Bipedal Reflex Coordination to Tactile Stimulation of the Sural Nerve During Human Running

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SUMMARY AND CONCLUSIONS

1. Cutaneous reflex responses were elicited during human running (8 km/h) on a treadmill by electrical stimulation of the sural nerve at the ankle. Stimulus trains (5 pulses of 1 ms at 200 Hz) at three nonnociceptive intensities, which were 1.5, 2.0, and 2.5 times perception threshold (PT), were delivered at 16 phases of the step cycle. For 11 subjects the surface electromyographic (EMG) activity of both the ipsilateral and contralateral long head of the biceps femoris (iBF and cBF, respectively), the semitendinosus (iST and cST), the rectus femoris (iRF and cRF), and the tibialis anterior (iTA and cTA) were recorded.

2. During human running, nonnociceptive sural nerve stimulation appears to be sufficient to elicit large, widespread and statistically significant reflex responses, with a latency of ~80 ms and a duration of ~30 ms. These reflex responses seem to be an elementary property of human locomotion. This is indicated by the occurrence of the responses in all subjects, the consistency of most of the reflex patterns across the subjects and, apart from a small amount of habituation, the reproducibility of the responses during the course of the experiment.

3. The responses are modulated continuously throughout the step cycle such that their magnitude does not increase in general covary with the background locomotor activities. This is observed most clearly in iST, iTA, and cTA for which statistically significant reflex reversals are demonstrated, and in cRF and cTA for which the responses are gated during most of the step cycle.

4. The response magnitude generally increases as a function of increasing intensity, whereas the phase-dependent reflex modulation is intensity independent.

5. A functional dissociation within the ipsilateral hamstring muscles is demonstrated: the iBF and iST show an antagonistic reflex pattern (facilitatory and suppressive, respectively) during the periods of synergistic background locomotor activity in the step cycle. Contralaterally, however, the cBF and cST are reflexively activated as close synergists during these periods.

6. The reflex responses and their phase-dependent modulation are different for the homologous muscles in the two legs. Yet, some similarities are observed. These are present rather with respect to the phase of the corresponding leg than with respect to the phase of the stimulated leg. Both observations suggest that the phase-dependent reflex modulation is controlled separately in the ipsilateral and contralateral legs.

7. The response simultaneity in all investigated muscles supports the notion of a coordinated cutaneous interlimb reflex during human running. This reflex coordination is intensity independent (within the range of nonnociceptive stimulation) and different from the locomotor coordination. The possible functional significance underlying the bipedal reflex coordination is discussed. It is suggested that tactile cutaneous feedback may be used to move the perturbed leg away from the stimulus, with the general constraint of preserving both the cadence and the balance at all times during the step cycle. The contralateral responses are thought to play an important, supportive role in promoting a smooth transition between these potentially conflicting requirements.

INTRODUCTION

Low-threshold cutaneous receptors, by virtue of their superficial location and their high sensitivity, seem to be the sensors "par excellence" for detecting small disturbances during normal locomotion (Burke et al. 1991). This putative, important role of cutaneous feedback is generally recognized in the literature and is supported by several combinations of experimental paradigms and preparations. However, as far as human locomotion is concerned, there is not much direct evidence in favor of the functional significance of cutaneous reflexes. There are four elements that are important in determining the outcome of reflex synergies. Fundamental changes in (patterns of) reflexes can be observed by changing either the stimulus location, the intensity, the preparation (species), or the task, as will be shown below.

First, although Lundberg et al. (1987) have proposed the idea of sensor fusion by means of the flexor reflex afferents (FRA) hypothesis, the afferent convergence may be restricted to highly specialized (so-called private) reflex pathways that, in the case of cutaneous feedback, correspond to different skin subregions (Lundberg 1975). This means that stimulation of different skin areas is expected to elicit different reflex strategies (Aniss et al. 1992; Duyssens and Loeb 1980; LaBella and McCrea 1990; Pratt et al. 1991; Schouenborg and Kalliomäki 1990).

Second, the reflex organization appears to be highly dependent on the intensity of cutaneous stimulation. An increase in stimulus strength activates the tactile (fast, group II) and the noxious (slow, group III and IV) cutaneous afferents in that order (Hugon 1973). The reflex control is assumed to change correspondingly from a balance-oriented to a withdrawal-oriented strategy (Duyssens et al. 1992; Forssberg 1979; Hugon 1973; Yang and Stein 1990), although some convergence of tactile and nociceptive input to common spinal interneurons has been demonstrated (Schouenborg et al. 1992).

