Adaptation of Cutaneous Stumble Correction When Tripping Is Part of the Locomotor Environment

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Haridas C, Zehr EP, Misiaszek JE. Adaptation of cutaneous stumble correction when tripping is part of the locomotor environment. J Neurophysiol 99: 2789–2797, 2008. First published April 16, 2008; doi:10.1152/jn.00487.2007. We recently showed that cutaneous reflexes evoked by stimulating the superficial peroneal (SP; innervates foot dorsum) nerve are modulated according to the level of postural threat. Context-related modulation was observed mainly in contralateral responses but not in the ipsilateral responses. This lack of effect on ipsilateral cutaneous reflexes might have been caused by the general nature of the whole body perturbation. We therefore hypothesized that context-relevant mechanical perturbations applied to the dorsum of the foot by an instrumented rod at early swing during walking would produce differences in ipsilateral cutaneous reflex amplitudes, consistent with the functional relevance of the SP nerve in cutaneous stumble responses. Subjects walked on a motorized treadmill under four conditions: 1) normal, 2) normal with mechanical perturbations at the foot dorsum, 3) arms crossed, and 4) arms crossed with mechanical perturbations at the foot dorsum. Electrical stimulation of the SP nerve was delivered at five phases of the step cycle, and cutaneous reflexes were compared between all conditions for each phase of the step cycle. Reflex responses were generally found to be modulated in amplitude during walking conditions in which mechanical perturbations were delivered, particularly in ipsilateral tibialis anterior (iTA), which showed a marked reduction in inhibition. The results indicated cutaneous reflexes in iTA and contralateral medial gastrocnemius (cMG) were influenced by the threat of a trip, induced by applying mechanical perturbations to the foot dorsum during walking. This task-related gating of cutaneous reflexes was not generalized to all muscles, thus suggesting a functional role in the maintenance of stability during locomotion.

INTRODUCTION

Spinal reflexes during human locomotion have been widely studied and have been shown to change in amplitude during walking (reviewed in Zehr and Stein 1999). Specifically, reflexes in the muscles of the legs evoked from electrical stimulation of cutaneous nerves in the foot are modulated according to the phase of the step cycle (Duyens et al. 1992; Van Wezel et al. 1997; Yang and Stein 1990; Zehr et al. 1997) as well as the task being performed (Duyens et al. 1993; Komiyama et al. 2000). Both Zehr et al. (1997) and Van Wezel et al. (1997) observed cutaneous reflexes in the muscles of the leg with electrical stimulation of the superficial peroneal (SP; innervating the dorsum of the foot) nerve during walking. During swing phase, SP nerve stimulation elicited a suppression of ankle flexor activity and excitation of the proximal muscles of the leg. These responses in the muscles were associated with a reduction in dorsiflexion and an increase in knee flexion. The authors suggested the evoked response was representative of a “stumbling corrective response” comparable to that first reported in the cat by Forssberg (1979). It was argued that this response served a functional role by withdrawing the foot and thereby allowing the swing limb to continue to progress forward despite encountering an obstacle during locomotion.

It has therefore been suggested that cutaneous reflexes serve to assist in maintaining stability during walking (Zehr and Stein 1999). If so, it follows that these reflexes should be altered when walking in an environment in which stability is challenged. A recent study in our laboratory showed that cutaneous reflexes evoked by electrical stimulation of the SP nerve were modulated to the context of the behavior being performed, primarily in the muscles of the nonstimulated (contralateral) leg (Haridas et al. 2005). Interestingly, cutaneous reflexes in the ipsilateral leg were less affected by varying the level of generalized postural threat induced by whole body perturbations applied at the waist. If the observed responses by Zehr et al. (1997) are indicative of a generalized role for stumble correction during walking as suggested above, the context-dependent modulation that was observed in the muscles of the contralateral leg in Haridas et al. (2005) should have also been observed in the muscles of the ipsilateral leg. Mechanical perturbations were delivered at the torso to create a general unpredictable environment in which stability was challenged (Haridas et al. 2005). These perturbations may have had little relevance for cutaneous feedback arising from the innervation area of the SP nerve, which is argued to be important for correcting swing leg trajectory to avoid stumbling (see Zehr and Stein 1999). It follows that mechanical perturbations delivered to the dorsum of the foot, which would affect ipsilateral swing limb motion during walking, would more closely emulate a perturbation for which the cutaneous feedback arising from SP nerve stimulation is specifically tuned. Therefore we hypothesized that cutaneous reflexes evoked by electrical stimulation of the SP nerve will be modulated when subjects walk in an environment in which...
mechanical perturbations were delivered to the cutaneous field innervated by the SP nerve, thereby creating a threat of a trip. Portions of these results have been reported in abstract form (Haridas et al. 2006).

