Context-dependent modulation of interlimb cutaneous reflexes in arm muscles as a function of stability threat during walking

Authors: Carlos Haridas\textsuperscript{1}, E. Paul Zehr\textsuperscript{2,3} and John E. Misiaszek\textsuperscript{1,4}

Affiliations: \textsuperscript{1}Centre for Neuroscience, University of Alberta, Edmonton, AB, Canada
\textsuperscript{2}Rehabilitation Neuroscience Laboratory, University of Victoria, Victoria, BC, Canada
\textsuperscript{3}International Collaboration on Repair Discoveries (ICORD), Vancouver, BC, Canada
\textsuperscript{4}Department of Occupational Therapy, Sensory-Motor Research Laboratory, 2-64 Corbett Hall, University of Alberta, Edmonton, AB, Canada T6G 2G4

Telephone: 780.492.6042
Facsimile: 780.492.4628
E-mail: john.misiaszek@ualberta.ca

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Abstract

Cutaneous reflexes evoked in the muscles of the arms with electrical stimulation of nerves of the foot ("interlimb reflexes") are observed during walking. These reflexes have been suggested to coordinate the actions of the legs and arms when walking is disturbed. Recently, we showed that cutaneous reflexes evoked in the leg muscles after stimulation at the foot are modulated according to the level of postural threat during walking. We hypothesized that the amplitude of interlimb cutaneous reflexes would similarly be modulated when subjects walk in unstable environments. Subjects walked on a treadmill under four walking conditions: 1) normal; 2) normal with unpredictable anterior-posterior (AP) perturbations; 3) arms crossed; 4) arms crossed with unpredictable AP perturbations. Interlimb reflexes evoked from electrical stimulation of the right superficial peroneal or sural nerves were recorded bilaterally, at four points of the step cycle. These reflexes were compared between conditions in which the arms were moving in a similar manner: i) normal vs. AP walking, and ii) arms crossed vs. arms crossed with AP perturbations. Differences in reflex amplitudes between arms crossed conditions were observed in most upper limb muscles when subjects were perturbed while walking compared to undisturbed walking. This effect was less apparent when the arms were swinging freely. The results indicate that the strength of interlimb connections is influenced by the level of postural threat (i.e. the context of the behaviour), thereby suggesting that these reflexes serve a functional link between the legs and arms during locomotion.
**Introduction**

Electrical stimulation of cutaneous nerves in the foot during human locomotion has been shown to elicit reflexes which are modulated in amplitude depending on the task being performed (Duysens et al. 1993; Komiyama et al. 2000) as well as the phase of the step cycle in which the reflex is elicited (Duysens et al. 1990, 1992; Van Wezel et al. 1997; Yang and Stein 1990; Zehr et al. 1997). It has been suggested that cutaneous reflex modulation is important in assisting the maintenance of balance during walking (Zehr and Stein 1999). For instance, electrical stimulation of the superficial peroneal (SP; innervates the dorsum of the foot) nerve during the swing portion of the step cycle has been shown to elicit reflex activity in the leg consistent with a “stumble corrective response”, which would allow smooth forward progression of locomotion to continue (Van Wezel et al. 1997; Zehr et al. 1997). Recently, we showed that cutaneous reflexes in the leg are modulated in a task-dependent manner according to the level of postural threat. We discussed this modulation in terms of “context-dependency”, in which the stability context plays a strong role in reflex modulation and also relates to the functional role of cutaneous reflexes (Haridas et al. 2005b). These results suggest cutaneous reflexes in the legs may assist in maintaining stability during walking.

A perturbation during walking may result in a corrective response that might include the use of the upper limbs to regain stability. For example, Marigold et al. (2002) demonstrated that an arm elevation strategy was typically incorporated in response to a slip during walking. Responses in the muscles of the arms have been shown to occur at latencies comparable to those in the legs following perturbations applied at the foot (Dietz et al. 2001; Marigold et al. 2003) or torso (Miaszek 2003) during walking. It is
argued that the responses in the arms contribute in whole-body responses to perturbations encountered during locomotion.

