RESEARCH ARTICLE

Reflex pathways connect receptors in the human lower leg to the erector spinae muscles of the lower back

J. M. Clair · Y. Okuma · J. E. Misiaszek · D. F. Collins

Abstract Reflex pathways connect all four limbs in humans. Presently, we tested the hypothesis that reflexes also link sensory receptors in the lower leg with muscles of the lower back (erector spinae; ES). Taps were applied to the right Achilles' tendon and electromyographic activity was recorded from the right soleus and bilaterally from ES. Reflexes were compared between sitting and standing and between standing with the eyes open versus closed. Reflexes were evoked bilaterally in ES and consisted of an early latency excitation, a medium latency inhibition, and a longer latency excitation. During sitting but not standing, the early excitation was larger in the ES muscle ipsilateral to the stimulation (iES) than in the contralateral ES (cES). During standing but not sitting, the longer latency excitation in cES was larger than in iES. This response in cES was also larger during standing compared to sitting. Responses were not significantly different between the eyes open and eyes closed conditions. Taps applied to the lateral calcaneus (heel taps) evoked responses in ES that were not significantly different in amplitude or latency than those evoked by tendon taps, despite a 75–94% reduction in the amplitude of the soleus stretch reflex evoked by the heel taps. Electrical stimulation of the sural nerve, a purely cutaneous nerve at the ankle, evoked ES reflexes that were not significantly different in amplitude but had significantly longer latencies than those evoked by the tendon and heel taps. These results support the hypothesis that reflex pathways connect receptors in the lower leg with muscles of the lower back and show that that the amplitude of these reflexes is modulated by task. Responses evoked by stimulation of the sural nerve establish that reflex pathways connect the ES muscles with cutaneous receptors of the foot. In contrast, the large volley in muscle spindle afferents induced by the tendon taps compared to the heel taps did not alter the ES responses, suggesting that the reflex connection between triceps surae muscle spindles and the ES muscles may be relatively weak. These heteronymous reflexes may play a role in stabilizing the trunk for maintaining posture and balance.

Keywords Human reflexes · Muscle spindles · Cutaneous afferents · Erector spinae muscle

Introduction

The neural control of human movement is mediated in part by reflex pathways through the spinal cord. Some of these pathways transmit signals from sensory receptors in one limb to the musculature of the other three limbs. These pathways form the substrate for interlimb reflexes that are thought to contribute to the coordination of all four limbs during tasks such as walking (Dietz et al. 2001; Dietz 2002; Zehr and Duysens 2004). Interlimb reflexes are often studied by activating receptors in one limb and recording responses in the remote, non-stimulated limbs (Dietz et al. 2001; Haridas and Zehr 2003; Kearney and Chan 1979,

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1981; Meinck and Piesiur-Strehlow 1981; Zehr et al. 2001). Such reflexes have been observed in muscles of the upper limb from ankle joint displacement (Kearney and Chan 1981) and in all four limbs from electrical stimulation of cutaneous nerves at the wrist and ankle (Zehr et al. 2001). Whether reflex connections also exist between sensory receptors in the limbs and the muscles of the trunk has not been explored.

Activity of the trunk musculature is important for maintaining upright posture and ensuring stability during standing and walking (Floyd and Silver 1955; Waters and Morris 1972). The lower erector spinae muscles (ES), in particular, provide stability of the lumbar spine and together with the transverse abdominus and internal obliques correct for changes in the center of mass (O'Sullivan et al. 2002) through a combination of spinal and cortical mechanisms. Spinal mechanisms include the stretch reflexes that can be demonstrated experimentally by taps applied over the ES muscles (Dimitrijevic et al. 1980; Zedka et al. 1999) or during more natural tasks, as a result of small movements of the trunk during arm movements (Zedka and Prochazka 1997). In contrast to these spinal mechanisms, after a more global postural perturbation ES activity has been characterized as part of an automatic postural response (Cordo and Nashner 1982) mediated in part through transcortical pathways (Diener et al. 1988). These responses are modulated by an interaction between central commands that depend on prior experience, and afferent feedback from the periphery (Deliagina et al. 2008; Horak et al. 1989; Jacobs and Horak 2007; Misiaszek 2006). Feedback from spindles in muscles around the ankle joint is thought to be especially important for postural control (Creath et al. 2005; Dietz et al. 1989; Fitzpatrick et al. 1992; Kavounoudias et al. 2001; Nashner 1976). Trunk muscle activity, in particular, is thought to be heavily influenced by signals from spindles in muscles acting on the ankle joint (Kearney and Chan 1981), however, the neural pathways that mediate this control have not been well-defined.

The present experiments were designed to test the hypothesis that there are spinal reflex pathways between sensory receptors in the lower leg and the ES muscles of the lower back. In particular, we thought that reflex pathways would connect spindles in the triceps surae muscles (TS) of the ankle and the ES muscles. To test this, brief taps were applied to the Achilles' tendon ("tendon taps") to activate TS muscle spindles and electromyographic (EMG) activity was recorded bilaterally from ES. After establishing the presence of the ES reflexes, we (1) investigated these reflexes during different tasks and conditions (i.e., sitting vs. standing, eyes open vs. eyes closed) to explore whether challenging the postural demands influenced their expression and (2) explored the afferent origin.

Methods

Sixteen subjects participated in this study (8 males and 8 females, 18–46 years) after providing informed, written consent. The study was conducted in two parts with ten subjects participating in the first part and eight in the second part. The experimental protocol was conducted in accordance with the standards set by the Declaration of Helsinki and was approved by the Health Research Ethics Board at the University of Alberta. All subjects reported no back pain or history of neurological disorders. Each experimental session lasted between 1.5 and 3 h.

Electromyography

Electromyography (EMG) was recorded from the right soleus and bilaterally from the lower ES using disposable bipolar surface EMG electrodes (2.54 cm^2, A10043-P, Vermed Medical, Bellows Falls, VT, USA). The soleus electrodes were placed below the gastrocnemius on the midline of the muscle. The ES electrodes were placed 2 cm lateral to the L4–L5 spinous processes according to the recommendations of Cholewicki et al. (1997). Reference electrodes (10.16 cm × 4.45 cm, Electrosurgical Patient Plate: Split, 3M Health Care, St Paul, MN, USA) were placed on both anterior superior iliac spines. Given that the stimulation was always delivered to the right foot, the right ES was defined as ipsilateral (iES) and the left ES as contralateral (cES). For the experiments in Part 1, EMG signals were amplified 1,000–5,000 times and band-pass filtered between 10 and 1,000 Hz (AMT-8, Bortec Biomedical, Calgary, AB, Canada). For the experiments in Part 2, EMG signals were amplified 1,000–5,000 times and band-pass filtered between 50 and 3,000 Hz (Neurolog System; Digitimer, Welwyn Garden City, UK). Data were sampled at 2,000 Hz using custom-written software (LabView, National Instruments, Austin, TX, USA) and stored on a computer for later analysis.

