Cutaneous Reflexes During Human Gait: Electromyographic and Kinematic Responses to Electrical Stimulation

E. P. ZEHR, T. KOMIYAMA, AND R. B. STEIN

Division of Neuroscience, University of Alberta, Edmonton, Alberta T6G 2S2, Canada; and Department of Health and Sport Sciences, Chiba University, Chiba 263, Japan

Zehr, E. P., T. Komiyama, and R. B. Stein. Cutaneous reflexes during human gait: electromyographic and kinematic responses to electrical stimulation. J. Neurophysiol. 77: 3311–3325, 1997. The functions of ipsilateral cutaneous reflexes were studied with short trains of stimuli presented pseudorandomly to the superficial peroneal (SP) and tibial nerves during human gait. Electromyograms (EMGs) of tibialis anterior (TA), soleus, lateral and medial gastrocnemius, vastus lateralis (VL), and biceps femoris (BF) muscle were recorded, together with ankle and knee joint angles. Net reflex EMG responses were quantified in each of the 16 parts of the step cycle according to a recently developed technique. After SP nerve stimulation, TA muscle showed a significant suppression during swing phase that was highly correlated to ankle plantarflexion. BF and VL muscles were both excited throughout swing and significantly correlated to knee flexion during early swing. Tibial nerve stimulation caused dorsiflexion during late stance, but plantarflexion during late swing. We argue that SP nerve reflexes are indicative of a stumbling corrective response to nonnoxious electrical stimulation in humans. The correlated kinematic responses after tibial nerve stimulation may allow smooth movement of the swing leg so as to prevent tripping during swing and to assist placing and weight acceptance at the beginning of stance.

INTRODUCTION

Peripheral sensory inputs have long been known to have powerful and often stereotyped reflex effects in many animals (Sherrington 1906). Much of the initial work on cutaneous reflexes was conducted in cats with various levels of reduction from decerebrate to intact walking preparations (for reviews, see Duysens and Tax 1994; Rossignol 1996). It was not until the work of Forssberg (1979), Prochazka et al. (1978), and Wand et al. (1980), though, that the functional role in terms of kinematic change was quantitatively assessed. These researchers found that cutaneous reflexes elicited in intact walking cats by electrical and mechanical perturbation of the dorsal surface of the distal hindlimb served to modify limb trajectory during swing such that stumbling was avoided; the “stumbling corrective reaction” (Forssberg 1979). Forssberg (1979) concluded that “...the reflex pattern and the induced corrective movements are adapted so that functionally meaningful movements are evoked in each phase of the step cycle.” Later, Drew and Rossignol (1987) described functionally relevant cutaneous reflexes in the cat forelimb. These studies illustrate an association between electromyographic (EMG) and kinematic data that suggests an important role of cutaneous receptors in modifying and correcting locomotor limb movement in the cat, particularly during swing.

The role of cutaneous reflexes is not so clear in the human. EMG responses have been measured in human leg muscles after nonnoxious stimulation of cutaneous nerves during walking. Such experiments have revealed that cutaneous reflexes are task dependent (e.g., phasic locomotor vs. tonic maintained activity) (Duysens et al. 1993; Kanda and Sato 1983; Lisin et al. 1973), intensity dependent (e.g., noxious vs. nonnoxious stimulation) (Belanger and Patla 1984; Crema and Frigo 1984; Duysens et al. 1990), and phase dependent (e.g., swing vs. stance) (DeSerres et al. 1995; Duysens et al. 1990, 1992; Yang and Stein 1990), and have contralateral as well as ipsilateral effects (Tax et al. 1995). However, with the exception of van Wezel et al. (1994), human studies have mainly examined reflex responses arising from stimulation of the distal tibial (plantar surface innervation) and sural (lateral foot border innervation) nerves. The reflex effects of stimulating the dorsal surface of the human foot [innervated by the primarily cutaneous superficial peroneal (SP) nerve], the same area as was described by Forssberg and colleagues (Forssberg 1979; Forssberg et al. 1975) in the cat, have not been studied.