The neural mechanisms involved in coordinating these whole-body corrective responses are not well understood. One possible mechanism is via intersegmental reflex circuits, such as interlimb cutaneous reflexes. Interlimb cutaneous reflexes in the muscles of the upper limbs (evoked with stimulation at the foot) have been found after electrical stimulation of cutaneous nerves in the foot during locomotion. Dietz et al. (2001) reported responses in the muscles of the upper limbs to electrical stimulation of the distal tibial cutaneous nerve, which were more prominent during walking compared to static tasks such as sitting and standing. Haridas and Zehr (2003) found that interlimb cutaneous reflexes in the muscles of the upper limbs arising from SP nerve stimulation at the foot displayed significant phase-modulation and sign-reversal during treadmill locomotion. These results suggest the existence of functional and coordinated reflex pathways from the cutaneous nerves of the foot to the muscles of the arms during locomotion.

The task and phase specific adaptations in the amplitude of these reflexes suggest they may assist in regulating arm responses as part of a whole-body corrective response. If so, then one expectation would be that these reflexes will be adapted to meet the specific postural demands of the task related to stability (e.g. “context-dependency”), similar to what we reported for cutaneous reflexes in the leg (Haridas et al. 2005b). Consequently, we hypothesize that interlimb cutaneous reflexes, elicited from stimulation of cutaneous nerves in the foot to muscles of the arm, will be facilitated when subjects
walk in an environment with an increased postural threat. Portions of these results have been reported in abstract form (Haridas et al. 2005a).
Materials and Methods

Subjects and protocol

Twelve subjects between the ages of 20 and 35, with no history of neurologic, orthopedic or metabolic impairment participated with informed, written consent in a protocol approved by the Human Research Ethics Board (Health Research) at the University of Alberta. In this study we examined cutaneous reflexes evoked by electrical stimulation of a) the superficial peroneal (SP) nerve or b) the sural nerve. Subjects visited the lab on two different occasions, once for each nerve stimulation protocol. The order of presentation of nerve stimulation was randomized across subjects.

Subjects were asked to walk on a motorized treadmill at a self-selected speed (typically between 0.8 – 1.2 m/s). Cutaneous reflexes were elicited during 4 walking conditions: 1) with the arms free; 2) with the arms free, but while receiving unpredictable anterior-posterior perturbations applied at the waist (AP); 3) with the arms crossed across the chest (arms crossed); 4) with the arms crossed and receiving unpredictable anterior-posterior perturbations (arms crossed + AP). The order of presentation of the walking conditions was randomized across subjects. The purpose of the anterior-posterior perturbations during walking was to create an environment in which stability was unpredictably challenged. Therefore, cutaneous reflexes were not elicited during such perturbations, but rather during periods of steady walking between the perturbations. Subjects were instructed that they were free to grab for safety rails located in front and to the sides (~ 45 cm from lateral edge of the arms, ~75 cm in front of the subject) if they felt the need to do so to prevent falling. The purpose for having the arms crossed was to increase the threat of falling, by constraining the arms from assisting in balance recovery.
Subjects reported feeling less stable when walking with their arms crossed or during conditions with anterior-posterior perturbations. We interpreted this to indicate that these manipulations achieved the objective of increasing the level of postural threat during walking. Subjects were informed before performing each walking condition as to whether perturbations would be elicited.

A detailed description of the device used for delivering the perturbations can be found elsewhere (Misiaszek and Krauss 2005). In brief, the perturbations were delivered by cables attached to a belt worn by the subject around the pelvis. From the belt, these cables ran in front and behind the subject to a drum to which a handle is attached. Pushing and pulling this handle caused anterior and posterior perturbations, respectively. A strain gauge placed on the lever arm of the handle was used to indicate when perturbations were applied. The magnitude of the perturbations was ~20% of the subjects’ body weight. However, as the perturbations were used only to create an unpredictable environment, the magnitude was not specifically controlled. Perturbations were delivered randomly throughout the step cycle, with a frequency of approximately 3-5 per minute. This resulted in approximately 50 perturbations delivered for each perturbation walking trial that lasted between 10-15 min. The direction of perturbation (anterior vs. posterior) was also randomized.