Maximal voluntary contractions

At the start of each session, subjects performed maximal voluntary contractions (MVCs) of soleus and ES while receiving verbal encouragement from the experimenters. For the soleus MVC, subjects were seated with their right knee and ankle at approximately 110° and 90°, respectively. The right foot was strapped to a stationary footplate and subjects performed maximal isometric plantarflexion contractions. For the ES MVC, a strap was looped around the subject's mid-back and attached to a metal frame in front of the subject. While seated, with a hip angle of approximately 90°, the subject extended their trunk (i.e., arched the lower back) against the strap to maximally

engage ES. One to two practice trials were performed for each muscle to permit subjects to become familiar with how to maximally activate each muscle.

Protocol

Part 1. Erector spinae reflexes evoked by Achilles' tendon taps

These experiments were designed to quantify reflexes in ES evoked by taps applied to the Achilles' tendon. Data were collected while subjects were (1) standing with eyes open, (2) sitting with eyes open, (3) standing with eyes closed, and (4) sitting with eyes closed. The sitting and standing trials were included to determine whether reflex amplitude was modulated according to task. The eyes closed condition was included to provide a greater challenge to postural stability and increase the reliance on feedback from peripheral receptors for postural control (Fitzpatrick et al. 1994; Nagano et al. 2006). We predicted that ES responses would be largest while standing with eyes closed due to the increased postural demands of the task. During standing, the subjects were instructed to stand with their feet shoulder width apart, place equal weight on each foot, look straight ahead, and rest their hands at their sides. Prior to data collection, the EMG activity in ES while standing was measured. Each subject matched this level of activity during seated trials by contracting the ES in the manner described for the MVC. During the eyes open trials, subjects used visual feedback of the low pass filtered EMG signal (0.3 Hz) displayed on a computer screen to maintain the desired level of activity. During the eyes closed trials, subjects received verbal cues from the experimenters when necessary to adjust their ES activity level to match the target level. The tendon taps were delivered manually by the experimenter, perpendicular to the right Achilles' tendon with a Taylor reflex hammer. The hammer was equipped with a force sensitive resistor and this signal was used to monitor the amplitude of the force applied during each tap, as well as to trigger data collection. The taps were delivered to evoke a consistent, robust stretch reflex in soleus as determined prior to data collection. Each trial consisted of 40 taps, separated by 3–5 s, delivered with a peak force of ~2N. A set of control trials was also collected, while subjects were standing with eyes open, in which taps ($n = 40$) were delivered to the right calcaneus, below the lateral malleolus ("heel taps") in a similar manner as the tendon taps. The purpose of these trials was to minimize the activation of muscle spindles in the triceps surae, while attempting to activate a similar proportion of cutaneous receptors as during the tendon tap. We predicted that the heel taps would evoke little or no reflex in soleus or ES. The five different trials were presented in a random order across subjects.

Part 2. Erector spinae reflexes evoked by cutaneous nerve stimulation

These experiments were conducted to address the unexpected finding that ES reflexes evoked by tendon taps and heel taps were not significantly different. Thus, in eight subjects, we investigated whether ES reflexes could be evoked by electrical stimulation of cutaneous afferents from the foot. The sural nerve was chosen because it is a purely cutaneous nerve that innervates the dorsal lateral region of the foot, including the area where the heel taps were applied. We compared the amplitude and latency of ES reflexes evoked by sural nerve stimulation, tendon taps, and heel taps. All data were collected while subjects were standing with eyes open. The taps were applied to the tendon and heel as described for Part 1 (above). The electrical stimulation (4-pulses, 1 ms pulse width, 300 Hz) was delivered using a Digitimer DS7A constant current stimulator (Neurolog System) through disposable bipolar electrodes (2.54 cm^2; A10043-P, Vermed Medical) placed over the sural nerve. One electrode was placed posterior and inferior to the lateral malleolus and the other inferior to the lateral malleolus. Placement was adjusted for each subject to find the site at which there was a clear radiating paresthesia into the area of skin innervated by the sural nerve at the lowest stimulation intensity [radiating threshold (RT)]. During data collection the stimulation was delivered at 2–3 times RT and the inter-stimulus interval was varied randomly between 3 and 5 s. This stimulation protocol is typical of that used to evoke cutaneous reflexes in previous studies (Zehr et al. 2001). In the present study, the stimuli were non-noxious and did not evoke contractions of the local musculature that could be attributed to the activation of motor axons. Subjects completed three trials in which they received either; (1) tendon taps, (2) heel taps, or (3) sural nerve stimulation. In each trial, they received 80 stimuli with an interstimulus interval of 3–5 s. The presentation order of the three different trials was randomized across subjects.

Data analysis

Data analyses were performed using custom-written Matlab software (The Mathworks, Natick, MA, USA). All EMG data were rectified and low pass filtered (40 Hz, dual-pass Butterworth). The EMG recorded during the MVC for each muscle was averaged over a 500 ms window centered around the peak EMG. To quantify reflexes evoked by the different stimuli (tendon tap, heel tap, electrical stimulation) for each subject, iES, cES, and soleus EMG were averaged over an interval from 100 ms before to 250 ms after the onset of the stimulus train. In two subjects who participated in Part 1 the ES EMG in some trials was contaminated by the signal associated with a heartbeat. The

heartbeat EMG signals were easily identified as large distinct waveforms appearing simultaneously in both ES channels at random times in relation to the stimulation. When this occurred, the sweep was removed from the analysis, thus average data for these subjects were calculated from 25 to 30 sweeps. For Part 2, 80 sweeps were collected in each trial and the first 40 sweeps that were not contaminated by signals associated with the heartbeat were used for analysis, thus all average data for Part 2 were calculated from 40 sweeps. For all muscles, the background muscle activity was calculated as the average EMG over the final 100 ms prior to stimulus delivery. Responses were analyzed over fixed epochs, relative to stimulus onset, that were determined based on visual inspection of the data (Fig. 1). For soleus, reflexes were analyzed over a window
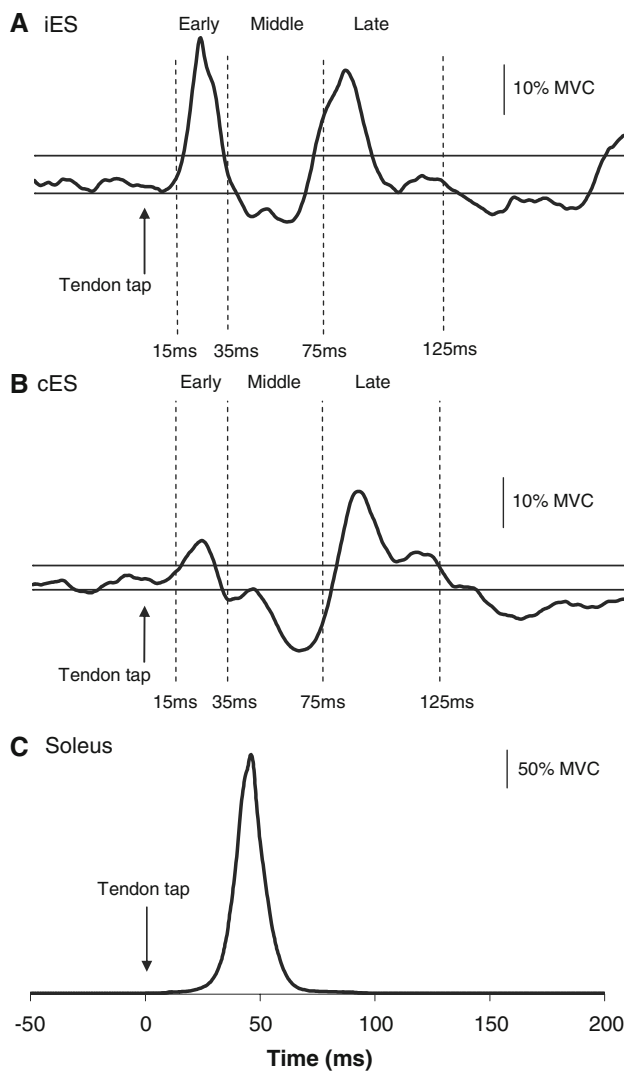