Reflex changes in ankle (Duysens et al. 1990, 1992) and knee (Duysens et al. 1992) trajectory were reported after stimulation of sural nerve. Only Duysens et al. (1992) performed a brief analysis of the mechanical effect and found a significant correlation between tibialis anterior (TA) EMG and increased dorsiflexion after sural nerve stimulation during walking. Also, some changes in ankle angle were described after tibial nerve stimulation (Duysens et al. 1990). In the other studies mentioned above, functional conclusions were based only on observed changes in one or more EMG waves without kinematic confirmation.

The purpose of the present paper was, therefore, to test the hypothesis that reflex EMG responses elicited in leg muscles after nonnoxious electrical stimulation of the other two main cutaneous nerves of the human foot, the SP and the tibial, during treadmill walking have a functional mechanical effect. This approach is quite different from that employed by other researchers, who have mainly examined the pathways and modulation of cutaneous reflexes without a detailed examination of reflex function. The current hypothesis is tested by correlating global reflex changes in the EMG activity with the kinematics and interpreting significant correlation in terms of possible functional roles, such as Forssberg’s (1979) stumbling corrective responses. Although electrical stimulation of a cutaneous nerve does not elicit
exactly the same afferent volley as natural stimulation, we argue that our results may mimic the responses to more natural perturbations. Portions of this work have previously been published in abstract form (Zehr et al. 1996a–c).

**METHODS**

**Subjects and general procedure**

Six subjects (5 male and 1 female), aged 24–36 yr, participated in the experiments with informed, written consent. Each subject participated in two separate experiments (1 for each nerve studied), each lasting ~3 h. Because there is often large intersubject variation in the magnitude and nature of reflex responses after stimulation, the same subjects were involved in each experiment. Then, variation in reflex responses could be ascribed to functional differences between the nerves. All experiments were conducted under an approved protocol for human subjects at the University of Alberta. During each session, subjects walked on the treadmill at speeds of 2 and 4 km/h for ~7–10 min at each speed. These two speeds were selected to provide a range of amplitudes of responses. Because future experiments involving stroke patients (who walk much more slowly than neurologically intact subjects) are planned, data on 2 km/h walking were collected. Approximately 400–600 steps were collected for each speed (including stimulated and control unstimulated steps).

**Nerve stimulation**

The SP and tibial nerves were stimulated with the use of a GRASS SD9 (Grass Instruments, Quincy, MA) isolated constant voltage stimulator with trains of three to six pulses at 200 Hz (pulse width 1.0 ms). The electrodes for the SP nerve were placed on the anterior surface of the leg just near the crease of the ankle joint, whereas the tibial nerve was stimulated on the medial surface of the ankle posterior to the medial malleolus. The location of the electrodes was such that strong radiating parasthesias were reported by the subjects in the appropriate cutaneous receptive fields; foot dorsum and plantar surface for SP and tibial nerves, respectively. Flexible 1-cm disposable ELECTROTTRACE (JASON, Huntington Beach, CA) Ag/AgCl surface EMG electrodes were used for cathodal stimulation. The threshold of stimulation in terms of the radiating threshold (RT; defined as a clear radiating parasthesia in the cutaneous field appropriate for each nerve) was determined in all subjects. The perceptual threshold (PT), defined as the lowest stimulation that was just detectable by the subject, was also determined. PT likely represents local activation of cutaneous receptors lying immediately underneath the recording electrodes. In contrast, RT likely represents electrical activation of fascicles in the underlying cutaneous nerve. In general, we had less variability between subjects in setting the intensity when measures of RT were used. Stimulation intensities were typically twice RT for each nerve. The intensity and number of pulses were varied somewhat in each experiment to obtain the strongest stimulation possible that was described as nonnoxious by the subject and was subthreshold for evoking a flexion reflex (a generalized withdrawal of the limb by flexion at the ankle, knee, and hip) during standing. There were no changes in responses observed that could be attributed to any variation in stimulus parameters within the range used in the present experiments.