Nerve stimulation

Cutaneous reflexes were evoked by trains (5 × 1.0 ms pulses @ 300 Hz) of isolated constant current stimulation (Grass S88 stimulator with SIU5 and CCU1 isolation and constant current units, AstroMed Inc.) applied to the SP or sural nerve of
the right (ipsilateral; ipsi) leg using flexible 1 cm disposable surface electrodes (A10043-P, Vermed). Electrodes for the SP nerve were placed in a bipolar configuration on the anterior surface of the leg, near the crease of the ankle joint. The electrodes for sural nerve stimulation were placed on the lateral surface of the ankle, between the lateral malleolus and the Achilles tendon. The intensity of stimulation was set as a multiple of radiating threshold (RT) for each subject, approximately $3 \times RT$ (actual means ($\pm$SEM): $2.8 \times RT \pm 0.12$ for SP, $2.9 \times RT \pm 0.07$ for sural), a value at which the stimulus is strong enough to evoke a reflex, yet is not perceived as painful by the subject. Radiating threshold was estimated as the lowest stimulus intensity at which the subject first perceived a clear radiating paresthesia into the innervation area of the nerve (SP: dorsum of foot; sural: lateral margin of the foot and plantar surface of the heel). This threshold value was checked between each walking trial to ensure that the stimulus properties remained similar throughout the experiment.

Stimuli were delivered such that no more than one stimulus was delivered within a single step cycle. Typically, stimuli were separated by approximately 2-6 s. Electrical stimuli were delivered at four points throughout the step cycle for SP nerve (contralateral (contra) toe-off, ipsi midstance, ipsi toe-off, and ipsi midswing) and sural nerve (ipsi heelstrike, ipsi midstance, ipsi toe-off, and ipsi midswing). These four points of the step cycle were chosen for the SP and sural nerve stimulation paradigms as they represent critical points in the phase-dependent pattern of modulation observed during walking (Haridas and Zehr 2003; Zehr et al. 1997, 1998). The timing of stimulus delivery was controlled manually by the experimenter to occur near the target points of the step cycle. The experimenter was provided real-time feedback of the accuracy of the stimulus timing
within the step cycle by viewing an oscilloscope display of the stimulus pulse along with the foot contact signals. Approximately 40 stimuli were delivered at each point in the cycle and then subsequently screened post hoc to select the stimuli occurring within the appropriate time points. This technique typically resulted in 15-30 stimuli being accepted for further analysis for each point in the step cycle for each walking condition (see below for the method used to screen the timing of the stimuli).

**Recording and Data Acquisition**

After shaving, abrad ing, and cleaning the skin with alcohol, disposable surface electrodes (A10012-60S, Vermed) were placed over the anterior deltoid (AD), posterior deltoid (PD), biceps brachii (BB), triceps brachii (TB), flexor carpi radialis (FCR), and extensor carpi radialis (ECR) of the arm ipsilateral (i) to the stimulation, as well as AD and PD of the contralateral (c) arm. Ground electrodes were placed over electrically neutral tissue. Signals were pre-amplified and bandpass filtered at 30 Hz - 3 kHz (P511 Grass Instruments, AstroMed Inc.). Kinematic data were collected using electrogoniometers (Biometrics, Inc.) placed across the ipsilateral ankle and elbow, secured with two-sided tape. Foot contact information was obtained from custom-made force sensitive resistors placed in the soles of the subject’s shoes. EMG, kinematic, foot force sensor, stimulation, and perturbation force data were collected at a sampling rate of 1000 Hz and saved to disk using a custom-written LabView v.5 data acquisition routine and a National Instruments data acquisition card (PCI-MIO-16E-4, National Instruments, Austin, Tex., USA). Post-hoc, the EMG signals were digitally full-wave rectified and
then low-pass filtered at 50 Hz (4th order dual-pass Butterworth filter), while the kinematic signals were low-pass filtered at 50 Hz.

**Data Analysis**

Data analysis for each subject began with the selection of 30 control step cycles for each walking trial (custom-written program, LabView v.5, National Instruments, Austin, TX, USA). Control steps were those for which no stimuli were applied and no perturbations occurred. Steps were also not included if a perturbation occurred within the preceding two steps. For each of the control steps, an 1800 ms data trace was captured starting at heelstrike of the ipsilateral foot, and averaged to produce an average control trace. Subsequently, reflex trials were selected and grouped into bins depending on the time at which the stimulus occurred within the step cycle. The four bins for each nerve stimulation protocol were defined as a time window spanning 10% of the average control step cycle duration, centered at that point in the step cycle (for example, if ipsilateral toe-off for a subject occurred at 56% of the step cycle, then stimuli applied between 51% and 61% of the step cycle were included). Ipsilateral heelstrike represented 0% of the step cycle. Once the stimulus trials were sorted into bins, the data traces were aligned to stimulus delivery, and averaged together. The average non-stimulated EMG trace was subtracted from the stimulated average trace, yielding a subtracted evoked EMG trace for each subject (Figure 1).