**M E T H O D S**

**Subjects and protocol**

Ten subjects (6 males and 4 females; age range, 22–33 yr), with no history of neurologic, orthopedic, or metabolic impairment, participated in this study. All procedures conformed to the Declaration of Helsinki for experiments on humans and were approved by the Human Research Ethics Board at the University of Alberta. All subjects provided informed written consent.

Subjects were asked to walk on a motorized treadmill at a self-selected speed (typically between 0.8 and 1.2 m/s). Cutaneous reflexes were elicited during four walking conditions: 1) normal; with the arms free (N); 2) normal while receiving mechanical perturbations to the dorsum of the ipsilateral foot (NP); 3) with the arms crossed across the chest (AC); and 4) with the arms crossed while receiving mechanical perturbations at the dorsum of the foot (ACP). The order of presentation of the walking conditions was randomized across subjects. Cutaneous reflexes were not elicited simultaneously with the mechanical perturbations but rather during periods of steady walking between perturbations. Safety rails were located around the treadmill (approximately 45 cm from the lateral edge of the arms, ~75 cm in front of the subject), and subjects were instructed to grab hold of the rails if they felt a fall was imminent. Subjects were informed before performing each walking condition whether perturbations would be elicited.

Mechanical perturbations were manually applied by tapping a steel rod against the dorsum of the right foot. The dorsum of the foot was selected for the location of the perturbation as it is also the innervation area for the SP nerve. A force sensor was attached to the steel rod to indicate when perturbations were applied. Perturbations were always delivered at early swing, because perturbations to the foot dorsum encountered naturally would likely occur at this point in the step cycle. Furthermore, the suggested functional role of the SP nerve in a “stumbling corrective response” has been noted during the swing phase (Van Wezel et al. 1997; Zehr et al. 1997). Perturbations were delivered in a random manner such that subjects were unable to predict which step cycle would be perturbed. This resulted in approximately four to six mechanical perturbations being delivered per minute. However, because perturbations were always delivered at the same point of the step cycle, subjects were able to anticipate the effect of encountering mechanical perturbations to the dorsum of the foot at early swing as the experiment progressed.

The researcher was positioned adjacent to the treadmill to the right and just behind the subject. Subjects were instructed to look forward during each walking condition. The subjects indicated that they were not able to observe the researcher or the rod delivering the perturbations to the dorsum of the foot. In addition, the researcher continually monitored each subject to ensure they maintained a forward gaze. The magnitude of the disturbance was not specifically controlled, because the purpose was to create an unpredictable and unstable environment. Shown in Fig. 1 is the effect of a single tap to the dorsum of the foot on the ankle and knee kinematics, as well as step cycle data for a single subject. Ankle and knee trajectories were altered as a result of receiving a perturbation compared with the trajectories observed during control steps. In addition, the duration of the step cycle in which a mechanical perturbation was delivered was prolonged compared with the duration of the average control step cycle. Consequently, the mechanical perturbations were sufficient to cause a disturbance in the walking pattern of the subjects, requiring an active correction, and therefore posed a sufficient threat to stability for the purposes of this study.

**Nerve stimulation**

Cutaneous reflexes were evoked by trains (5 × 1.0-ms pulses at 300 Hz) of isolated current stimulation (Grass S88 stimulator with SIU5 and CCU1 isolation and constant current units, AstroMed) applied to the SP nerve of the right (ipsilateral) foot using flexible 1-cm disposable Ag/AgCl surface EMG electrodes. The electrodes were placed in a bipolar configuration on the anterior surface of the foot, near the crease of the ankle joint. The intensity of the electrical stimulation was set at two times the radiant threshold (RT) as described elsewhere (Zehr et al. 1997). Stimuli at this intensity create a clear, radiating, nonnoxious paresthesia in the innervation area of the nerve.

