In contrast, during the OPPOSE task (dotted lines in Fig. 6), the handles are also initially displaced but reverse their motion back toward the starting position as the subjects resist the displacement. It is important to note that the initial displacement of the handles was similar between tasks and that the reversal of direction observed with the OPPOSE task occurred 200–300 ms after the initial onset of the displacement. In addition, the acceleration traces (derived from the position traces) from the two tasks overlapped each other during the first 150 ms of the displacement of the handles. To compare the features of the perturbation of the handles we measured the displacement of the handles in the first 150 ms and the peak acceleration for each TASK and PHASE across subjects. On average, the displacement of the handles in the first 150 ms ranged between 6.6 and 7.6 cm across tasks and phases. Separate two-way ANOVAs for FWD and BWD perturbations did not reveal any significant effects of TASK and PHASE on handle displacement, with F values ranging between 0.51 and 1.38. Similarly, no differences in the peak acceleration were detected, with F values ranging between 0.17 to 1.27. The average peak acceleration varied between 1.1 and 1.3 m/s² across the tasks and phases.
The horizontal force recorded at the handles is described by a single peak in the first 150 ms of the perturbation with a return to baseline thereafter during the COMPLY task. In contrast, during the OPPOSE task a second deflection in the trace emerges later. This second peak during the OPPOSE task is related to the reversal of the direction of handle displacement. The initial peak in the force trace during the first 150 ms of the perturbation overlaps between the COMPLY and OPPOSE tasks.

Two-way ANOVAs of the initial peak force revealed no significant effects of TASK and PHASE, with $F$ values ranging between 0.35 and 0.85. The average initial peak forces varied between 7.3%BW and 9.2%BW across tasks and phases.

**DISCUSSION**

The primary purpose of the present study was to investigate the reactions in muscles of the arm and the leg following perturbations delivered at the hands during walking. The main findings of this study were that 1) perturbations applied at the hands resulted in early latency responses in arm muscles when subjects were instructed to OPPOSE but not when they were instructed to COMPLY to the perturbations; 2) the responses evoked during OPPOSE involved activation of muscles in the arm as well as muscles in the leg; and 3) when instructed to COMPLY to the perturbations, most subjects presented re-
responses in muscles of the leg notwithstanding that there was no activation of muscles in the arm.

How do these results compare to other studies? A previous study by Cordo and Nashner (1982) found that unexpected forward handle pulls applied to standing subjects resulted in short-latency (<100 ms) activation of arm and leg muscles when subjects were instructed to "resist" the perturbation. In contrast, the authors reported that short-latency responses in the arms were usually small or absent when subjects were asked to "not resist" the perturbation, while short-latency responses in the legs continued to be expressed. These results are very similar to our results during treadmill walking, except that in our study responses in the arm muscles were never observed during the COMPLY ("not resist") task. This subtle difference in the likelihood of observing responses in the arm muscles during the COMPLY task between the two studies could be attributed to differences in how responses were identified from the EMG traces. Alternatively, the absence of evoked responses in the arms in our study during COMPLY could be related to the fact that our subjects were walking on a treadmill. It is well documented that many short-latency responses throughout the body, including reflexes in the arms, are modulated during locomotion or locomotor-like activities, compared with static or stationary tasks (Zehr and Duyens 2004). Additionally, subjects in the Cordo and Nashner (1982) study were required to hold a steady load prior to the onset of the perturbation. This increase in background activity would be expected to increase the excitability of the target motoneuron pool and increase the excitability of any responses mediated by those motoneurons. Nevertheless, both studies report the expression of responses in the leg muscles to perturbations of the handles, regardless of whether the subjects were asked to COMPLY or to OPPOSE the disturbance. Therefore, the external displacement of the arms initiates a rapid (<100 ms) response in the legs, regardless of whether a response is observed in the arms themselves. This rapid interlimb response observed in the leg muscles is preserved during walking, despite the fact the legs are actively involved in stepping.