Cutaneous reflexes were calculated from the subtracted traces for each muscle. A reflex response was identified if the subtracted trace exceeded, for 5 ms continuously, the 95% confidence interval around the mean for the 50 ms preceding the stimulus artifact.
The middle latency component of the reflex was calculated for the time window of 80-120 ms post-stimulus. Cutaneous reflex amplitudes for each subject were normalized to the maximum EMG amplitude occurring during the step cycle for each muscle and expressed as a percentage. Ongoing background EMG activity and the ankle and elbow angles were also calculated for each of the walking conditions. These were calculated as the average full-wave rectified EMG amplitude or the absolute joint angle occurring during each of the four bins of interest in the step cycle (see above).

Statistics

Since the arms are moving rhythmically in some conditions and restricted in other conditions, the pattern of muscle activation varied greatly between conditions. As a result, comparisons were made between tasks in which the arms were either allowed to swing in a natural manner (normal vs. AP), or were crossed in front of the subject (arms crossed vs. arms crossed + AP). This allowed for comparisons between tasks in which the background EMG of the arm muscles was similar (Figure 2). Statistical analysis was performed using the averaged normalized values for each subject, from each part of the step cycle. For each nerve stimulation paradigm and for each muscle studied, a two-way repeated measures analysis of variance (condition [2] x bin [4]) was used to isolate the sources of variance. Using the experimental error calculated by the ANOVA, planned comparisons were then performed for the reflex amplitudes between the two conditions of comparison at each bin. Similar analysis was performed on the background EMG as well as ankle and elbow joint angles. One-way repeated measures ANOVAs were also
performed on step cycle durations for the group average data. Statistical significance was set at $p < 0.05$. 
Results

In this study, we were interested in understanding the context-dependent modulation of interlimb reflexes. Interlimb cutaneous reflexes are usually not expressed if the muscle is not active, in particular, inhibitory reflexes cannot be observed without some level of activity. In our analysis, we only included data from a muscle for each subject if there was a clear response to the stimulation (see Materials and Methods) in at least one condition for at least one point in the step cycle. This led to data from a variable number of subjects being included in the statistical analysis for each muscle. In the figures showing the group averaged data the numbers of subjects included in the analysis is detailed in the figure legend. It should also be noted that any of the task-related differences reported below for the group averaged data were observed in all of the individual subjects included in the analysis.

Background EMG and kinematics

While walking on the motorized treadmill, subjects were asked either to swing their arms in a normal manner (normal and AP conditions), or to cross the arms in front (arms crossed and arms crossed + AP conditions). Shown in Figure 2 is single-subject average background EMG data during the step cycle for the normal (arms swinging; left column) and arms crossed (right column) walking conditions. The arms crossed conditions generally displayed relatively tonic EMG activity in some muscles, whereas in the arms free conditions some muscles displayed phasic modulation. Therefore, we compared the background EMG for each muscle between conditions in which the arms were being similarly used. Consequently, comparisons were only made between the two conditions for which the arms were free (normal versus AP conditions), or between the
two conditions for which the arms were crossed (arms crossed versus arms crossed + AP conditions).

There was no main effect of walking condition \((p > 0.05)\) on ipsilateral ankle and elbow angles between tasks of similar arm movement across all subjects. One-way repeated measures ANOVAs revealed no significant differences \((p > 0.05)\) in step cycle durations between walking conditions.

**Arms swinging rhythmically**

When the arms were moving rhythmically (similar to normal walking), middle latency interlimb cutaneous reflex amplitude values did not show many significant differences between the normal and AP walking conditions. A similar pattern of modulation was observed for each walking condition across the step cycle. Shown in Figures 3 and 4 are the average middle latency interlimb cutaneous reflex amplitude values (and corresponding average background EMG values) for muscles in which significant differences between the normal and AP walking conditions were found during the SP and sural nerve stimulation protocols respectively. The general trend observed was that the reflex amplitude during the AP walking condition was lower as compared to normal walking. A good example of this is seen in iECR with SP nerve stimulation (Figure 3). The only significant difference observed between the two walking conditions in this muscle was observed at ipsi toe-off, where the reflex amplitude was lower during the AP condition compared to the normal walking condition. In contrast, the background EMG activity for iECR was found to be significantly higher at ipsi midswing during the AP walking condition.
With the sural nerve stimulation paradigm, only three out of eight muscles recorded displayed significant differences in reflex amplitude values between walking conditions (Figure 4). Similar to SP nerve stimulation, the middle latency interlimb cutaneous reflex amplitude with sural nerve stimulation was significantly lower during the AP condition as compared to the normal walking condition in all three muscles, with iFCR and iTB displaying these differences at ipsi heelstrike, and at ipsi toe-off for iECR. The corresponding background EMG activity between the normal and AP walking conditions were comparable, with the only significant difference in background EMG activity for all these muscles across the step cycle was observed in iTB at ipsi midstance, where the EMG activity was significantly lower during the AP walking condition compared to the normal condition.