Electrical stimuli were delivered approximately every three to eight step cycles, and no more that one stimulus was delivered within a single step cycle. In addition, stimuli were delivered such that they did not occur at the same time as a mechanical perturbation. The mechanical perturbations occurred infrequently, approximately once every 10–15 steps. The timing of the electrical stimuli relative to the mechanical perturbations was not specifically controlled. Stimuli were delivered at five points in the step cycle: heelstrike, midstance, toe-off, early swing, and midswing of the ipsilateral leg. The timing of stimulus delivery was controlled manually by the experimenter to occur near the targeted 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 20 stimuli were delivered at each of the five points in the step cycle and subsequently screened off-line to select the stimuli that occurred within the appropriate time points. Stimuli were excluded from the
subsequent analysis if they occurred within one step cycle following a mechanical perturbation.

**EMG**

The sites on the skin that were used for recording EMG were first shaved, abraded, and cleaned using alcohol swabs. Disposable 1-cm Ag/AgCl surface electrodes (A10012, Vermed) were placed longitudinally parallel to the predicted path of the muscle fibers in a bipolar configuration over the tibialis anterior (TA), soleus (SOL), medial gastrocnemius (MG), vastus lateralis (VL), and biceps femoris (BF) of the right leg ipsilateral (i) to the stimulation, as well as TA and MG of the left, contralateral (c) leg. Ground electrodes were placed over electrically neutral tissue. Signals were preamplified and band-pass filtered at 30 Hz to 3 kHz (P511 amplifiers, using [1/2] amplitude high and low-pass filters, Grass Instruments, AstroMed).

**Kinematics and step cycle detection**

Kinematic data were collected using electrogoniometers (Biometrics) placed across the ipsilateral ankle and knee, using two-sided tape. Custom-made force sensitive resistors placed in the sole of the subject’s right shoe provided foot contact information (e.g., heelstrike, toe-off).

**Data acquisition and analysis**

EMG, kinematic, foot contact, stimulation, and the onset of perturbation data were collected at a sampling rate of 1,000 Hz and saved to disk using a custom-written LabView v.5 data acquisition program and a National Instruments data acquisition card (PCI-MIO-16E-4, National Instruments). The EMG signals were digitally full-wave rectified and low-pass filtered at 50 Hz (4th-order dual-pass Butterworth filter). Kinematic signals were low-pass filtered at 50 Hz.

Approximately 40 control step cycles for each walking condition were selected for each subject using a custom-written LabView v.8 program. Control steps were those in which no stimulus or perturbation occurred. In addition, control steps were not selected if a perturbation or stimulus was delivered within the preceding two steps or if the data traces contained artifacts. An 1,800-ms data trace was captured for each control step starting at ipsilateral heelstrike, and an average control trace was calculated from all selected control steps.

For each subject, the data traces were preprocessed to ensure that the foot was flat on the floor and aligned to the onset of the stimulation. The ongoing background EMG activity and the angles for the ankle and knee were selected for each control step starting at ipsilateral heelstrike, and an average control trace was calculated from all selected control steps.

After the control steps were selected, the stimuli were grouped into five bins according to their time of occurrence in the step cycle. Each bin, with the exception of one, was defined as a time window of 10% of the average step cycle duration. Every bin was centered at the five points of interest in the step cycle (e.g., if midstance for a subject occurred at 31% of the step cycle, and stimuli applied between 26 and 36% of the step cycle were included). The time window for early swing was defined using a time window of 6%, which was centered at a value midway between toe-off and midswing. Because early swing occurs shortly after toe-off and before midswing, this smaller time window was used to prevent overlapping of the preceding and subsequent bins. Stimulation occurred 0% of the step cycle. This procedure resulted in ~17 stimuli in each bin being used for analysis (mean = 17.51; SD = 3.1). Once the stimuli were sorted into bins, the corresponding data traces were aligned to the stimulus onset and averaged together. The average control EMG trace was subtracted from the average stimulated data trace to produce a subtracted evoked EMG trace, which represented the pure reflex response for each subject. Figure 2 shows the process in which a subtracted EMG trace is produced, with the average control and stimulated data taken from cMG during the ACP walking condition for a single subject. Examples of the subtracted traces produced by this method are depicted in Fig. 4 comparing the AC and ACP conditions.