Fig. 1 Reflexes evoked in iES, cES and soleus by taps applied to the right Achilles' tendon in a single subject while sitting with eyes open. Each trace represents the average of 40 reflexes. *Horizontal lines* depict ±2 SD of the background EMG recorded during the 100 ms prior to stimulus delivery

25–75 ms after stimulus onset, consistent with a short-latency stretch reflex. For reflexes in ES in Part 1, data were sorted into early (15–35 ms), middle (35–75 ms), and late (75–125 ms) epochs. For the tendon tap and heel tap responses of Part 2, the latency of the late epoch was shifted slightly earlier (70–125 ms) to more accurately capture the peak responses in this group of subjects. To quantify responses to stimulation of the sural nerve in Part 2 the epochs were slightly later (early 25–45 ms, middle 45–85 ms, late 85–125 ms). For each response epoch, the peak latency, amplitude, and sign were calculated. Peak latency was calculated as the time from stimulus onset to the point of maximal excitation or inhibition. Amplitude was calculated by subtracting the average EMG over a 10 ms period, centered around the point of maximal excitation or inhibition, from the mean pre-stimulus EMG, and was expressed as a %MVC. The sign of the response was determined by whether the peak response was larger (positive) or smaller (negative) than the mean pre-stimulus EMG.

Statistical analysis

For each subject in Part 1, χ^2 analyses were used to determine whether there were significantly more excitatory responses compared to inhibitory responses, or vice versa, for each epoch. A response was considered significant when the EMG in a given epoch remained outside of a ±2 SD band, centered around the mean pre-stimulus EMG activity, for a minimum of 5 ms. This 5 ms criterion has been used in previous studies for the analysis of cutaneous reflexes (Zehr et al. 2001; Haridas and Zehr 2003).

The subtracted and signed EMG values were used for statistical analyses of reflex responses across the group. Planned comparisons were used to identify significant differences between ES reflex amplitudes between the different conditions in Part 1. A three-way repeated measures analysis of variance (rmANOVA; Task: sitting and standing; Eyes: open and closed; Muscle: iES and cES) was performed for each epoch to provide the experimental error value for the planned comparison analyses. To compare the ES reflexes evoked by tendon taps with those by heel taps in each epoch, the error value for planned comparisons was extracted from a two-way rmANOVA (Stimulation: tendon taps and heel taps; Muscle iES and cES). A two-way rmANOVA was used to compare soleus reflexes between conditions (Task: sitting and standing; Eyes: open and closed). For the experiments described in Part 2, separate two-way rmANOVAs (Muscle: iES and cES; Stimulation: tendon taps, heel taps and sural nerve stimulation) were used to compare ES response amplitudes and latencies evoked by tendon taps, heel taps and sural nerve stimulation for each epoch. Responses in soleus were compared using a one-way rmANOVA (tendon taps, heel taps and sural nerve

stimulation). In Parts 1 and 2, background contraction levels for both soleus and ES were compared between conditions using rmANOVAs. Tukey's HSD tests were used for post hoc comparisons of the ANOVA results when significant main effects or interactions were identified. For all statistical analyses, the significance level was $p \leq 0.05$. Descriptive statistics are reported as the mean $\pm$ 1SD.

Results

Part 1. Tendon taps

Reflexes recorded from ES and soleus in one subject while sitting with eyes open and holding a bilateral background contraction in ES are shown in Fig. 1. For this subject, responses exceeded the 2 SD band centered around the prestimulus EMG (horizontal lines) and thus were considered significant in all three epochs for iES and cES. Figure 2 shows responses recorded from cES in another subject and highlights the qualitative similarity of reflexes recorded during sitting (panel A) and standing (panel B) with eyes open (thick lines) and closed (thin lines). For the sake of clarity, the 2 SD bands are not shown in this figure.

The taps applied to the Achilles' tendon elicited a stretch reflex in soleus in all subjects (Figs. 1c, 3d). These reflexes were always excitatory, with an average amplitude of $160 \pm 83\%$ MVC and a peak latency of 48 ± 3 ms while standing with the eyes open. There were no significant differences in the amplitude (Fig. 3d) or latency of the reflexes recorded in soleus between conditions. There was also no significant difference between the background EMG activity in soleus when the subjects were standing during the tendon tap trials with the eyes open ($6 \pm 5\%$ MVC) and eyes closed ($6 \pm 4\%$ MVC).

Taps applied to the Achilles' tendon evoked significant reflexes in iES and cES in all subjects. Significant reflexes consisted predominantly of early excitation followed by a middle latency inhibition and a subsequent period of excitation. Table 1 summarizes the frequency, sign and latency of significant ES responses evoked by tendon taps for the group of 10 subjects. In iES, significant responses were evoked in 80, 93, and 88% of all trials for the early, middle, and late epochs, respectively. Significant responses were recorded from cES in 70, 83 and 95% of all trials for the early, middle, and late epochs, respectively. For iES, responses were excitatory (30/40 trials) in the early epoch significantly more often than they were inhibitory (2/40) [χ^2 (1, $N = 32$) = 24.53, $p \leq 0.001$]. There was also significantly more excitatory responses in the early epoch for cES [22/40 excitatory vs. 6/40 inhibitory; χ^2 (1, $N = 28$) = 9.18, $p \leq 0.01$]. During the middle epoch, iES responses were more often inhibitory (25/40 trials) than excitatory (12/40 trials) [χ^2 (1, $N = 37$) = 4.59, $p \leq 0.05$]. The middle latency responses recorded from cES were also more often inhibitory (25/40 trials) than excitatory (8/40 trials) [χ^2 (1, $N = 33$) = 8.79, $p \leq 0.01$]. For the late epoch, excitatory responses predominated for both iES [26/40 excitatory vs. 7/40 inhibitory; χ^2 (1, $N = 35$) = 12.63; $p \leq 0.001$] and cES [35/40 excitatory vs. 3/40 inhibitory; χ^2 (1, $N = 38$) = 26.97, $p \leq 0.001$].