Arms crossed

In contrast to the walking conditions in which the arms were moving rhythmically, there were more significant differences observed between walking conditions in which the arms were restricted from moving (arms crossed). The overall trend observed was higher middle latency interlimb cutaneous reflex amplitude values for the arms crossed + AP walking condition, the more unstable of the two walking conditions in which the arms were crossed. Figures 5 and 6 shows muscles that displayed significant differences in reflex amplitude values between the two arms crossed walking conditions with SP and sural nerve stimulation respectively. The average background EMG values are also displayed. During the SP nerve stimulation paradigm, significantly higher middle latency reflex amplitude values for the arms crossed + AP walking condition were observed in iAD at ipsi toe-off, iECR and cPD at contra toe-off, and iFCR
at ipsi midswing (Figure 5). These differences in reflex amplitude were observed despite background EMG levels that were similar between the two conditions. The only significant difference in background EMG activity was observed for iFCR, with the EMG during the arms crossed + AP condition being higher at ipsi toe-off.

Similarly, the majority of muscles recorded displayed significant differences in reflex amplitude values between the two walking conditions during the sural nerve stimulation protocol (Figure 6). Significant differences were observed at ipsi midstance for iAD and iTB, and at ipsi toe-off for iFCR and iECR. Ipsilateral PD showed significant differences at two points of the step cycle, ipsi heelstrike and ipsi midstance. Despite these differences in reflex amplitudes, the EMG activity between the two arms crossed walking conditions was similar during sural nerve stimulation. The exception to this was observed in iECR, where significant differences in background EMG were seen at all points of interest in the step cycle. Significant differences were also observed at ipsi midstance for iAD, and iPD at ipsi heelstrike and ipsi toe-off.

In addition, a reversal in reflex sign was observed between walking conditions with both nerve stimulation paradigms in the muscles of the wrist. With SP nerve stimulation, reflex reversal was observed in iFCR at contra toe-off and ipsi midswing, and in iECR at contra toe-off (Figure 5). At each of these occurrences, inhibitory middle latency reflex amplitude values were observed during the arms crossed condition, in contrast to the facilitatory reflexes for the arms crossed + AP walking condition. Reflex reversal was also observed during the sural nerve stimulation paradigm, in which iECR displayed a facilitatory middle latency reflex amplitude value at ipsi heelstrike during the arms crossed walking condition, which became inhibitory during the arms crossed + AP
condition (Figure 6). Of the four occurrences of reflex reversals observed between tasks for both nerve stimulation paradigms, two were found to be significantly different (SP nerve: iFCR at ipsi midswing; iECR at contra toe-off). These reflex reversals in the muscles of the wrist were not observed in walking conditions when the arms were not restricted. For these walking conditions (normal, AP), interlimb cutaneous reflexes evoked with SP and sural nerve stimulation were always excitatory.
Discussion

The arms have been shown to contribute in whole-body corrective responses to perturbations encountered during walking. Interlimb cutaneous reflexes could assist in coordinating these corrective responses, as they have been found in the arms with cutaneous nerve stimulation at the foot (Dietz et al. 2001; Haridas and Zehr 2003). If so, these reflexes should be regulated in a context-dependent manner, as a function of the level of threat to stability, as we observed with cutaneous reflexes (Haridas et al. 2005b). This study investigated the amplitude of interlimb cutaneous reflexes in the arms evoked from electrical stimulation of the SP and sural nerves in the foot during walking while varying the degree of stability. The main observations were i) that varying the level of stability during walking influenced the amplitude of interlimb cutaneous reflexes in the upper limbs, and ii) the differences observed between walking conditions were dependent upon the nerve being stimulated and the demands of the task.