Third, differences in the reflex synergies of various species are to be expected because of the different demands that are imposed on bipedal, plantigrade and quadrupedal, digitigrade progression. Moreover, anatomic differences seriously hamper a simple comparison of (reflex) data relating to different species. For example, the biarticular parts of the biceps femoris differ considerably for cats and humans. In humans, the largest lever arm is at the hip (the long head)
jects (Duysens et al. 1991), and to the upper leg muscle principle, it is possible that the afferent input during gait determined by ipsilateral or contralateral step-cycle events. In addition, the reflex modulation of the biceps femoris (1 subject during 4-km/h walking) (Tax et al. 1991, 1993). Moreover, for different tasks different sets of muscles may be selected to participate in a cutaneous reflex (Aniss et al. 1992; Burke et al. 1991; Palla and Belanger 1987; Pratt et al. 1991). Hence the reflex responses are generally not stereotyped but are continuously adapted according to the actual task. This flexibility cannot generally be accounted for by traditional ideas of servocontrol, servo-assistance, or stiffness control. In fact, this has led Stein (1991) to advocate the notion of a quite complex strategy of adaptive control.

The main objective of this study is to investigate the role of tactile reflexes during human running by electrically stimulating the purely cutaneous sural nerve. The resulting reflex responses are usually studied by determining changes of electromyographic (EMG) activity in ipsilateral muscles. In the ipsilateral muscles investigated (mainly the lower leg muscles tibialis anterior, soleus, and medial gastrocnemius), the very first, pronounced reflex responses are evoked at a latency of 70–90 ms, and they show evidence of premotorneuronal modulation as a function of the phase in the step cycle during either walking or running (Duysens et al. 1990a,b–1993; Yang and Stein 1990). These responses may affect the kinesiology of the limb and as a result postural stability. Therefore any responses contralateral to the side of stimulation may have to be an integral part of a coordinated interlimb reflex strategy (for review see Duysens and Tax 1994; a more general review on interlimb coordination in humans see Dietz 1992).

Such an integrative action of contralateral responses to tactile stimulation of cutaneous afferents has been studied in cats (Duysens and Loeb 1980; Duysens and Stein 1978; Duysens et al. 1980; Forssberg et al. 1977). Like their ipsilateral counterparts, the contralateral responses appear to be phase dependent too. Direct experimental evidence in case of human locomotion, however, is less well documented, mainly restricted to the lower leg muscles soleus and gastrocnemius, which show a considerable variability across subjects (Duysens et al. 1991), and to the upper leg muscle biceps femoris (1 subject during 4-km/h walking) (Tax et al. 1990). The question is whether contralateral responses (like ipsilateral responses) show evidence of premotorneuronal modulation and, if so, whether this modulation is determined by ipsilateral or contralateral step-cycle events. In principle, it is possible that the afferent input during gait is modulated by ipsilateral sources (interactions between different types of afferents or influences from a central pattern generator) before it crosses the midline. Alternatively, it is possible that all the phase-dependent modulation of the contralateral responses is due to contralateral interventions. In the latter case, one would expect the phase-dependent modulation of the contralateral responses to depend exclusively on contralateral step-cycle events. It is, therefore, of interest to know whether one can find invariants for the modulation patterns.

Furthermore, little is known about the coordination between the ipsilateral responses and the concomitant contralateral responses in humans. This limits an adequate interpretation of the functional role of cutaneous feedback during human locomotion in terms of general concepts such as strategies of withdrawal (Hagbarth 1960; Sherrington 1910), assistance (Duysens et al. 1992), placing (Hugon 1973), or balance preservation (Yang and Stein 1990). Therefore, in this paper, attention will be directed to both the ipsilateral and contralateral reflex modulation in the biarticular thigh muscles, i.e., the long head of the biceps femoris (iBF and cBF, respectively), the semitendinosus (iST and cST), and the rectus femoris (iRF and cRF), after nonnociceptive sural nerve stimulation during human running (8 km/h). We concentrate on these muscles because they are important for preserving balance during normal locomotion (Winter 1984) and for directing the force exerted on the environment (Jacobs and Van Ingen Schenau 1992; Van Ingen Schenau 1990). In addition, the reflex modulation of the tibialis anterior (iTA and cTA) was studied on both sides. The iTA is studied once more to thoroughly investigate the previously reported intersubject variability after sural nerve stimulation (Duysens et al. 1992, 1993) and to check whether a concomitant variability is observed in the other muscles. A first attempt will be made to interpret the human cutaneous feedback system in terms of a synchronous bipedal synergism.