One other study has reported on the corrective reactions in the legs and arms induced by displacement of a set of handles during treadmill walking (Nashner and Forssberg 1986). Nashner and Forssberg (1986) reported that forward displacement of the handles resulted in short-latency (<100 ms) responses in the gastrocnemius and biceps muscles when subjects were instructed to resist the perturbation. These results are comparable to the present findings. However, Nashner and Forssberg (1986) only tested the handle displacement perturbations in two subjects and only with the subjects instructed to resist the perturbation. In addition, these authors only reported data for perturbations that occurred at around midstance. The present study confirms the findings of Nashner and Forssberg (1986) but also shows that the amplitude of the responses elicited in the legs, but not the arms, is modulated across the step cycle and that responses in the legs are evident when subjects are asked to COMPLY with the perturbation.

Activation of responses to perturbations applied at the hands. Perturbations applied during walking by rapid displacement of a handle result in postural responses involving activation of muscles in the arms and the legs (Hirschfeld and Forssberg 1991; Nashner and Forssberg 1986). It has been argued that such perturbations trigger reflex responses in muscles of the arms and legs that are most likely activated from afferents in muscles of the arms. Our results could be interpreted with a similar approach. Perturbations delivered at the hands during the OPPOSE task resulted in direction-specific activation of muscles in the arm and the leg following the displacement of the handles. One possible mechanism by which the direction specificity in the activation of the arm muscles could be explained is that responses to backward perturbations could be initiated by muscle afferents in AD and TB, while responses to forward perturbations could be initiated by muscle afferents in PD and BB. However, in Fig. 6 it is shown that any appreciable movement of the handles did not occur until well after the onset of acceleration and a change in the load applied at the hands. Therefore, it is possible that the onset of the perturbation could be detected by the change in acceleration preceding the displacement of the handles. Muscle spindle afferents are sensitive to changes in acceleration, and therefore the acceleration associated with the displacement of the handles could be detected by muscle afferents from the stretched muscles (Prochazka 1996). Alternatively, the application of the load at the hands associated with the applied perturbation would activate cutaneous receptors in the skin of the hand. Mechanoreceptors in the skin can encode detailed information about the surface in contact with the hand, not only related to the shape and texture of the contacted surface but also related to the dynamics of the contact between the hand and the surface. These receptors can respond to changes in shearing forces with latencies under 25 ms (Johansson and Flanagan 2009). Tactile feedback from the hand has been found to strongly influence postural control. Body sway is largely reduced by touch of a stable surface even when the load applied at the surface is not sufficient to provide mechanical support (Jeka and Lackner 1994; Kouzaki and Masani 2008; Krishnamoorthy et al. 2002). Hence, it is possible that cutaneous information from the hands can be used by the nervous system.
perhaps in conjunction with stretch reflexes from the arms, to activate the direction-specific responses observed with the displacement of the handles.

Task and phase modulation of arm and leg responses. Important differences in the responses evoked in arms and legs from perturbations delivered at the hands were found in association with the task. In particular, strong responses in the arms were observed during the OPPOSE task but were absent during the COMPLY task. The displacement and acceleration of the handles in the first 150 ms of the perturbation were comparable regardless of task. Therefore, there were no differences in the characteristics of the perturbations before the onset of the responses. In addition, there were no differences in background EMG in the arm muscles between tasks, suggesting that no changes in elbow or shoulder joint stiffness were linked to the task. The differences in the responses between the OPPOSE and COMPLY tasks are likely related to changes in functional requirements of the tasks. In other words, the responses might be suppressed during COMPLY as part of the instruction set to permit the handles to be moved without the resistance that would be generated by activation of the arm muscles and facilitated during OPPOSE as a means to rapidly resist the movement of the handles.

The responses in the arms during the OPPOSE task were accompanied by activation of muscles in the legs. The responses observed in the legs were comparable to those observed in other balance disturbance studies during walking. For example, corrective reactions evoked during walking from backward pulls applied at the waist (Misiaszek 2003; Misiszek and Krauss 2005), sudden deceleration of the treadmill belt (Berger et al. 1984), or forward translations of the support surface (Tang et al. 1998) consist of early activation of TA and VL with a distal to proximal temporal organization. It has been argued that the fact that comparable corrective reactions are evoked independently from the locus of the perturbation suggests that the reactions are due to a common centrally coordinated response (Misiaszek 2003). Accordingly, the results observed in the present study during the OPPOSE task suggest that balance-corrective reactions evoked from the displacement of the handles activate the same response, suggesting that responses evoked in the legs to perturbations applied at the hands are balance-corrective responses.