Mechanisms of adaptation

To our knowledge, this study is the first to describe the modulation of interlimb cutaneous reflex amplitude in relation to walking in an environment in which postural stability is challenged. That is, in which the general constraints and requirements of the task (walking) are unchanged, but the context within which the task is performed is altered. Recent work has described the influence of walking in such an environment on cutaneous reflexes in the legs (Haridas et al. 2005b). In the present study, the general finding was interlimb cutaneous reflexes evoked from the foot were facilitated when postural threat was greatest with the arms crossed. In contrast, when the arms were
swinging freely, these reflexes were generally suppressed when postural threat was greatest. While walking with the arms crossed, the amplitude of interlimb cutaneous reflexes evoked with both SP and sural nerve stimulation were significantly greater when perturbations were also delivered. This finding was not observed in all muscles recorded, but rather isolated in muscles of the shoulder and wrist. When the arms were allowed to swing freely, the interlimb cutaneous reflexes observed in the muscles of the arms were relatively similar regardless of whether perturbations were delivered. This difference in the influence of postural threat on these reflexes in relation to the task of the arms (free vs. crossed) suggests that similar to previous findings with cutaneous reflexes (Haridas et al. 2005b), specific interlimb cutaneous reflex pathways are regulated appropriate to the task requirements and context, rather than some generalized reflex adaptation.

Differences in reflex amplitude between walking conditions could be due to differences in the ongoing EMG activity, which is representative of changes in motoneuronal pool excitability. The significant differences in interlimb cutaneous reflex amplitudes between tasks in which the arms were crossed were generally not associated with differences in the level of ongoing EMG activity. There were only three occurrences in which a significant difference between the two walking conditions in both background EMG and reflex amplitude value were observed. For one of these occurrences (Figure 6: sural nerve; iAD at ipsi midstance), the reflex was facilitated during the arms crossed + AP walking condition, despite significantly lower background EMG. For all other changes in interlimb cutaneous reflex amplitude values noted, the background EMG was similar between conditions. This also holds true for the occurrences of reflex reversals noted when the arms were crossed. For example with SP nerve stimulation, reflex
reversals in the muscles of the wrist were observed at points in the step cycle where the corresponding background EMG activity was similar between walking conditions (Figure 5). Thus, the significantly higher interlimb cutaneous reflex amplitudes observed during walking conditions with the greatest postural threat are not simply due to an increase in ongoing muscle activity.

Reversal of cutaneous reflexes has previously been shown during locomotion in the cat (Duysens, 1977; Forssberg et al. 1975) and human (Duysens et al. 1990; Van Wezel et al. 1997; Yang and Stein 1990). In these studies, there was a reversal in the sign of reflexes in the legs which was dependent on the phase of the step cycle. Cutaneous reflexes in the legs have also been shown to undergo reflex reversals between different tasks. Komiyama et al. (2000) reported that during standing, inhibitory cutaneous reflexes were predominant in contrast to mainly facilitatory reflexes observed during walking. To our knowledge, this is the first study to report reversal of interlimb cutaneous reflexes that are dependent upon the level of postural threat (i.e. context-dependency) during walking. Phase-dependent cutaneous reflex reversals occurring in the legs during cat locomotion has been attributed to parallel inhibitory and excitatory pathways to motoneurons (Andersson et al. 1978; Duysens 1977). Similarly, DeSerres et al. (1995) suggested the cutaneous reflex reversal observed in tibialis anterior during human locomotion might be due to a shift in the weighting of parallel excitatory and inhibitory pathways from cutaneous afferents to the motor units of the muscle. A comparable mechanism is suggested for the context-dependent reflex reversal noted in the present study.
The results of the present study suggest specific regulation of interlimb cutaneous reflex pathways in a task-dependent manner as opposed to a generalized change in reflex excitability. Cutaneous reflexes in the muscles of the arms have been shown during rhythmic movements such as arm cycling (Zehr and Kido 2001) and human walking (Zehr and Haridas 2003). Zehr et al. (2004) suggested that these reflexes found in the muscles of the upper extremities are under the control of a central pattern generator (CPG). However, the similar pattern of phase-dependent interlimb cutaneous reflex modulation between walking conditions suggests it is unlikely that the differences in interlimb cutaneous reflex amplitude values observed between walking conditions are due to differential CPG control of reflex pathways. The specific regulation of interlimb cutaneous reflex pathways could be mediated by descending sources such as the corticospinal tract, as cutaneous reflexes in the muscles of the leg during walking have been shown to be facilitated with cortical stimulation (Pijnappels et al. 1998). The transmission of interlimb cutaneous reflexes may partially involve propriospinal projections connecting the upper and lower limbs (Zehr et al. 2001). In addition, the latency range (80 – 120 ms) in which these reflexes were observed allows for a supraspinal transmission of these responses (Christensen et al. 1999; Nielsen et al. 1997). Therefore, it is likely that supraspinal effects contribute to the task-related modulation of interlimb cutaneous reflexes observed in this study.