To check whether the observed reflex coordination is intensity independent, as suggested for stepping humans (Kanda and Sato 1983) and for walking cats (Loeb et al. 1987), we applied three levels of nonnociceptive stimulation. These stimulus strengths cause tactile sensations on the lateral side of the foot, which corresponds to the innervation area of the sural nerve.

Preliminary data have been published in abstract form (Tax et al. 1991, 1993).

METHODS

Experimental setup

Experiments were performed in two laboratories (Freiburg and Nijmegen). A group of 11 normal subjects (10 male, 1 female), between the ages of 21 and 45, was tested. The experiments were carried out in conformity with the declaration of Helsinki for experiments on humans. All subjects had given informed consent and had no known history of neurological or motor disorder. During all experiments the subjects wore a safety harness that was fastened to the ceiling.

The experimental setups in Freiburg (described in Berger et al. 1984; Dietz et al. 1986) and Nijmegen were completely comparable except for the treadmill configuration and the detection of foot contact. In Freiburg the latter information was obtained via two built-in force plates, corresponding to the split-belt configuration of the treadmill. In Nijmegen very thin insole foot-switch systems (designed in collaboration with Algra Fotometaal b.v., Wormerveer) were used.

Bipolar EMG activity was recorded in both legs by means of surface electrodes [PPG Hellige: silver/silver chloride, contact area 10 mm diam; mean interelectrode distance 4.2 ± 0.5 (SD) cm], over the long head of the BF, over the ST, the RF, and TA. The stimulation electrodes (interelectrode distance 2.0 cm) were positioned on the left leg approximately halfway between the exter-
nal malleolus and the achilles tendon, where the sural nerve is close to the skin surface. An electrical stimulus consisted of five rectangular pulses of 1-ms duration given at 200 Hz. A custom-made constant-voltage stimulator provided the desired stimulus amplitude.

**Experimental protocol**

An experimental session typically started with several short periods of running on the treadmill. In these periods the subject was trained to run at a comfortable, constant pace with the belt speed set at 8 km/h. Between these periods, during quiet standing, the perception threshold (PT) was determined psychophysically by gradually increasing (to above PT) and decreasing (to below PT) the stimulus amplitude in at least three series.

In the main experiment the stimuli were varied both with respect to the timing of presentation in the step cycle and with respect to the intensity (i.e., voltage amplitude). For variations in timing, ipsilateral or contralateral footfall could trigger the computer to release a (constant-voltage) stimulus after 1 of 8 different preprogrammed delays such that a reproducible stimulation at 16 equidistantly distributed phases in the step cycle was delivered. The corresponding stimulus currents appeared to be independent of the phase of stimulation. For variations in intensity, the PT was used as the unit of stimulation. Stimulus intensity could take on the values 0 PT (control), 1.5 PT, 2.0 PT, and 2.5 PT, yielding significantly different corresponding current levels.

Every stimulus condition was presented 10 times in the main experiment. All 640 trials occurred in random order. The successive stimulus presentations were separated by a random interval of 2–5 s, which corresponded to at least two cycles of unperturbed running.

**Data sampling and analysis**

The EMG signals were (pre-)amplified (by a total factor of 105), high-pass filtered (cutoff frequency at 3 Hz), full-wave rectified (Inman et al. 1952) and then low-pass filtered (cutoff frequency at 300 Hz). The resulting EMG envelopes, together with the stimulus voltage and current (measured with a sample-and-hold circuit), the ipsilateral and contralateral ground contact forces (or foot-switch signals), and a digital code referring to the stimulus condition were AD converted (500 Hz) and stored on hard disk for each trial (starting 100 ms before stimulation and lasting for 1,600 ms).

The 10 different trials of each stimulus condition were averaged. The average control trials were subtracted from the corresponding average reflex trials to obtain the “pure” reflex responses (subtracted trials or shortly “subtractions”). For the responses at each stimulus intensity and for each muscle, one single optimal time window was set for all 16 stimulus phases (Belanger and Patla 1987; Duyens et al. 1991; Yang and Stein 1990). When a muscle showed no or hardly any responses, no adequate window could be set. In that case an average window was used, calculated from the data windows used to measure responses in (in order of priority) the same muscle at other intensity levels, other nearby muscles in the same leg, or the same muscles in other subjects.