The stimulator was driven by a pseudorandom pulse generator with a minimal repeat time of 1.8 s and a maximum of 4 s. In this way we were able to collect many unstimulated steps between stimulated steps and no step had more than one stimulus. Outputs from both the trigger pulse generator and the Grass stimulator were sent to a 12-bit A/D converter and then into a 486 66-MHz microcomputer running AXOTAPE (Axon Instruments) data acquisition software.

**EMG**

After light abrasion and cleansing of the skin with alcohol, disposable ELECTROTTRACE (JASON, Huntington Beach, CA) Ag/AgCl surface EMG electrodes were applied in bipolar configuration longitudinal to the predicted path of the muscle fibers (inter-electrode distance ~ 2 cm) over the soleus (SOL), lateral and medial gastrocnemius (LG and MG, respectively), TA, vastus lateralis (VL), and biceps femoris (BF) muscles. SOL electrodes were placed distal to the termination of the gastrocnemius muscles, whereas MG and LG electrodes were placed over the medial and lateral heads of the gastrocnemius. TA electrodes were placed over the largest girth of the TA muscle. For VL, the distal electrode was placed ~4–6 cm proximal to the lateral margin of the patella, and for BF placement was over the muscle belly at approximately one-third the distance from the knee to the hip. Because the tibial nerve has a motor branch in the plantar nerve, we recorded motor responses of the intrinsic muscles by placing electrodes on the plantar foot surface and we monitored these responses to evaluate stimulus stability throughout a walking trial. This check was not available for SP nerve. For SP nerve, though, the position of the stimulating electrodes was such that it typically produced some minor facilitation of the nearby extensor digitorum brevis muscle. We therefore monitored the EMG from this muscle to check that its stimulation remained constant throughout the cycle. Variation in stimulation across the step cycle was generally <10%. Ground electrodes were placed over electrically neutral tissue, such as the knee. EMG signals were preamplified and high-pass filtered at 100 Hz. Then they were full-wave rectified, thus yielding components down to DC, and low-pass filtered at 100 Hz. This filtering process provided a good linear envelope with little spread of the stimulus artifact (which could then be digitally removed off-line, see below). The processed output was then sent to a 12-bit A/D converter and then into a microcomputer running AXOTAPE (Axon Instruments) data acquisition software.

**Kinematics and step cycle timing**

Angular position of knee and ankle were recorded with custom-made potentiometric electrogoniometers placed over the joint and secured with plastic tape and fabric straps. Signals obtained from custom-made force sensors located in the insole of the subject’s shoe were used to establish step cycle parameters (e.g., heel contact, toeoff). This technique, based on force-sensing resistors, has been previously described (Zehr et al. 1995b). Angle and force signals were preamplified at the subject (the subject wore a small pouch and belt to hold the amplifiers) and then sent directly to the AXOTAPE computer system.

**Data acquisition and analysis**

The data were sampled continuously at 500 Hz and stored on hard disk for off-line analysis. Custom-written software programs were used to separate the step cycle into 16 separate parts, beginning with heel contact. The stimuli occurred randomly throughout the step cycle. All responses to stimuli occurring in the same part of the step cycle were averaged together and aligned to stimulus delivery within that part of the step cycle. The values obtained for each of the 16 averages after stimulation were subtracted from the corresponding averages from unstimulated steps during the same trial (Fig. 1).
EMG analysis