For the group, there was no significant effect of task (standing vs. sitting) on the magnitude of responses in the early, middle, or late epochs for iES (Fig. 3). The cES muscle also showed no significant effect of task for responses in the early and middle epochs. In contrast, cES responses in the late epoch during standing were significantly larger than during sitting (Fig. 3c). Responses in ES were not significantly different between eyes open and eyes closed for any condition. There were no significant differences in background ES EMG activity between conditions and the average background ES EMG activity measured for the group across conditions was 21% MVC (range 17–24%).

Responses evoked in iES and cES were significantly different in amplitude and these differences depended on task. In the early epoch, responses in iES were larger than

Fig. 2 Data recorded from cES for a single subject. Reflexes were evoked by Achilles' tendon taps while the subject was seated (**a**) and standing (**b**) with the eyes open or eyes closed
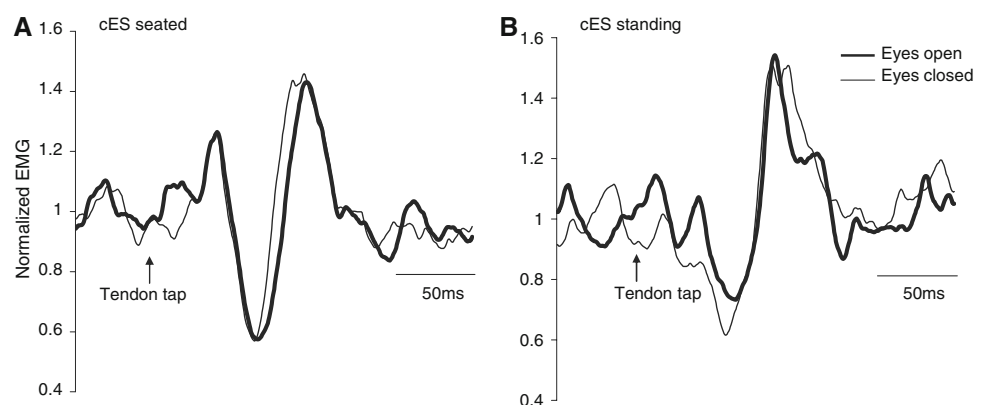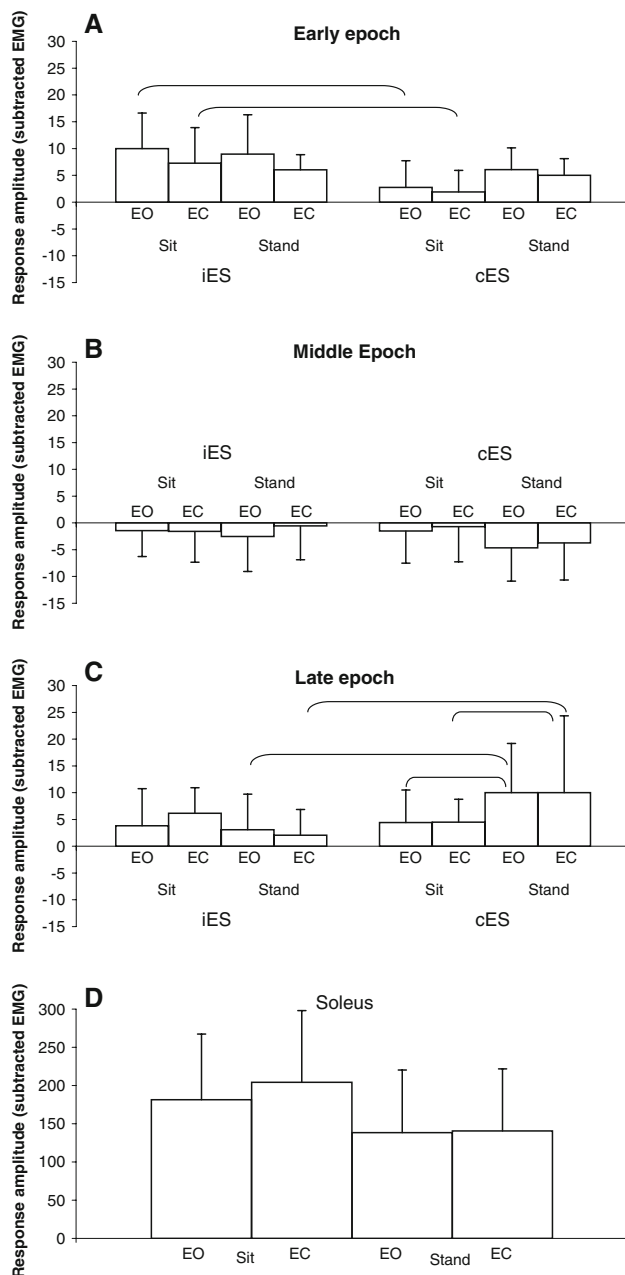
Fig. 3 Amplitude of responses recorded from ES [early epoch panel (**a**), middle epoch panel (**b**), late epoch panel (**c**) and soleus (**d**) averaged across the group for all conditions]. Values are means ± SD. *Brackets* identify responses that are significantly different from each other ($p \leq 0.05$). EO-eyes open, EC-eyes closed

those recorded in cES while sitting with eyes open and eyes closed (Figs. 1, 3a), but during standing there were no significant differences between the early responses in iES and cES (eyes open or closed). As shown in Fig. 3b, responses in the middle epoch were not significantly different between iES or cES regardless of task. For the late epoch, the ES responses showed task-dependent changes that were opposite to those found for the early epoch. While standing (eyes open and eyes closed), the late responses in cES were

larger than those in iES, but during sitting there were no significant differences in the late responses between iES and cES (eyes open or eyes closed) (Fig. 3c).

Tendon taps versus heel taps

In an additional set of trials, taps were applied to the lateral calcaneus while subjects were standing with eyes open. Figure 4 shows data for the group of ten subjects averaged over the interval from 50 ms before to 200 ms after the taps (left panels) and quantified for each reflex epoch (right panels). The heel taps evoked reflexes in soleus that were 75% smaller than those evoked by the tendon taps ($p \leq 0.05$). In contrast, there were no significant differences in ES reflexes evoked by tendon taps or heel taps in any epoch. Background soleus and ES EMG activity were not significantly different between the tendon tap and heel tap trials.