In the present study, interlimb cutaneous reflexes were elicited by delivering electrical stimulation to nerves in the foot to subjects while they walked under varying levels of postural threat. During the sural nerve stimulation protocol, more significant differences in reflex amplitude between tasks in which the arms were allowed to swing
freely were observed as compared to SP nerve stimulation. This observation may serve as an example of nerve-specificity, which has been reported previously (Komiyama et al. 2000; Van Wezel et al. 1997; Zehr et al. 1997). The suggested nerve-specificity reported in this study may be explained by the innervation area of the nerves stimulated. The sural nerve innervation area includes a portion of the plantar surface of the heel. Sensory information from this region of the foot may contribute to regulation of foot placement (Kostov et al. 1999), which would be important when walking in an unstable environment and therefore be regulated in a context-dependent manner. In contrast, the innervation area of the SP nerve provides sensory information from the dorsum of the foot, which may not be of functional relevance in the current experimental context. It may be that more context-related perturbations (i.e. at the dorsum of the foot) could affect reflexes elicited with SP nerve stimulation to a greater extent than observed in the present study.

*Evidence of a functional role for interlimb cutaneous reflexes?*

In contrast to the walking conditions in which the arms were swinging freely, there were markedly more significant differences between the arms crossed and arms crossed + AP walking conditions. This was observed for both SP and sural nerve stimulation. One possibility for the difference noted may be the different number of muscles that are active for each arm position. As shown in Figure 2, more muscles are active when the arms are crossed, in contrast to when the arms are allowed to swing rhythmically. The greater number of muscles in the arms being activated would increase the probability of interlimb cutaneous reflexes being elicited, as cutaneous reflexes
generally require activity in the muscles to be expressed. Consequently, there is a greater likelihood of observing task-dependent differences in reflex amplitudes.

Interlimb cutaneous reflex amplitudes were generally facilitated for the arms crossed + AP walking condition as compared to the arms crossed condition (Figure 5 and 6), and these differences were observed primarily in the muscles of the shoulder girdle and wrist. In contrast, there was a general suppression of interlimb cutaneous reflexes while the arms were swinging rhythmically, where during the AP walking condition these reflexes were suppressed compared to normal walking (Figure 3 and 4), observed primarily in the muscles of the wrist. This trend in reflex amplitude due to the task of the arms may be indicative of a functional role for the interlimb cutaneous reflexes observed. When the arms are allowed to swing rhythmically, they are available to contribute towards any needed corrective responses in response to a perturbation. Furthermore, since the arms are allowed to move freely, there are multiple strategies in which they may be used to participate in a corrective response. The diversity of options available to execute a corrective response (e.g. reaching for safety rails around the treadmill) may lead to increased variability, which may contribute to the lack of significant differences observed between the normal and AP walking conditions. This may be particularly true for the muscles of the shoulder girdle, which may be more relevant for executing a gross movement of the arm related to regaining stability. This variability with the arms swinging freely is similar to findings by Misiaszek (2003), who noted inconsistent responses in the muscles of the arms between subjects in response to perturbations received during walking.
In contrast, having the arms crossed in front of the body limits their contribution to assisting in any corrective responses. To use the crossed arms for maintaining stability during walking, all subjects would have to first uncross them regardless of the next course of action. This standardization of arm utilization, at least initially, may account for the more consistent results across subjects and the changes noted. It follows that the higher interlimb cutaneous reflex amplitudes observed bilaterally in the muscles of the arms during the arms crossed + AP condition may serve to assist in a coordinated corrective response, such as to uncross the arms to allow a reaching movement towards the safety rails positioned around the treadmill. The significantly higher reflex value in iTB during sural nerve stimulation could also contribute in an uncrossing and reaching response. In addition, the higher interlimb reflex values in the muscles of the wrist could facilitate in a guided reaching response towards a stable support.
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References


Figure legends

Figure 1: Subtracted EMG traces for iPD after sural nerve stimulation for a single subject following electrical stimuli occurring at ipsilateral heelstrike. Both traces represent walking conditions in which the arms were crossed; arms crossed (thick black line), arms crossed + AP (thick grey line). The vertical dashed line indicates onset of stimulation. Rectangular box indicates the 80-120 msec post-stimulus) time window in which the middle latency reflex was analyzed. Arms crossed: walking with the arms folded across the chest, AP: walking with the arms folded across the chest while being perturbed.