For each trial, the mean EMG value was calculated within the applicable window. Then the average and standard error (n = 10 trials) were determined from the EMG measurements of corresponding stimulus conditions. The same procedure held for the subtracted trials. The resulting data underwent both an amplitude normalization procedure so that a proper intersubject comparison could be made. For the amplitude normalization, the EMG data were scaled for each muscle to the maximum control value in the step cycle (i.e., the maximum spontaneous activity during 8 km/h running). For the normalization of the time axis, the step cycle was subdivided into 16 equal intervals. The reflex responses investigated will be presented according to their appearance in 1 out of these 16 intervals. This, in fact, corresponds to the usual procedure of normalizing the time axis with respect to the step-cycle time (Inman et al. 1981; Winter and Yack 1987; Yang and Stein 1990). To decide whether the sign of the observed reflex responses is significantly positive (i.e., facilitation) or negative (i.e., suppression), the subtracted responses underwent a Wilcoxon signed-rank test. For low numbers, which is the case in this experiment (in the order of 10), this nonparametric statistical test is preferable to the Student’s t-test.

**RESULTS**

**Normal locomotion patterns**

For each muscle the underlying background locomotor pattern is generally similar for the homologous muscles in both legs and similar for different subjects. This is a prerequisite for a proper comparison of the different reflex responses. The observed general characteristics of the BF, ST, RF, and TA locomotor patterns appear to be in agreement with the literature (see, for instance, Inman et al. 1981) and are shown on top of Figs. 2 (ipsilateral) and 4 (contralateral).

The BF and ST, both muscles of the hamstring group, have synergistic tasks with respect to knee flexion and hip extension, and antagonistic tasks with respect to rotation of the lower leg (the BF providing for exorotation and the ST for endorotation). During running the BF and ST are activated as close synergists. This is revealed by their coactivation during the two activity periods (end swing and midstance) in the step cycle. This coactivation is generally assumed to decelerate the forward swinging leg during end swing in preparation for stance and to provide for propulsive force during midstance.

The RF, the biarticular muscle of the quadriceps group, is also active during two activity bursts in the step cycle. These two bursts occur largely antagonistically with respect to the bursts in BF and ST. One burst appears during the transition from swing to stance imposing an extensor force on the knee to restrict knee flexion at and after footfall. The other activity burst appears during the beginning of swing to assist hip flexion and prevent abnormal knee flexion after toe-off.

The TA is predominantly active during the second half of stance and the entire swing period. In the period from end stance to the beginning of swing, this activity is used to assist the lifting of the foot by dorsiflexing the ankle. During the middle of the swing phase, the TA is activated to work against gravity keeping the foot in the air. At end swing the activity is usually largest to gently “float” the foot over the floor immediately before initial foot contact and subsequently gradually “ease down” the foot and keep it from slapping down on the floor immediately after initial foot contact.

**General reflex characteristics**

Reflex responses were found in all subjects (n = 11) and all muscles investigated. An example is shown in Fig. 1 for both the iBF and cBF of subject I. For each stimulus intensity, 16 subtraction traces are shown corresponding to the 16 phases of stimulation in the step cycle (Fig. 1, B and C). Several general characteristics emerge.

The earliest responses are found ipsilaterally and have a latency of ~50 ms and a duration of ~20 ms (most clearly seen in Fig. 1B, traces 6 up to 16 for 2.0 PT and 2.5 PT).
FIG. 1. Biceps femoris (BF) of subject 1 (JD). A: ipsilateral and contralateral BF (iBF and cBF, respectively) background locomotor activity in relation to the stance (signal up) and swing phases of both legs. Stick diagrams are shown on top. One single step cycle is subdivided into 16 equal intervals, the beginning of the 1st interval coinciding with ipsilateral footfall (see methods). B: for the iBF a typical set of 48 average (n = 10 trials) subtraction traces is shown. This set is subdivided into 3 subsets that refer to the 3 different levels of stimulation [1.5 perception threshold (PT), 2.0 PT, and 2.5 PT]. Bold lines indicate the time of stimulation, whereas dashed lines refer to a delay of 100 ms with respect to the onset of stimulation. The number on the left side of each subtraction trace indicates in which of the 16 step-cycle intervals the middle-latency response occurs. In fact, the responses occur during ipsilateral stance in trace 1–6 and during contralateral stance in trace 9–14. C: same procedure as in B, but now for the cBF. All panels: time calibration 100 ms; electromyographic (EMG) calibration 1 mV. Note: the size of the ipsi- and contralateral calibration bars is different to match the amplitudes of the corresponding background EMG signals in A. This matching allows a direct visual comparison of the reflex magnitudes in B and C.