Part 2: Erector spinae reflexes evoked by cutaneous nerve stimulation

To determine whether the responses recorded from ES could be evoked by the activation of cutaneous receptors, a second series of experiments was conducted in which the amplitude and latency of ES reflexes evoked by tendon taps, heel taps and sural nerve stimulation were compared in eight subjects while standing with eyes open. The group traces in Fig. 5 show responses in ES elicited by all three stimuli. There were no significant differences in the amplitudes of responses in any epoch between the different stimulus types. Similarly, there were no significant differences in the amplitudes of responses in either the early or late epochs between iES and cES. In the middle epoch, responses to tendon taps and heel taps were smaller in iES than cES. Responses to sural nerve stimulation were not significantly different between iES and cES in the middle epoch. The latency of the responses in each epoch were not different between iES and cES. However, response latencies in all three epochs for the sural nerve stimulation were significantly longer than responses to the tendon taps and the heel taps, which were not significantly different from each other. The mean latencies to the peak responses in the early epoch (averaged across iES and cES) were 24 ± 7, 26 ± 8, and 33 ± 7 ms for tendon tap, heel tap, and sural nerve stimulation, respectively. In the middle epoch, latencies were 54 ± 8, 51 ± 8, and 66 ± 11 ms for tendon tap, heel tap and sural nerve stimulation, respectively. Response latencies in the late epoch were 90 ± 12, 87 ± 13, and 106 ± 11 ms for tendon tap, heel tap, and sural nerve stimulation, respectively. Responses in soleus evoked by tendon taps were significantly larger than those elicited by heel taps and sural nerve stimulation, which were not significantly different from each other (Fig. 5e, f). Soleus reflexes

Table 1 Response frequency, prevalence of excitatory and inhibitory responses, and average response latencies for ES responses to Achilles' tendon taps for the different conditions in Part 1

Conditions	iES			cES		
	Early epoch	Middle epoch	Late epoch	Early epoch	Middle epoch	Late epoch
Standing eyes open (N = 10)	7	9	9	6	10	10
	7+/0−	2+/7−	6+/3−	6+/0−	1+/9−	10+/0−
	24 ± 8 ms	57 ± 4 ms	99 ± 4 ms	20 ± 8 ms	59 ± 7 ms	93 ± 10 ms
Standing eyes closed (N = 10)	9	10	9	7	8	10
	9+/0−	5+/5−	7+/2−	6+/1−	1+/7−	10+/0−
	22 ± 5 ms	57 ± 8 ms	104 ± 14 ms	23 ± 6 ms	57 ± 8 ms	100 ± 14 ms
Seated eyes open (N = 10)	7	9	8	8	8	9
	7+/0−	2+/7−	7+/1−	5+/3−	3+/5−	7+/2−
	24 ± 4 ms	60 ± 12 ms	96 ± 11 ms	28 ± 6 ms	59 ± 10 ms	99 ± 11 ms
Seated eyes closed (N = 10)	9	9	9	7	7	9
	7+/2−	3+/6−	8+/1−	5+/2−	3+/4−	8+/1−
	26 ± 5 ms	59 ± 12 ms	91 ± 8 ms	28 ± 8 ms	61 ± 10 ms	97 ± 12 ms

For example, to describe responses in the early epoch for iES standing eyes open (*first row*), response frequency was 7 (i.e., 7 out of 10 subjects displayed a significant ES response in that epoch). Out of these 7 significant responses, 7 were excitatory (7+) and 0 were inhibitory (0−). The average response latency was 24 ms and the standard deviation was ±8 ms

evoked by the heel taps were on average 94% smaller than those evoked by tendon taps. The sural nerve stimulation generated a small net inhibition in soleus at this reflex epoch. There were no differences in the amount of soleus or ES background activity between the three stimulation conditions.

Discussion

These experiments are the first to characterize reflexes in muscles of the lower back initiated by the activation of sensory receptors in the lower leg. Taps applied to the right Achilles' tendon evoked reflexes bilaterally in ES, in addition to the well-known stretch reflex in ipsilateral soleus. Contrary to our prediction, taps applied over the lateral calcaneus ("heel taps") and electrical stimulation of the sural nerve (a cutaneous nerve of the foot) evoked reflexes in ES that were not significantly different in amplitude from those evoked by the tendon taps. We propose the reflexes in ES arise at least in part from the activation of cutaneous receptors in the foot and may contribute to the neural strategies used for the maintenance of posture and balance.

Taps applied to the Achilles tendon evoked reflexes bilaterally in the ES muscles in all subjects. In most cases, these reflexes consisted of a period of excitation in the early epoch, inhibition in the middle epoch, and excitation in the late epoch. This response pattern is qualitatively similar to the pattern observed for "interlimb" reflexes evoked in many muscles of the arms and legs by activation of sensory receptors in a stimulated limb, remote from the recording site (Kearney and Chan 1979; Zehr et al. 2001). The early

excitation in ES, which was maximal at a latency of 20–28 ms, and the middle epoch inhibition, maximal at a latency of 57–61 ms, are both consistent with transmission along pathways restricted to the spinal cord. The longer latency excitation peaked at 91–104 ms and may involve transcortical pathways (Nielsen et al. 1997).