Figure 2: Average EMG for 30 control steps (starting at ipsi heelstrike) taken from a single subject. Left column displays EMG during the normal walking condition, and EMG during the arms crossed condition is shown in the right column. This subject displayed relatively tonic activity of the arm muscles during the arms crossed walking conditions, contrasting the more rhythmic activity observed during the normal walking conditions. EMG is scaled equally between the two walking conditions shown. Horizontal black line at the bottom of each column represents the stance phase of the step cycle.

Figure 3: Group averaged data for the middle latency interlimb cutaneous reflexes arising from SP nerve stimulation between conditions in which the arms
were not restricted for the only muscle in which a significant difference was found. The four points of the step cycle investigated are shown on the abscissa. Average middle latency interlimb cutaneous reflex amplitude values are depicted as black (normal) and grey (AP) bars, with the standard error shown. Values for middle latency reflexes are shown on the left ordinate. Data from 7 subjects contributed to this figure. Average background EMG is represented by the black (normal) and grey (AP) lines, with its values along the right ordinate. Both reflex and background EMG values are normalized to the maximum EMG produced during normal, undisturbed walking. *: significant difference ($p < 0.05$) in middle latency interlimb cutaneous reflexes; ‡: significant difference ($p < 0.05$) in background EMG.

Figure 4: Group averaged data for the middle latency interlimb cutaneous reflexes arising from sural nerve stimulation for muscles in which a significant difference was found between conditions in which the arms were not restricted. The four points of the step cycle investigated are shown on the abscissa. Average middle latency interlimb cutaneous reflex amplitude values are depicted as black (normal) and grey (AP) bars, with the standard error shown. Values for middle latency reflexes are shown on the left ordinate. These data were derived from 12, 11 and 9 subjects, for iTB, iFCR and iECR, respectively. Average background EMG is represented by the black (normal) and grey (AP) lines, with its values along the right ordinate.
ordinate. Both reflex and background EMG values are normalized to the maximum EMG produced during normal, undisturbed walking. *: significant difference ($p < 0.05$) in middle latency interlimb cutaneous reflexes; ‡: significant difference ($p < 0.05$) in background EMG.

Figure 5: Group averaged data for the middle latency interlimb cutaneous reflexes arising from SP nerve stimulation for muscles in which a significant difference was found between conditions involving the arms being crossed. The four points of the step cycle investigated are shown on the abscissa. Average middle latency interlimb cutaneous reflex amplitude values are depicted as black (arms crossed) and grey (arms crossed + AP) bars, with the standard error shown. Values for middle latency reflexes are shown on the left ordinate. These data were derived from 10, 6, 5 and 9 subjects, for iAD, cPD, iFCR and iECR, respectively. Average background EMG is represented by the black (arms crossed) and grey (arms crossed + AP) lines, with its values along the right ordinate. Both reflex and background EMG values are normalized to the maximum EMG produced during the arms crossed walking condition. *: significant difference ($p < 0.05$) in middle latency interlimb cutaneous reflexes; ‡: significant difference ($p < 0.05$) in background EMG.

Figure 6: Group averaged data for the middle latency interlimb cutaneous reflexes arising from sural nerve stimulation for muscles in which a significant difference was found between conditions involving the arms being...
crossed. The four points of the step cycle investigated are shown on the abscissa. Average middle latency interlimb cutaneous reflex amplitude values are depicted as black (arms crossed) and grey (arms crossed + AP) bars, with the standard error shown. Values for middle latency reflexes are shown on the left ordinate. These data were derived from 9, 10, 9, 10 and 8 subjects, for iAD, iPD, iFCR, iECR and iTB, respectively. Average background EMG is represented by the black (arms crossed) and grey (arms crossed + AP) lines, with its values along the right ordinate. Both reflex and background EMG values are normalized to the maximum EMG produced during the arms crossed walking condition. *: significant difference ($p < 0.05$) in middle latency interlimb cutaneous reflexes; ‡: significant difference ($p < 0.05$) in background EMG.
SP n. (N vs. AP)

iECR

REFLEX AMPLITUDE (% OF MAX EMG)

BACKGROUND EMG (% OF MAX EMG)

contra toe-off  |  ipsi midstance  |  ipsi toe-off  |  ipsi midswing

■ Normal  
□ AP

*  †