To obtain smoother records, stimulus artifacts were digitally removed and then the EMGs were filtered with a five-point digital moving average filter. The unstimulated control EMGs for each part of the step cycle were subtracted from the corresponding stimulated step cycle parts to yield subtracted evoked EMG traces. The evoked EMGs for each subject were analyzed for the net reflex effect with the use of the average cumulative reflex EMG after 150 ms (ACRE150). This technique was employed because the major focus in this study was to evaluate the function of cutaneous reflexes. Thus it was necessary to compare the net control signal (i.e., the net EMG reflex effect) with the net mechanical outcome (i.e., movement kinematics, see below). Further, previous studies on cutaneous reflexes (see INTRODUCTION) have focused mostly on an analysis of responses occurring at a given restricted range of latencies and with durations typically ~30 ms. If a facilitation for 30 ms were followed by an equal suppression for the next 30 ms, there would be no net effect and any transient would have its fundamental at ~16 Hz, which is above the physiological range. By measuring the net response over the entire reflex period of 150 ms, we can expect a realistic association with movement kinematics, which are the filtered output of the entire system. As previously described (see Komiyama et al. 1995; Zehr et al. 1995a), the ACRE150 technique is a modified cumulative sum (CUSUM) based on the technique commonly employed to examine effects in post-stimulus time histograms (Ellaway 1978). In brief, the analysis program calculates the subtracted, residual reflex EMG traces and digitally removes the stimulus artifact. The poststimulus data were then sequentially summed and any significant facilitation or suppression was identified as positive or negative deflections in the CUSUM record. The value obtained at 150 ms after stimulation

![Graph showing EMG analysis](image-url)
FIG. 2. Subtracted EMGs of TA (top left), SOL (top right), LG (bottom left), and MG (bottom right) muscles after superficial peroneal (SP) nerve stimulation for 1 representative subject. Throughout, stimulus artifact has been suppressed and replaced by a flat line, atop which has been placed a thick dashed line. Each trace runs from 50 ms before stimulation to 250 ms after stimulation. Numbers at far left: specific portions of step cycle. Solid vertical line: stance. Dashed vertical line: swing.
FIG. 3. Grouped data (n = 6; means ± SE) for average cumulative reflex EMG after 150 ms (ACRE150) values for SOL (A), LG (B), MG (C), and TA (D) muscles, along with stimulus-induced changes in ankle joint angle (E) throughout the step cycle after SP nerve stimulation. Note that ACRE150 values are expressed as a percentage of maximum EMG for each muscle during the step cycle and angle changes as a percentage of maximum excursion of the joint. Asterisks: effects statistically different from 0 at P < 0.05. Solid and dashed lines at bottom: stance and swing phases. Labeled numbers: specific portions of step cycle. Dorsiflexion and plantarflexion are as indicated by arrows.
was then divided by the time interval of integration to measure an overall reflex effect in microvolts (i.e., negative values indicate overall suppression and positive values indicate overall facilitation). Because we were interested in reflex effects, a 150-ms post-stimulus interval was chosen since it preceded any significant voluntary activation (see Zehr et al. 1995a). To reduce problems arising from individual differences or electrode placement, the ACRE150 values for each subject were normalized to the peak EMG value (averaged over a 40-ms time window) occurring during the entire step cycle for each muscle at each walking speed and expressed as percentages.

Results

SP nerve

Average rectified and integrated EMG and angle data are plotted in Fig. 1 from an individual subject walking without stimulation. The typical pattern of EMG activities seen in the subjects is shown for the six knee and ankle muscles studied here, together with the changes in angle at the corresponding joints. The responses to stimulation of the SP nerve in each of 16 parts of the step cycle are shown for four muscles acting at the ankle in Fig. 2. The solid vertical line indicates those parts that fall in the stance phase and the dashed vertical line indicates those parts that fall in the swing phase. Typically, the stance phase is parts 1–8 and the swing phase is parts 10–15. The stance-to-swing transition occurs in part 9 and the swing-to-stance transition in part 16. The stimulus artifacts (representing the period of stimulation) have been removed for clarity, but the period is indicated by the horizontal dashed lines. The EMG without stimulation from Fig. 1 has been subtracted from each trace so that positive deflections represent facilitation and negative deflections represent suppression of EMG activity from the control values. Note that complex patterns of facilitation and suppression are often seen extending for >100 ms.