Cutaneous reflexes were calculated from the subtracted EMG traces for each muscle. The cutaneous reflex amplitude was calculated as the average value of the subtracted trace within the middle latency time period (80–120 ms after stimulus), similar to Haridas et al. (2005). Example data from one subject are shown in Fig. 4. For the data shown in Fig. 4, the middle latency response in ITA was characterized by an initial inhibitory response with a subsequent positive deflection in the AC condition (gray trace). In the presence of the perturbation (ACP), the positive deflection became a clear excitatory response. Not all subjects showed this clear excitatory response during the perturbation conditions. Four of the 10 subjects showed this excitatory response during the perturbation conditions, which was not present in the N or AC conditions. The other six subjects included a positive deflection within the general inhibitory response. The maximum background EMG value that occurred during the middle latency time window (80–120 ms after stimulus) was used to calculate the maximum background EMG value that occurred during the middle latency time window. This value is used to normalize the maximum background EMG value that occurred during the step cycle for each muscle and expressed as a percentage. The maximum background EMG activity was estimated from the peak-to-peak difference in EMG activity detected in any of the 40 control steps used to generate the average control EMG trace.

The ongoing background EMG activity and the angles for the ipsilateral ankle and knee were also calculated for each walking condition. These were calculated from the unstimulated steps at the time at which the reflexes for each bin would have been observed. Ongoing EMG and joint angles from the ankle and knee were averaged for 40 ms during the control step cycle data, starting 80 ms after the average occurrence of the stimulus onset taken from the stimulation trials for each bin.

![FIG. 2. Process by which subtracted EMG traces were produced for analysis. Data are taken from a single subject for contralateral medial gastrocnemius (cMG) during the walking condition with the arms crossed while receiving mechanical perturbations at the dorsum of the foot (ACP). Stimuli were delivered at toe-off; solid vertical lines represent occurrence of stimuli. A: step cycle EMG activity for cMG during the ACP walking condition. Average stimulated step cycle data (thick black line) is shown superimposed onto average control step cycle data (thin black line). B: subtracted EMG trace resulting from the subtraction of average control step cycle EMG data from the average stimulated step cycle EMG data (for data shown in A). Data are aligned to the onset of stimulus. The middle latency time window in which cutaneous reflexes were analyzed is shown by the rectangular box. Vertical scale line represents 10% of maximum EMG.](http://jn.physiology.org/doi/10.1152/jn.00439.2007)
Changes in ipsilateral ankle and knee joint angle were calculated similar to the cutaneous reflex data described above. The subtracted kinematic change was calculated over a time window of 120–200 ms after stimulus (Haridas and Zehr 2003; Zehr et al. 1997) and normalized to the maximum range of motion over the control step cycle for each subject.

Statistics

Statistical analysis was performed using the averaged normalized cutaneous reflex amplitudes for each subject from each part of the step cycle. In this study, we specifically hypothesized that walking in an environment in which mechanical perturbations were applied to the dorsum of the foot would modulate the amplitude of cutaneous reflexes derived from SP nerve stimulation. Consequently, to guard against type II error, planned contrasts were performed comparing reflex amplitudes between each condition at a particular bin. That is, a total of six contrasts were made at each bin. For each muscle studied, a two-way repeated-measures ANOVA [condition (4) × bin (5)] was used to parse the sources of variance. The mean square error term derived from the ANOVA was used in the denominator for the tests of the contrasts. Similar planned contrasts were performed on the kinematic changes in the ankle and knee evoked by the SP nerve stimulation. A priori, we did not predict that the different walking environments would lead to changes in the background EMG, ankle and knee joint angles, or step cycle durations of the control steps. Therefore these variables were compared using repeated-measures ANOVAs to test for main effects of condition or condition × bin interaction effects. Statistical significance was set as \( P < 0.05 \). A Bonferroni correction was used for the multiple planned contrasts at each bin.