However, these “early-latency” responses are small and are not found consistently in all muscles and all subjects. Consistent responses (in all 8 muscles and all subjects) are found at a latency of ~80 ms with a duration of ~30 ms. These “middle-latency” responses are mostly facilitatory and can be very large, sometimes larger than the maximum background locomotor activity, even during periods of the step cycle when the muscle is inactive (compare Fig. 1, A with B and C). Suppressive responses, predominantly in iST, iTA, and cTA, do occur as well. In general, these suppressive responses are followed by a rebound excitation (see, for example, Fig. 3B), whereas no (or small and not consistent) responses are observed after middle-latency facilitations (Fig. 1, B and C). In this paper attention will
be focused on the earliest consistent responses, thus with latencies of ~80 ms.

Averaged over the whole population of subjects and all intensities the absolute magnitudes of the iBF, iST, iRF, and iTA responses are 2.9 ± 1.6, 1.0 ± 0.3, 3.0 ± 1.8, and 2.5 ± 1.2 (mean ± SD) times larger, respectively, than the absolute response magnitudes of their contralateral homologues. The difference is statistically significant for BF (Wilcoxon signed-rank test: \( P < 0.01 \)), RF (\( P < 0.05 \)), and TA (\( P < 0.01 \)). For the ST thus no difference was found. This may be due to the predominantly suppressive responses found in iST and the predominantly facilitatory responses found in cST (see further).

In general, the magnitude of the responses varies across different phases, in contrast to the latency. No significant effect of stimulus intensity (for stimulation below the nociceptive threshold) on the middle latencies is observed (see, for example, Fig. 1). For each muscle the window settings averaged across all subjects are given in Table 1. A comparison between the ipsilateral and the contralateral window settings reveals a statistically significant longer latency for the contralateral responses (Wilcoxon signed-rank test: \( P < 0.01 \)). Averaged over all subjects the difference is 5 ± 4 (SD) ms. On both sides, no significant differences are observed between the three proximal muscles. Because these muscles are located between hip and knee, whereas the TA resides between ankle and knee, one could expect longer loop times for TA. A small difference is indeed found, but only ipsilaterally (Table 1).

On average, the latency of the iTA responses is 5 ± 4 (SD) ms larger than the average latency of the three ipsilateral proximal muscles (Wilcoxon signed-rank test: \( P < 0.01 \)). Despite the above-mentioned differences in response latency, it is clear that, taking the response durations (~30 ms) into account, all responses largely overlap in time.

In the following sections the phase-dependent modulation of the responses at all three intensities will be described in detail for each muscle. Subsequently, the intensity dependence of the magnitude of the responses will be described. Finally, the time dependency of the reflex responses will be investigated by means of a habituation analysis.

### Phase-dependent reflex modulation

Results of the ipsilateral and contralateral responses at all stimulus intensities are given in Figs. 2 and 4, respectively. This is done by plotting, for each investigated muscle, averages and standard errors of the subtracted responses as a function of the phase in the step cycle. It is clear that the response magnitude increases with increasing intensity of stimulation. This increase in response magnitude is generally accompanied by an increasing number of phases in the step cycle for which the level of significance is reached. For instance, the iRF of subject 1 (Fig. 2A) shows significant responses from phase 7 up to 10, 11, and 13 at 1.5, 2.0, and 2.5 PT stimulation, respectively.

On top of the panels of Figs. 2 and 4 "control" and mean (i.e., intensity averaged) "reflex" data are shown to facilitate a direct comparison between the responses and the background locomotor pattern. Whether the difference in the control and mean reflex data is statistically significant (Wilcoxon signed-rank test: \( P < 0.05 \)) is indicated by the open squares. In general, the statistical description of the phase dependency of the reflex responses is given with respect to these results.