The overall response (ACRE150; see METHODS) has been calculated for each subject walking at 2 and 4 km/h and
FIG. 5. SP nerve grouped data for ACRE<sub>150</sub> values for VL (A) and BF (B) muscles, along with changes in knee angle (C) throughout step cycle. Asterisks: statistical significance at <i>P</i> < 0.05. Knee flexion and extension are as indicated by arrows. ACRE<sub>150</sub> values are expressed as a percentage of maximum EMG for each muscle during the step cycle and angle changes as a percentage of maximum excursion of the joint.

averaged over the six subjects studied. The values are summarized in Fig. 3, together with the corresponding changes in ankle angle. There are few consistent effects of SP stimulation at this intensity on any of the muscles during the stance phase and little change in ankle angle. However, MG but not LG is suppressed (asterisks represent values that are significant at <i>P</i> < 0.05) in some parts of the stance phase. Thus there is a differential effect of SP stimulation in the human gastrocnemius muscle. Duysens et al. (1996) have recently shown a differential response in MG (facilitation) and LG (suppression) after sural nerve stimulation during human gait, but the function of these differential responses
remains unclear. In the early part of swing phase, stimulation produces a suppression of TA activity of ~20% (all values are measured relative to the peak activity observed during the step cycle without stimulation) and this is correlated with a negative change in angle (a reduction in dorsiflexion, labeled as a change in the plantarflexion direction in Fig. 3). A small but significant facilitation is observed in the triceps surae muscles (SOL, LG, and MG), which should result in the generation of knee flexor/ankle plantarflexor torque in some later parts of the swing phase, but it is not enough to produce a change in ankle angle. This confirms the importance of measuring kinematic changes before attributing functional effects to changes in EMG.

Figure 4 shows data for the knee muscles (VL and BF) in one subject. In contrast to the ankle muscles, the responses are overwhelmingly facilitatory, particularly for BF. The average values for the six subjects are shown in Fig. 5, together with the changes in knee angle. As with the ankle, the changes during the stance phase are small, although a significant correlation in the knee flexor BF is associated with some knee flexion during several parts of the stance phase (5–7). Larger changes are observed during much of the swing phase in both muscles, and this is again associated with significant knee flexion in several parts (12–16). An interesting point is that increased activity in both the knee extensor (VL) and the knee flexor (BF) is associated with knee flexion. The increases in BF activity (~20%) are larger than in VL activity (~10%), so that the knee flexor action dominates. The coactivation of antagonist muscles will increase the stiffness of the knee joint.

A second method of analyzing the changes is to run the correlations between EMG activity and angle change for each subject at both speeds in each part of the step cycle. All the data are plotted in Fig. 6, and correlations up to \( R = 0.9 \) (part 11) are seen between TA EMG and ankle angle. Although there is actually a slightly higher correlation with the changes in knee angle. As with the ankle, the changes during the stance phase are small, although a significant correlation in the knee flexor BF is associated with some knee flexion during several parts of the stance phase (5–7). Larger changes are observed during much of the swing phase in both muscles, and this is again associated with significant knee flexion in several parts (12–16). An interesting point is that increased activity in both the knee extensor (VL) and the knee flexor (BF) is associated with knee flexion. The increases in BF activity (~20%) are larger than in VL activity (~10%), so that the knee flexor action dominates. The coactivation of antagonist muscles will increase the stiffness of the knee joint.

Figure 6 shows data for the knee muscles (VL and BF) in one subject. In contrast to the ankle muscles, the responses are overwhelmingly facilitatory, particularly for BF. The average values for the six subjects are shown in Fig. 5, together with the changes in knee angle. As with the ankle, the changes during the stance phase are small, although a significant correlation in the knee flexor BF is associated with some knee flexion during several parts of the stance phase (5–7). Larger changes are observed during much of the swing phase in both muscles, and this is again associated with significant knee flexion in several parts (12–16). An interesting point is that increased activity in both the knee extensor (VL) and the knee flexor (BF) is associated with knee flexion. The increases in BF activity (~20%) are larger than in VL activity (~10%), so that the knee flexor action dominates. The coactivation of antagonist muscles will increase the stiffness of the knee joint.