RESULTS

Background EMG and kinematics

Shown in Fig. 3 are the average control traces for one subject for the NP and ACP conditions compared with the N condition. The general walking pattern was observed to be similar across conditions. In particular, the muscles crossing the ankle joint showed little difference in activity between conditions. The EMG activity between the N and NP walking conditions seems to be dissimilar for iBF near the swing phase, where the background activity is greater for the N condition. Higher EMG activity is also seen during the ACP condition compared with the N walking condition in iVL around heel-strike. However, these isolated differences in background EMG activity were not consistent across subjects. Repeated-measures ANOVAs did not identify any main effects of condition or condition × bin interaction effects of the background EMG activity in any of the muscles tested (\( P > 0.05 \)). Similarly, the ankle and knee angles for one subject were comparable between all walking conditions (Fig. 3). Repeated-measures ANOVA did not identify any main effects of condition or condition × bin interaction effects for the group averaged ongoing ankle and knee angles at the time of stimulus delivery.

SP nerve cutaneous reflexes

Stimulation of the SP nerve evoked middle latency cutaneous reflexes in all muscles. The reflex amplitudes were modulated across the step cycle, similar to previous findings with SP nerve stimulation (Haridas and Zehr 2003; Haridas et al. 2005; Van Wezel et al. 1997; Zehr et al. 1997). For instance, inhibitory cutaneous reflexes were observed at the stance-swing and swing-stance transition points of the step cycle in iTA during normal (N) walking, and excitatory reflexes were observed during swing in cMG.

The amplitudes of middle latency reflexes evoked from SP nerve stimulation differed across conditions for some muscles. Figure 4 shows the subtracted EMG traces taken from a single subject for iTA and cMG during the AC and ACP walking conditions with SP nerve stimulation delivered at toe-off. The amplitude of the inhibitory middle latency response in iTA was suppressed when walking in an environment in which a threat of tripping was present (ACP). Also, the excitatory response in
cutaneous reflexes elicited during the NP and ACP excitatory reflex amplitudes was observed in cMG from toe-off shown by planned contrasts (Fig. 5). A clear enhancement of reflex values across the step cycle for all walking conditions was present.

During the AC condition was facilitated when perturbations (with respect to the innervation area of the SP nerve) on the N and AC walking conditions. At toe-off, the group average amplitude for the NP condition was also significantly higher than that for both the AC and NP walking conditions. The differences described above and identified by the planned contrasts for the group average data were consistently observed in all subjects tested.

Kinematic effect of SP nerve stimulation

It has been previously shown that, with SP nerve stimulation, there is an increase in plantar flexion at the stance-swing transition and an increase in knee flexion during swing, which is indicative of a stumbling corrective response (Haridas and Zehr 2003; Van Wezel et al. 1997; Zehr et al. 1997). In this study, similar findings were observed. The effect of SP nerve stimulation on both ipsilateral ankle and knee kinematics are displayed in Fig. 6. In the ipsilateral ankle (top), an overall trend of decreased stimulus-induced plantar flexion was observed during walking conditions in which mechanical perturbations were delivered compared with conditions with no perturbations from toe-off to midswing. Plantar flexion was significantly lower \((P < 0.05)\) during the NP and ACP conditions compared with the AC walking condition at toe-off and early swing. A significant difference was also observed at early swing between the N and NP walking conditions, with plantar flexion being lower during the NP condition. For the ipsilateral knee (bottom), significant differences between walking conditions were observed at early swing, where the degree of flexion that was induced by SP nerve stimulation was lower during the AC walking condition compared with the N, NP, and ACP conditions.

DISCUSSION

In a recent study from this laboratory, we showed that cutaneous reflexes evoked in the leg with SP nerve stimulation during walking were modulated according to the level of postural threat (Haridas et al. 2005). However, this finding was mainly isolated to the muscles of the contralateral leg, and it was thought that the lack of differences in ipsilateral cutaneous reflexes was caused by the locus of the perturbations. In this study, we investigated the influence of context-specific perturbations (with respect to the innervation area of the SP nerve) on cutaneous reflexes in the muscles of the legs during walking. When walking under conditions in which mechanical perturbations were delivered to the dorsum of the foot, cutaneous reflex amplitude values were facilitated compared with walking during conditions with no mechanical perturbations. In
FIG. 5. Group averaged data for middle latency cutaneous reflexes in all recorded muscles for each point of the step cycle. Reflex amplitudes are normalized to the maximum EMG observed for each muscle across the step cycle. The 5 points in the step cycle studied are located on the abscissa. Each of the 4 walking conditions tested is represented by a different symbol: ○, normal; ●, normal while receiving mechanical perturbations to the dorsum of the ipsilateral foot (NP); □, with the arms crossed across the chest filled circle (AC); ■, ACP. Error bars represent SE. *Significant differences ($P < 0.05$) between walking conditions.
addition, the findings suggest that not only are local cutaneous reflexes influenced by the presence of context-specific perturbations, but they are also gated according to the phase of the step cycle. Furthermore, inhibitory cutaneous reflexes were shown to be essentially abolished in iTA when walking in the presence of mechanical perturbations. This context-specific effect suggests cutaneous reflex responses in the lower limbs may be gated out or deleted when extraneous to the locomotor task.