**Ipsilateral BF.** Basically three periods of facilitatory responses can be discerned. One period is observed during midstance. The response amplitude decreases at end stance, with a minimum at the beginning of swing before contralateral footfall. During swing, two response periods can be observed, one with a maximum around phase 10 and one with a maximum around phases 15 and 16. These two periods are separated by a remarkable minimum around phase 14, where no significant response is found for the population (Fig. 2B). Most subjects show this minimum of facilitatory responses during this period. Subject 1, for example, shows an almost zero response in phase 13 (Fig. 2A). For this subject phase 13 is the only phase in which no significant iBF response was elicited at all three intensities. For two subjects this decrease in response amplitude even led to small (but statistically significant) suppressive responses.

Obviously the responses are not strictly correlated with the control activity. This is revealed by the fact that the reflex gain (magnitude of the pure reflex divided by the magnitude of the control activity) is considerably different for different phases. Subject 1, for example, shows the response minimum in phase 13, a period in which the control activity is large, whereas response maxima are found when the control activity is low (e.g., phases 10 and 16; see Fig. 2A).

**Ipsilateral ST.** The iST responses can also be subdivided into three periods. Significant suppressions occur during midstance and the latter half of swing. Significant, small facilitations are found during the first half of swing. These phase-dependent reflex reversals demonstrate that also for the ST there is no strict correlation between the response and the corresponding control activity in the step cycle.

During the two background activity bursts, the responses of iBF and iST are opposite in sign. The reflex coordination of iBF and iST during these periods is thus of an antagonistic nature, in contrast with their spontaneous activity pattern during unperturbed locomotion, when they are synergistically activated.

**Ipsilateral RF.** In the iRF two statistically significant facilitatory response periods can be discerned. Basically, these occur from end swing to midstance and from end stance to...
midswing, during both background activity bursts. In between these periods the responses are smaller. In one subject this decrease even led to small (but statistically significant) suppressive responses during end swing. Although the largest responses occur during the background activity bursts, there is no strict correlation. For subject 1, for example, the response in phase 2 is significantly larger than the response in phase 1, in contrast to the corresponding control activities (Fig. 2A).

**A**  
SUBJECT 1

![Graphs showing subtracted responses for different stimulus intensities.]

**FIG. 2.** Corresponding to the different stimulus intensities used (1.5, 2.0, and 2.5 PT), the subtracted responses (±SE) are plotted for all 4 ipsilateral muscles as a function of the phase in the step cycle. Phases 1 and 9 correspond to the onset of ipsilateral and contralateral stance, respectively. On top of these figures mean (of the 3 intensities used) "reflex" data (large squares) and the corresponding "control" data (small squares) are shown. In addition, the statistical significance of the reflexes (Wilcoxon signed-rank test: \( P < 0.05 \)) is indicated by the large squares being filled (not significant) or open (significant). The data are normalized with respect to the maximum background locomotor activity of each muscle (see methods). Black bars indicate the ipsilateral and contralateral stance phases (±SD). Note the different vertical scales in **A** and **B**.

**IPSILATERAL TA.** For subject 1 the iTA shows no or only small responses during stance, whereas statistically significant suppressions are seen during almost the entire swing phase (Fig. 2A). These suppressions reach a maximum in the latter half of the swing phase, during phases 14 and 15. Averaged across the subjects the iTA shows a reflex reversal (Fig. 2B). Facilitatory responses are observed from end stance up to midswing and suppressive responses during end swing. However, the standard errors are very large, which
indicates a large amount of intersubject variability. The intersubject variability is so large that even none of the facilitations is statistically significant. The reason for this lack of significant responses across all subjects is that several different modulation patterns of iTA responses can be distinguished. The first type of modulation pattern is based on responses that are predominantly suppressive, similar to the response pattern observed in subject 1: no or only small responses are observed during stance and only suppressive responses during swing (TA1: 5 subjects). The second modulation pattern is a mixture of suppressive and facilitatory responses. No or only small responses are seen during stance, facilitatory responses during early to midswing, and suppressive responses during end swing (TA2: 4 subjects). The third modulation pattern is predominantly facilitatory: no or only small responses are present during stance and only facilitatory responses during swing (2 subjects). In Fig. 3A the average iTA responses of the two largest subgroups of subjects are plotted.
A possible explanation for the existence of different subgroups can be derived from Fig. 3 B. Subtracted EMG traces during midswing are shown for the iTA of subject 1. A superposition of both facilitation (−80 to −110 ms) and suppression (−65 to −135 ms) is observed. The relative amount of facilitation, however, is small. Hence, despite the presence of excitatory signals, the net responses are always suppressive (Fig. 2A). In this context it is interesting that this subject, when tested 1.5 yr later, showed a reflex pattern that resembled that of the reflex reversal (whereas the reflex modulation patterns of the other muscles did appear to be reproducible).