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Taken together, the results of SP stimulation show three major points: 1) there is little effect on the EMG or kinemat-
with large values of $R$ but that there is not a significant change in ankle angle (Fig. 8), presumably resulting from the increased activity in SOL that would counteract the TA effect.

The other significant ankle change in Fig. 8 is a plantarflexion in parts 14 and 15 of the swing phase that is associated with an increased activity of the triceps surae (SOL, LG, and MG) and small changes in the TA. Yang and Stein (1990) and Duysens et al. (1990) found an actual reversal of TA activity with tibial nerve stimulation producing suppression at a middle latency response, but this can be more than balanced by the early and later facilitation in some subjects. Thus it is important to use an overall measure such as the ACRE$_{150}$. There is a significant $R$ value of 0.63 at part 14 of the cycle (Fig. 9). Whereas there was generally good agreement in data obtained in different subjects (e.g., see error bars in all grouped data figures), there was variability in the responses at this part of the step cycle after tibial nerve stimulation. In some subjects there was a net suppression and in others a net facilitation in TA, and the angle changes varied accordingly (Fig. 10). The predominant movement is plantarflexion, associated with the increase in triceps surae muscles. Thus tibial nerve stimulation does produce a functional reversal with dorsiflexion during the transition from stance to swing and a plantarflexion during late swing.

The results at the knee are shown in Fig. 11. Again, the predominant effect is facilitation, particularly during the swing phase, and this is associated with a flexion of the knee during this phase. However, looking at the Pearson $R$ values in Fig. 9, there is only one significant correlation. Thus much of the flexion of the knee must be coming from other sources, such as being secondary to flexion at the hip.

**DISCUSSION**

In this paper we show that volleys in cutaneous pathways to leg muscles from electrical stimulation of two major lower leg cutaneous nerves during human gait can elicit EMG and kinematic responses. The third nerve, the sural, has previously been studied in some detail by Duysens et al. (1992). Here, the overall responses were generally larger during the swing phase and transitional phases than during stance. Furthermore, we show a significant correlation between the net EMG and mechanical measures of stimulus-induced changes in ankle and knee joint angle trajectory after stimulation of each nerve. Below we argue for the functional relevance of the observed responses and discuss the relative contribution of cutaneous input during the various phases of human gait.

**Are the responses functional?**

SP NERVE RESULTS. As was mentioned in the introduction, Forssberg (1979) spoke of a ‘‘stumbling corrective response’’ in the feline preparation as one in which a given stimulus elicited robust reflex EMG responses that had mechanical effects permitting undisturbed locomotor progression. This response was essentially increased knee, hip, and ankle flexion, a pattern quite suited to the more stable nature of quadrupedal locomotion. This response allowed the animal to continue movement of the swing limb with little...
Fig. 8. Tibial nerve grouped data for ACRE values for SOL (A), LG (B), MG (C), and TA (D) muscles, along with stimulus-induced changes in ankle joint angle (E) throughout the step cycle during 2- and 4-km/h walking. Same format as in Fig. 5. Asterisks: statistically significant net responses at $P < 0.05$. 
overall disturbance to the act of walking. Our observed responses to electrical stimulation of SP nerve in human subjects showed some similarities and some differences. The only way for the innervation area of SP nerve (foot dorsum) to be strongly activated during walking, particularly during swing, would be for contact with some form of impediment. In our experiments stimulation of the SP nerve elicited radiating paraesthesia that resembled, to some extent, banging the foot on an obstacle. The sensation is not pain, but rather pressure and tingling. If one were to catch the foot on an obstacle during early swing phase, the responses observed here would allow for smooth leg movement as shown schematically in Fig. 12, middle. A suppression of normal TA muscle activity would allow for passive plantarflexion (a reduction in dorsiflexion, as mentioned previously), which we observed to be functionally concomitant with slight knee flexion, to lift the limb over the obstacle. In contrast, if normal muscle activity and swing leg kinematics were maintained, movement would be blocked and a fall could result. Thus this is a stumbling corrective response to electrical stimulation in humans. A difference between this result and that described by Forssberg (1979) is that, although in the cat knee and ankle flexion result, we observed knee flexion and reduced ankle dorsiflexion in our human subjects. It is postulated that this occurs as a result of inherent differences in balance control and stability that exist in quadrupeds and bipeds. Therefore, although the general quality of the response may be similar across species, the details at crucial joints (i.e., the ankle joint) may be different.