Functional context-dependent gating of cutaneous reflexes

Numerous studies have reported the existence of a stumbling corrective response in both cats (Buford and Smith 1993; Forssberg 1979; Forssberg et al. 1975, 1977; Prochazka et al. 1978) and humans (Eng et al. 1994; Lam et al. 2003; Schillings et al. 2000; Van Wezel et al. 1997; Zehr et al. 1997), which serves to clear an encountered obstacle thus allowing for stability to be maintained during walking. In humans, inhibition of iTA during swing in response to electrical stimulation of the foot dorsum is a defining feature of a stumbling corrective response (Van Wezel et al. 1997; Zehr et al. 1997). In this study, the inhibitory reflexes observed in iTA from toe-off to midswing during walking conditions with no mechanical perturbations were suppressed such that the reflex amplitude values were closer to zero during walking conditions in which a threat of a trip existed. Increasing instability by crossing the arms did not result in reflex changes; only the threat of a trip was associated with the changes observed in cutaneous reflex amplitudes. This is in stark contrast to our previous findings in which a generalized threat to stability by perturbations delivered to the torso did not affect the reflexes of the ipsilateral leg (Haridas et al. 2005).

Here we report that repeated exposure to perturbations to the dorsum of the foot modulates the cutaneous reflexes from the foot. Bastiaanse et al. (2006) recently reported that a prestimulus pulse delivered before a reflex-evoking pulse train led to reduced sural nerve cutaneous reflex amplitudes. Taken together, these results suggest that prior knowledge of the arrival of sensory information leads to modulation of their influences, indicating that reflexes are adapted with contextual expectation. In turn, this can lead to reshaping of evoked responses...
Mechanisms of context-dependent reflex modulation

The context-dependent differences in cutaneous reflex amplitude were specific to certain muscles at specific points in the step cycle. This reflex modification can thus not be explained by a generalized change in the state of cutaneous reflex pathways. In addition, changing the context of the task led to a few minor adaptations in the profile of the background EMG of some muscles (e.g., iVL and iBF in Fig. 3) over the step cycle, suggesting a change in the behavioral set (Prochazka 1989). However, the changes in cutaneous reflex amplitudes observed in iTA and cMG occurred in the absence of changes in background EMG. Therefore, the differences in reflex amplitudes cannot be explained directly by differences in motoneuronal pool excitability, suggesting that changes in reflex amplitude must be related to factors associated with walking in the imposed conditions and altered behavioral state (Misiaszek 2006).

One possible mechanism for the context-dependent modulation observed involves supraspinal pathways projecting onto reflex pathways of the muscles of the legs. Pijnappels et al. (1998) reported the amount of cortical facilitation onto cutaneous reflex pathways varied according to the phase of the step cycle, suggesting that cortical input is able to generate the differential modulation observed. Similarly, Bretzner and Drew (2005) showed differential modulation of cutaneous reflexes according to the nerve and cortical site stimulated in intact cats at the onset of swing. Responses in some muscles were facilitated, whereas responses in other muscles were depressed, suggesting that cortical and cutaneous pathways have specific terminations to various interneuronal networks residing in the spinal cord. The convergence of cortical input onto interneurons of the reflex pathways could serve to modify the magnitude of reflex responses in relation to context. Corticospinal tract neurons in the cat have been shown to increase their firing rate when walking over a series of barriers compared with level walking (Beloozerova and Sirota 1993). Bretzner and Drew (2005) suggested that this increased rate of firing could allow for greater modulation of cutaneous reflex excitability and thus function as a mechanism to facilitate or inhibit reflexes that assist or interfere with stable locomotion. Taken together, descending cortical input is likely involved in the context-dependent modulation of cutaneous reflexes observed in this study.

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