Responses in the legs were also observed during the COMPLY task but were markedly smaller than those observed during the OPPOSE task. However, as described above, the characteristics of the applied perturbation in the first 150 ms of the disturbance were comparable between tasks. Therefore, the difference in the amplitude of the responses in the legs between tasks is related to the difference in the task requirements. During the OPPOSE task, when the disturbance to balance is expected to be greater, the responses in the legs are more pronounced. In contrast, during the COMPLY task the threat to balance by the displacement of the arms is less, resulting in an appropriately scaled reaction. This task-specific scaling of the corrective reactions is consistent with the concept of “postural set” (Prochazka 1989). In this way, the balance reactions in the legs initiated by disturbances applied at the hands are scaled to meet the demands of the task engaged in by the hands at the time of the disturbance. Therefore, it would seem that the balance control system adapts the reactions elicited in the legs to accommodate for the constraints and restrictions placed upon whole-body stability by the tasks engaged in by the arms (Misiszek and Krauss 2005).

The amplitude of the responses in the legs showed a clear effect of the point in the step cycle at which the disturbance of the handles was applied. This was most evident during the OPPOSE task, but the smaller responses seen during the COMPLY task tended to show a similar phase-dependent modulation in response amplitude. Generally, responses in the legs were largest when the disturbance occurred at heel strike. This is very similar to the phase-dependent modulation of response amplitude reported for perturbations applied at the waist during treadmill walking (Bolton and Misiszek 2012; Misiszek 2003; Misiszek and Krauss 2005). The increase in response amplitude in the legs at heel strike appears to be related to the inherent instability with the establishment of a new base of support to receive and support the mass of the body (Bolton and Misiszek 2012). In contrast, the responses evoked in the arms during the OPPOSE task were not systematically larger in amplitude at heel strike. Indeed, the analysis did not reveal a statistically significant effect of PHASE on the amplitude of the responses in the arm muscles. However, the responses in the arm muscles tended to show a modest suggestion of phase dependence in the response amplitudes in all four muscles that tended to follow the subtle variations in the background EMG. This is in contrast to what is observed for the responses evoked in the legs, which were largest at heel strike regardless of the level of background EMG. Consequently, the pronounced phase-dependent regulation of the responses evoked in the leg muscles is not mirrored by a similar phase-dependent regulation of the responses in the arms. The implication is that the regulation of the amplitude of the responses in the arms and legs is governed independently, despite the common threat to instability introduced by forming a new base of support at heel strike.

Conclusions. The results from this study showed that balance reactions can be elicited in the legs in response to perturbations at the arms. However, the task engaged in by the arms influences the expression of the responses in the legs. That is, when a demand to maintain stability at the arms is part of the task (OPPOSE), then the responses are facilitated. Functionally, this difference would be important for tasks in which the arms themselves are engaged in maintaining balance. For example, when a walking aid, such as a cane or walker, is being used to assist with stability, disturbances to the arms would threaten the upright balance of the user. A whole-body corrective reaction, including at the arms and legs, would be required to stabilize the walking aid, while also maintaining balance. For those individuals with compromised balance control and who would therefore be most likely to utilize an assistive device, the appropriate initiation, organization, and scaling of the whole-body response might also be compromised. For example, Bateni and Maki (2005) found that, despite the mechanical advantages of using walking aids, these devices are themselves associated with an increased risk of falling. We have shown that in young healthy adults the rapid coordinated responses in the arms and legs triggered by disturbances to the arms during walking are scaled to meet the demands of the task performed by the arms. Facilitation of the corrective responses in the legs when the hands are engaged in other tasks might be a critical function of the nervous system for maintaining bipedal support, particularly when grasping for
an external support is limited by activity engaged in by the hands (Bateni et al. 2004).

REFERENCES