Although it is difficult to compare our results arising from electrical stimulation with naturally occurring stumbling, Schillings et al. (1996) have recently described stumbling reactions to obstacles encountered during human treadmill locomotion. They describe kinematic changes that, although of larger amplitude, are quite similar to our electrically stimulated responses. Schillings et al. demonstrated increased plantarflexion and knee flexion responses in concert with enhanced BF activity. Eng et al. (1994) described various corrective responses to actual physical obstacles during swing, and their data, although time shifted somewhat from the present data (e.g., TA suppression is noted in a late swing lowering response by Eng et al.), seem qualitatively quite similar. These findings corroborate our assertion that electrically “simulated” perturbations may elicit functionally relevant reflexes in the swing leg during human walking.

The question remains, though, as to why the knee extensor VL undergoes a net facilitation at the same time the functionally relevant net BF facilitation is occurring. The increased activity across the knee joint may serve to increase the stiffness of the knee joint in case the distal modification at the
ankle is unsuccessful. If the reduction in resistance to ankle joint dorsiflexion is not enough to allow smooth swing across the obstacle, stumbling and tripping could occur. If so, increased loading of knee extensors in the swing leg will ensue. The nervous system may be anticipating this possible outcome, and the increased activation of the knee extensors along with the knee flexors would provide a finer control of knee joint trajectory and a larger safety margin in case of a stronger perturbation. Also, the increased knee joint stiffness along with reduced ankle joint stiffness may force the perturbation to be accommodated at the distal limb segment. Thus the perturbation will have a smaller destabilizing effect on the whole swing leg. Interestingly, although they did not report data on the VL muscle specifically, Schillings et al. (1996) have reported enhanced rectus femoris (a knee extensor synergist of VL, but also a hip flexor) activation in their mechanical stumbling paradigm. Also, in the cat, Drew and Rossignol (1987) reported coactivation of forelimb flexors and extensors after superficial radial nerve stimulation. They suggested that their results might be interpreted in terms of control over the inertia of the distal segment. This may also play a role in the present experiments. Here coactivation was seen in the more proximal muscles, controlling the larger inertia of the proximal and distal leg segments, and not in the distal muscles (i.e., SOL, LG, MG, and TA), controlling the smaller inertia of the most distal segment. However, it must also be noted that we measured one knee extensor (VL) and one hip extensor/knee flexor (BF) of the many
muscles that cross the knee in the anterior and posterior compartments. Therefore, although we believe the current explanation to be plausible, caution must be exercised in extending the results too far, particularly as regards potential differences between electrical and more natural stimulation.

TIBIAL NERVE RESPONSES. We observed significant kinematic correlation between the net effect in TA muscle and ankle joint trajectory during the stance-to-swing transition and throughout swing (see Fig. 9, top) after tibial nerve stimulation. However, the kinematic association switched