We hypothesized that reflex pathways connect sensory receptors in the lower leg with the ES muscles of the lower back. Specifically, we thought that reflexes would arise from the activation of spindles in the TS muscles that plantarflex the ankle. This idea was based on the well-established hypothesis that signals from muscle receptors around the ankle joint provide important information for posture and balance and play a key role in triggering responses for balance correction (Creath et al. 2005; Diener et al. 1988; Dietz et al. 1989; Fitzpatrick et al. 1992; Kavounoudias et al. 2001; Nashner 1976; Schweigart and Mergner 2008). However, the tendon taps we utilized to activate TS muscle spindles will have also activated muscle spindles and cutaneous receptors over a large area of the leg and foot, as well as some TS Golgi tendon organs (Burke et al. 1983). Thus, to explore the afferent origin of the ES reflexes, "heel taps" were delivered to the right calcaneus directly below the lateral malleolus and electrical stimulation was applied to the sural nerve. We predicted the heel taps would activate a similar proportion of cutaneous receptors as the tendon taps, but fewer TS spindles (and no Golgi tendon organs), and responses in ES and soleus would be reduced accordingly. The sural nerve stimulation was chosen to provide a cutaneous input from the same region of the foot as the heel taps that, unlike the tendon and heel taps, was not contaminated by the activation of afferents from muscle spindle
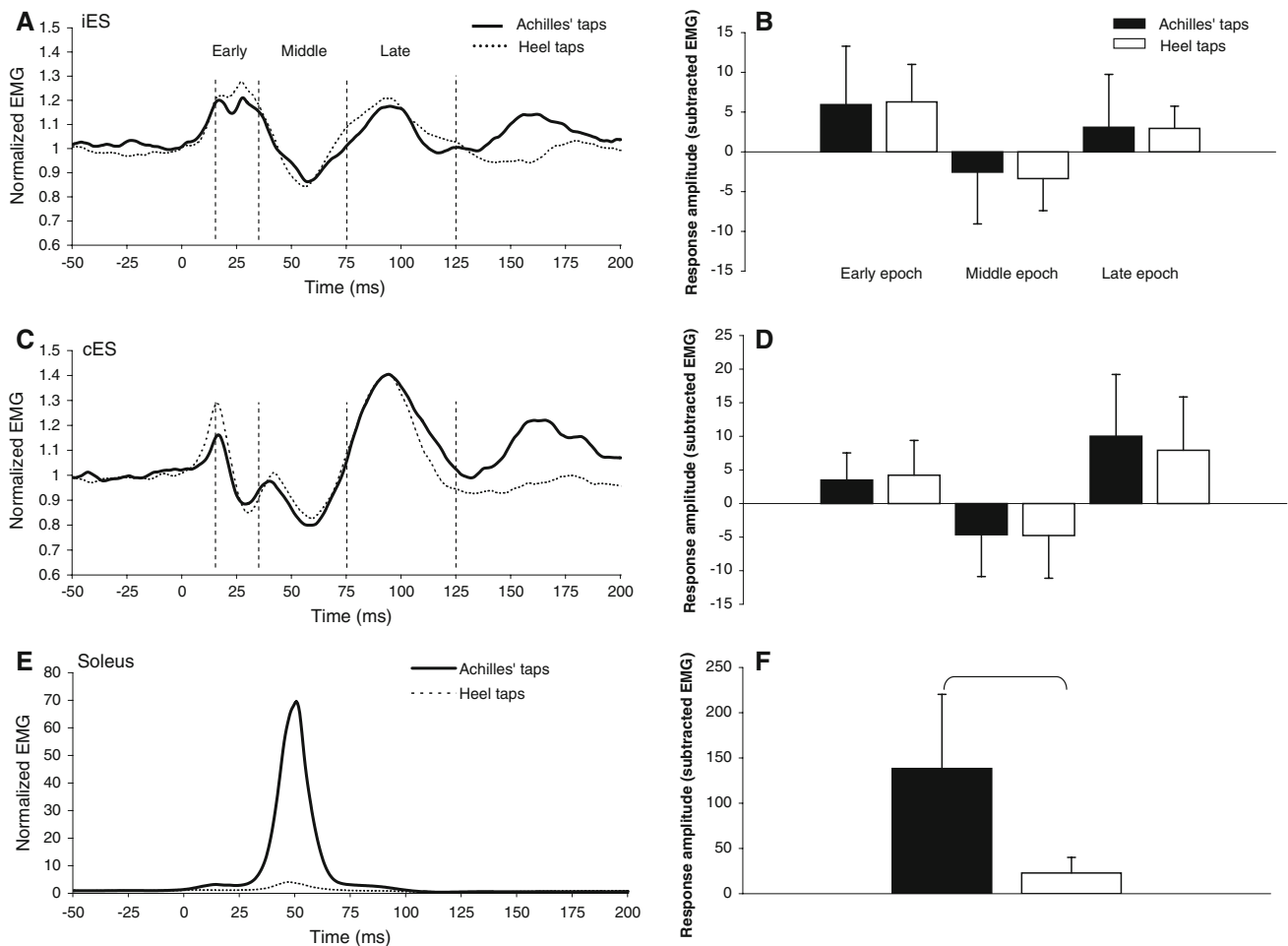
Fig. 4 Reflexes recorded from iES (**a**, **b**), and cES (**c, d**) and soleus (**e, f**), evoked by Achilles' tendon taps and heel taps applied to the lateral calcaneus while subjects were standing with eyes open. Data are averaged over the group of 10 subjects. Values are means ± SD. *Brackets* identify responses that are significantly different from each other ($p \leq 0.05$)

receptors or Golgi tendon organs. Despite a 75–94% reduction in the amplitude of the soleus stretch reflex elicited by heel taps, the ES reflexes were not significantly different in amplitude or latency than those evoked by tendon taps. The amplitude of ES responses in each epoch evoked by the tendon taps and heel taps were not significantly different from those evoked by the cutaneous volley generated by the sural nerve stimulation. However, the latencies of the responses in each epoch evoked by sural nerve stimulation were significantly longer than those evoked by tendon taps and heel taps. These results raise several possibilities regarding the origin of the ES responses. (1) The ES reflexes may be part of a generalized startle response initiated by all three stimulus types. We do not believe this is the case because the responses occurred at a much shorter latency than would be expected from a traditionally defined startle response (Brown et al. 1991). Additionally, startle responses typically habituate within the first 2–6 stimuli (Brown et al. 1991) and thus could not account for the robust responses seen in individual subjects' data which represent the mean

responses to 40 stimuli. (2) Both tendon and heel taps may have generated a wave of vibration through the musculoskeletal system activating muscle spindles in ES and generating a local stretch reflex in ES. However, the ES responses evoked by sural nerve stimulation, when there would be no vibration argue against this possibility. Similarly, the ES responses to the heel taps and the sural nerve stimulation suggest the ES responses are not initiated by the movement associated with the soleus stretch reflex. (3) The responses evoked by sural nerve stimulation confirm that reflex pathways connect cutaneous receptors in the foot and ES motoneurons. Responses evoked by the tendon and heel taps were not significantly different in amplitude from those evoked by sural nerve stimulation, but had shorter peak latencies. The differences between the responses evoked by the taps and the sural nerve stimulation likely reflect differences in the afferent volley. The taps will have activated a different proportion of cutaneous receptors in a different temporal pattern than the electrical stimulation and will also have activated muscle receptors (Burke et al. 1983).
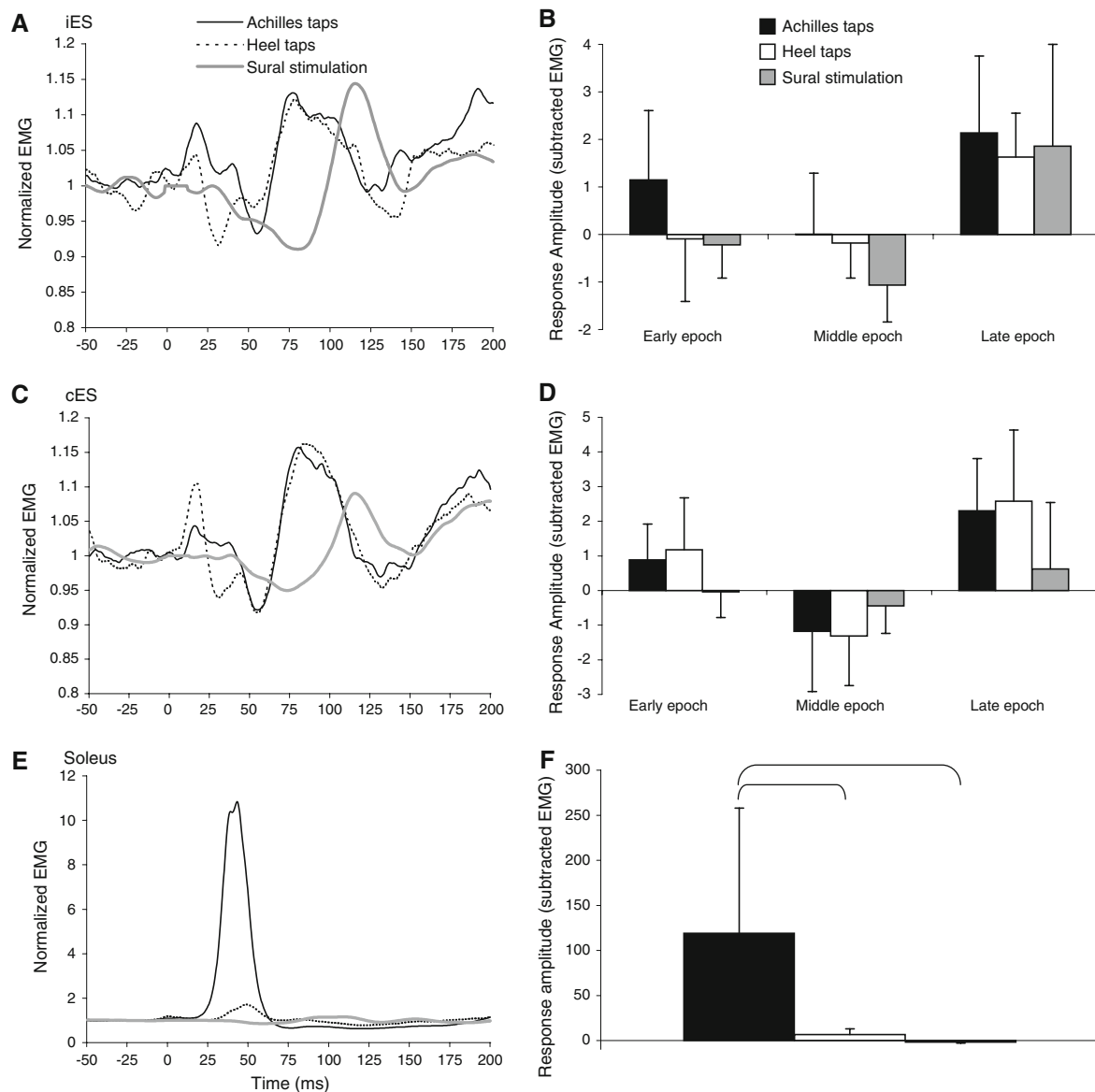
Fig. 5 Reflexes evoked by Achilles' tendon taps, heel taps and sural nerve stimulation. Mean data are shown for responses recorded from iES (**a**, **b**), cES (**c**, **d**) and soleus (**e**, **f**). *Brackets* identify responses that are significantly different from each other ($p \leq 0.05$)