FIG. 11. Tibial nerve grouped data (n = 6 subjects; means ± SE) for ACRE100 values for VL (A) and BF (B) muscles, along with stimulus-induced changes in knee angle (C) throughout the step cycle during 4-km/h walking. Same format as in Fig. 5.
from being one in which significantly \((P < 0.05)\) increased ankle joint dorsiflexion was observed (Fig. 8E, part 9) to one in which increased plantarflexion was noted (late swing, parts 14 and 15). This is similar to the kinematic changes reported in some subjects by Duysens et al. (1990) after tibial nerve stimulation. However, in that study a correlational analysis such as plotted in Fig. 10 between EMG index and angle change was not conducted. The reversal in kinematic correlation can be clearly seen in Fig. 10, top, in which responses from stance transition (part 9, filled circle) all lie above zero (increased ankle joint dorsiflexion), whereas those from late swing (part 14, open circle) are mainly below zero and thus represent increased ankle joint plantarflexion. We interpret the effects observed during the stance-to-swing transition (Fig. 12, left) as follows. During this phase the normal pattern of tactile input to the foot sole should be reduced (as in the cat, Popovic et al. 1993), not increased as our stimulation would emulate, in preparation for swing phase. The linkage between increased TA activation and increased ankle dorsiflexion should lift the foot off the ground to avoid scuffing of the foot and potential tripping when swing phase begins. We also observed increased plantarflexion during late swing (Fig. 12, right). At this time, input to the sole of the foot would also indicate ground contact. However, the functionally relevant response might not be to increase dorsiflexion as observed earlier in the step cycle. Rather, ground contact is expected and weight is being transferred toward this limb. Therefore our observed plantarflexion may be interpreted in terms of a form of placing reaction to get the foot firmly on the ground once foot contact is sensed, again to accept weight and prevent tripping.

The correlations were less numerous and sizeable between reflex effects and knee joint trajectory after tibial nerve stimulation, so functional responses at the knee may not be as prominent after nonnoxious stimulation of this nerve. As pointed out earlier, some of the kinematic changes may be secondary to movements at other joints, such as the hip. Patla and Prentice (1995) indicated that voluntary, visually cued corrections to obstacles during human gait may act by altering the hip moment. Therefore changes measured at the ankle and knee might be more passive processes, within which suppression (e.g., SP effects on TA muscle as described above) may be as important as facilitation of normal locomotor activity. This is an issue worthy of further study.

**Why are there smaller kinematic effects during stance and larger effects during swing?**

During locomotion in cats the afferent volley in SP nerve has two bursts of activity, one when the paw hits the ground and a second when the paw is lifted from the ground (Popovic et al. 1993). However, there is continuing activity during the stance phase as the skin surface is stretched or wrinkled as the ankle extends or flexes. Afferent activity is low during swing phase at a time when the receptive field is in an opportune location for detecting foot contact with external obstacles. Unexpected inputs relevant to the control of locomotion during this phase could have a more marked effect on the progress of locomotion, as demonstrated here. Alternatively, such inputs could be gated out either by a central oscillator (Duysens et al. 1990) or perhaps a peripheral modulation making use of interposed interneurons or presynaptic inhibition, as has been demonstrated for the monosynaptic H reflex (Stein 1995). The cutaneous nerves can provide cognitive information during stance about pressure on the foot and the ground surface that would be involved in the planning of subsequent steps but that is beyond our reflex time scale. In contrast, obstacles encountered during swing need rapid, reflex responses to maintain secure, stable walking, and the responses observed here may be important for this reflex function. Lastly, it must also be pointed out that during stance the foot is planted firmly on the ground and one might expect less movement than when the limb is free to move during swing.

In conclusion, we have documented that electrical stimulation of the tibial and SP nerves, which have distinct and anatomically opposed cutaneous innervation areas, elicits prominent net EMG and kinematic reflex effects. We have also argued for a simple functional interpretation (Fig. 12) in terms of integrated responses whereby cutaneous reflexes can functionally stabilize human gait. For example, contrast the plantarflexor response and mechanical correlation seen after early swing SP nerve stimulation (Fig. 3E) with the dorsiflexion response seen after tibial nerve stimulation (see Fig. 8E). Interestingly, these results are quite similar to those reported by Buford and Smith (1993) when they applied mechanical and electrical perturbations to the ventral and dorsal foot surfaces during forward and backward walking in the cat. They found antagonistic EMG and mechanical reflex responses that were specific to the forward or back-
ward walking pattern and anatomic responses of the cutaneous receptive field and that were functionally relevant to allow continued gait. We agree with a functional role of these cutaneous reflex responses in prevention of stumbling and tripping during critical transitional and swing phases of human gait.

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Address for reprint requests: E. P. Zehr, Division of Neuroscience, 513 HMRC, University of Alberta, Edmonton, Alberta T6G 2S2, Canada.

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