Responses in ES evoked by the tendon and heel taps were not significantly different, despite the heel taps evoking a substantially smaller soleus stretch reflex consistent with the activation of fewer TS muscle spindles than the tendon taps. Thus, the responses in ES do not appear to be dominated by the robust input from TS muscle spindles evoked by the tendon tap as we had initially predicted but rather they may be predominantly cutaneous in origin. This is consistent with the emerging idea that feedback from force sensitive receptors in the skin of the foot may play a more important role in the control of human stance than feedback from ankle proprioceptors (Cnyrim et al. 2009).

Roles for feedback from cutaneous receptors of the foot in balance control have been proposed based on microneu-

rographic recordings from the human tibial nerve (Kennedy and Inglis 2002) or sural nerve (Trulsson 2001) during stimulation of the foot sole. Cutaneous mechanoreceptors in the sole of the foot assist in detecting ground contact (Magnusson et al. 1990) and changes in the distribution of pressure (Kavounoudias et al. 1998). Postural sway increases when cutaneous input from the foot is reduced or eliminated through cooling of the foot (Magnusson et al. 1990) or ischemic block induced by an inflated cuff around the leg (Asai et al. 1992). Similarly, anesthesia of the sole of the foot resulted in significantly different EMG responses to perturbations applied during standing when compared with trials in which the foot was not anesthetised. Mechanoreceptors located along the lateral border of the

foot, the region innervated by the sural nerve and the sites where the tendon and heel taps were applied, have been shown to be important in maintaining upright stance and postural control (Meyer et al. 2004; Trulsson 2001; Vedel and Roll 1982).

Increasing postural instability by having subjects stand with their eyes closed, which has been shown to increase body sway (Fitzpatrick et al. 1994; Nagano et al. 2006) did not alter the expression of the ES reflexes in the present study. It may be that the eyes closed condition did not present enough of a challenge to the postural system to result in a change in reflex expression. This is similar to other studies in which postural perturbations delivered during eyes open and closed conditions did not produce any differences in transmission through stretch reflex and transcortical pathways utilized for balance corrective responses (Carpenter et al. 1999; Keshner et al. 1987).

The ES muscles stabilize the spine and assist in postural corrections during sitting (Forssberg and Hirschfeld 1994; Preuss et al. 2005; Zedka et al. 1998) and standing (Cresswell et al. 1994). Presently, sensory input from one leg evoked ES reflexes bilaterally during sitting and standing. Thus, ongoing discharge of sensory receptors in the legs may contribute through these pathways to the continuous background synaptic drive to ES motoneurons. These heteronymous ES reflexes may also contribute to the generation of postural corrections such as the bilateral ES activation that distributes forces on the pelvis and helps maintain a consistent distribution of the center of mass (Dofferhof and Vink 1985; White and McNair 2002) during rotational perturbations (Carpenter et al. 1999) and walking (Dofferhof and Vink 1985). Although it is presently not known how these reflexes are expressed during walking, the amplitudes of responses in ES were affected by the changes in task, particularly the late responses in cES as there was a significantly larger late cES response during standing compared to sitting. Comparisons between iES and cES responses in both the early and late epochs revealed differences in amplitude between sides that were also task-dependent. Such task-dependent differences in response amplitude may reflect a reweighting of sensory inputs to meet the demands of the task (Cnyrim et al. 2009; Mahboobin et al. 2009; Misiaszek 2006; Schweigart and Mergner 2008). A bilateral, but asymmetrical activation in ES has been demonstrated in other studies during rotational perturbations (Carpenter et al. 1999) and walking (Dofferhof and Vink 1985). Waters and Morris (1972) showed that the cES was significantly more active than the iES at heel strike which would counteract the rotational forces of the pelvis. The ES reflexes presently observed were driven by at least some of the same receptors that would be activated at heel strike.

Summary

These experiments characterize reflexes in the ES muscles of the lower back evoked by the activation of sensory receptors in the lower leg. These heteronymous reflexes were expressed bilaterally and changed in amplitude between sitting and standing. A comparison of reflexes evoked by tendon taps, heel taps and sural nerve stimulation showed that reflex pathways connect cutaneous receptors of the foot and ES motoneurons and suggest that reflex connections from TS muscle spindles may be relatively weak. These reflex pathways between the legs and lower back may play a role in the neural control of posture and balance.

References

Asai H, Fujiwara K, Toyama H, Yamashina T, Tachino K, Nara I (1992) The influence of foot soles cooling on standing postural control analyzed by tracking the center of foot pressure. In: Posture and gait: control mechanisms, vol II. University of Oregon Institute of Neuroscience, Eugene, OR, pp 151–154

Brown P, Rothwell JC, Thompson PS, Britton TC, Day BL, Marsden CD (1991) New observations on the normal auditory startle reflex in man. Brain 114:1891–1902

Burke D, Gandevia SC, McKeon B (1983) The afferent volleys responsible for spinal proprioceptive reflexes in man. J Physiol 339:535–552

Carpenter MG, Allum JH, 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

Cholewicki J, Panjabi MM, Khachatryan A (1997) Stabilizing function of trunk flexor-extensor muscles around a neutral spine posture. Spine 22:2207–2212

Cnyrim C, Mergner T, Maurer C (2009) Potential roles of force cues in human stance control. Exp Brain Res 194:419–433

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

Creath R, Kiemel T, Horak F, Peterka R, Jeka J (2005) A unified view of quiet and perturbed stance: simultaneous co-existing excitable modes. Neurosci Lett 377:75–80

Cresswell AG, Oddsson L, Thorstensson A (1994) The influence of sudden perturbations on trunk muscle activity and intra-abdominal pressure while standing. Exp Brain Res 98:336–341

Deliagina TG, Beloozerova IN, Zelenin PV, Orlovsky GN (2008) Spinal and supraspinal postural networks. Brain Res Rev 57:212–221

Diener HC, Horak FB, Nashner LM (1988) Influence of stimulus parameters on human postural responses. J Neurophysiol 59:1888–1905

Dietz V (2002) Do human bipeds use quadrupedal coordination? Trends Neurosci 25:462–467

Dietz V, Horstmann GA, Berger W (1989) Significance of proprioceptive mechanisms in the regulation of stance. Prog Brain Res 80:419–423

Dietz V, Fouad K, Bastiaanse CM (2001) Neuronal coordination of arm and leg movements during human locomotion. Eur J NeuroSci 14:1906–1914

Dimitrijevic MR, Gregoric MR, Sherwood AM, Spencer WA (1980) Reflex responses of paraspinal muscles to tapping. J Neurol Neurosurg Psychiatry 43:1112–1118

Dofferhof AS, Vink P (1985) The stabilising function of the mm. iliocostales and the mm. multifidi during walking. J Anat 140:329–336

Fitzpatrick RC, Gorman RB, Burke D, Gandevia SC (1992) Postural proprioceptive reflexes in standing human subjects: bandwidth of response and transmission characteristics. J Physiol 458:69–83

Fitzpatrick R, Rogers DK, McCloskey DI (1994) Stable human standing with lower-limb muscle afferents providing the only sensory input. J Physiol 480:395–403

Floyd WF, Silver PH (1955) The function of the erectores spinae muscles in certain movements and postures in man. J Physiol 129:184–203

Forssberg H, Hirschfeld H (1994) Postural adjustments in sitting humans following external perturbations: muscle activity and kinematics. Exp Brain Res 97:515–527

Haridas C, Zehr EP (2003) Coordinated interlimb compensatory responses to electrical stimulation of cutaneous nerves in the hand and foot during walking. J Neurophysiol 90:2850–2861

Horak FB, Diener HC, Nashner LM (1989) Influence of central set on human postural responses. J Neurophysiol 62:841–853

Jacobs JV, Horak FB (2007) Cortical control of postural responses. J Neural Trans 114:1339–1348

Kavounoudias A, Roll R, Roll JP (1998) The plantar sole is a 'dynamometric map' for human balance control. Neuroreport 9:3247–3252

Kavounoudias A, Roll R, Roll JP (2001) Foot sole and ankle muscle inputs contribute jointly to human erect posture regulation. J Physiol 532.3:869–878

Kearney RE, Chan CW (1979) Reflex response of human arm muscles to cutaneous stimulation of the foot. Brain Res 170:214–217

Kearney RE, Chan CW (1981) Interlimb reflexes evoked in human arm muscles by ankle displacement. Electroencephalogr Clin Neurophysiol 52:65–71

Kennedy PM, Inglis JT (2002) Distribution and behaviour of glabrous cutaneous receptors in the human foot sole. J Physiol 538:995–1002

Keshner EA, Allum JH, Pfaltz CR (1987) Postural coactivation and adaptation in the sway stabilizing responses of normals and patients with bilateral vestibular deficit. Exp Brain Res 69:77–92

Magnusson M, Enbom H, Johansson R, Pyykkö I (1990) Significance of pressor input from the human feet in anterior-posterior postural control. The effect of hypothermia on vibration-induced bodysway. Acta Otolaryngol 110:182–188

Mahboobin A, Loughlin P, Atkeson C, Redfern M (2009) A mechanism for sensory re-weighting in postural control. Med Biol Eng Comput (in press). doi:10.1007/s11517-009-0477-5

Meinck HM, Piesiur-Strehlow B (1981) Reflexes evoked in leg muscles from arm afferents: a propriospinal pathway in man? Exp Brain Res 43:78–86

Meyer PF, Oddsson LI, De Luca CJ (2004) Reduced plantar sensitivity alters postural responses to lateral perturbations of balance. Exp Brain Res 157:526–536

Misiaszek JE (2006) Neural control of walking balance: if falling then react else continue. Exerc Sport Sci Rev 34:128–134

Nagano A, Yoshioka S, Hay DC, Himeno R, Fukashiro S (2006) Influence of vision and static stretch of the calf muscles on postural sway during quiet standing. Hum Mov Sci 25:422–434

Nashner LM (1976) Adapting reflexes controlling the human posture. Exp Brain Res 26:59–72

Nielsen J, Petersen N, Fedirchuk B (1997) Evidence suggesting a transcortical pathway from cutaneous foot afferents to tibialis anterior motoneurones in man. J Physiol 501:473–484

O'Sullivan PB, Grahamslaw KM, Kendell M, Lapenskie SC, Möller NE, Richards KV (2002) The effect of different standing and sitting postures on trunk muscle activity in a pain-free population. Spine 27:1238–1244

Paquet N, Tam F, Hui-Chan CW (1996) Functional modulation of the human flexion and crossed extension reflexes by body position. Neurosci Lett 209:215–217

Preuss RA, Grenier SG, McGill SM (2005) Postural control of the lumbar spine in unstable sitting. Arch Phys Med Rehabil 86:2309–2315

Schweigart G, Mergner T (2008) Human stance control beyond steady state response and inverted pendulum simplification. Exp Brain Res 185:635–653

Trulsson M (2001) Mechanoreceptive afferents in the human sural nerve. Exp Brain Res 137:111–116

Vedel JP, Roll JP (1982) Response to pressure and vibration of slowly adapting cutaneous mechanoreceptors in the human foot. Neurosci Lett 34:289–294

Waters RL, Morris JM (1972) Electrical activity of muscles of the trunk during walking. J Anat 111:191–199

White SG, McNair PJ (2002) Abdominal and erector spinae muscle activity during gait: the use of cluster analysis to identify patterns of activity. Clin Biomech 17:177–184

Zedka M, Prochazka A (1997) Phasic activity in the human erector spinae during repetitive hand movements. J Physiol 504:727–734

Zedka M, Kumar S, Narayan Y (1998) Electromyographic response of the trunk muscles to postural perturbation in sitting subjects. J Electromyogr Kinesiol 8:3–10

Zedka M, Prochazka A, Knight B, Gillard D, Gauthier M (1999) Voluntary and reflex control of human back muscles during induced pain. J Physiol 520:591–604

Zehr EP, Duysens J (2004) Regulation of arm and leg movement during human locomotion. Neuroscientist 10:347–361

Zehr EP, Collins DF, Chua R (2001) Human interlimb reflexes evoked by electrical stimulation of cutaneous nerves innervating the hand and foot. Exp Brain Res 140:495–504