Besides the large differences, the iTA response patterns do show similarities (Figs. 2 and 3A). First, in all subjects either small or no responses occur at the beginning of stance. Second, at end swing a similar tendency in the modulation pattern of all subjects can be observed. The subjects with predominantly suppressive responses show the largest suppressions during end swing, the subjects with the reflex reversal show the suppressions during end swing, and finally, the subjects with predominantly facilitatory responses show the smallest facilitations (relative to the background activity) during end swing. The similarity of this reflex modulation is also indicated by the fact that the population-averaged suppression in phase 15 is statistically significant (Fig. 2B).

**Contralateral BF.** Two periods of facilitatory responses can be discerned during the step cycle (Fig. 4B). During the background activity burst of late swing (phases 5 up to 8), the responses are rather small. During the background activity burst of midstance (phases 11 up to 13), larger responses are elicited, although the level of background activity is similar to that seen during late swing. For subject 1 the difference between the two response periods is even more pronounced (Fig. 4A). Hence the magnitude of the responses is not strictly correlated with the background activity.

The responses in phases 5 and 6 are not statistically significant (Fig. 4B), although the magnitude is comparable with the neighboring phases. In fact, the gain ("subtracted" response divided by the corresponding "control") is smallest in those two phases during end swing. As far as the limb configuration is concerned, these phases correspond to phases 13 and 14 of the ipsilateral leg. The latter phases are the very two phases for which the iBF gain is smallest during the step cycle.

**Contralateral ST.** The cST responses are comparable with those of the cBF, although the cST responses are statistically significant in more phases of the step cycle. The reflex coordination of the cBF and cST is thus in general synergistic during the step cycle. As in the cBF, the gain of responses reaches a local minimum in phases 5 and 6.

**Contralateral RF.** In general, the subjects show small and few responses during the step cycle. In the cRF of subject 1 a period (phases 15 to 3) can be discerned for which small facilitatory responses are statistically significant (Fig. 4A). However, after population analysis statistically significant facilitatory cRF responses can only be distinguished (Fig. 4B) during midswing (phases 4, 5, and 6). The background activity during this period is low. During the periods with high background activity, however, practically no responses are elicited.
A phase-dependent reflex reversal is observed in the cTA. By analogy with results found for the iTA, statistically significant suppressive responses are found during end swing (phases 6 and 7), whereas statistically significant but very small facilitatory responses are found during early stance (phase 9). On average, small facilitatory responses are elicited during the first half of swing (phases 15 to 1, see Fig. 4B). Although these responses are larger than those observed in phase 9, they do not reach statistical significance, because of the intersubject variability during this period.

Intensity dependence

Figures 2 and 4 indicated that the response magnitude increases with increasing intensity. This is further elaborated in Fig. 5. An impression of the intensity dependence can be gained by means of step-cycle averages: for each subject the
responses of the 16 phases in the step cycle are averaged. The results of a subsequent population averaging is illustrated in Fig. 5A. Ipsilaterally, the dominant upper leg synergy appears to be a combination of facilitation in iBF and iRF and suppression in iST. This synergy can be accompanied by a suppression (for subgroup TA1) as well as a facilitation (for subgroup TA2) in iTA. Contralaterally, a combination of facilitation in cBF, cST, and cRF and suppression in cTA appears to be the dominant synergy. Both patterns of reflex coordination are independent of the level of stimulation.

A further analysis is performed on the responses in different periods of the step cycle. It is shown in the previous section that the step cycle can be subdivided into one (cRF, cTA), two (iRF, iTA, cBF, cST), or three (iBF, iST) periods on the basis of the sign, magnitude, and significance level of the reflex responses (Figs. 2 and 4). The intensity dependence of the average reflex responses within each period is presented in Fig. 5, B (ipsilateral) and C (contralateral).

For the ipsilateral upper leg muscles the response increase in the investigated periods is significant both when 0 PT and
FIG. 5. A: population averages of the mean subtracted response in the step cycle are plotted (±SE) in histogram style for all muscles (in case of the iTA, the 2 largest subgroups are plotted). This is done for each level of stimulation separately. Calibration bar indicates 0.25 of the maximum background locomotor activity. B: population average of the mean response magnitude (±SE) in different periods of the step cycle (see text) as a function of stimulus intensity. The period concerned is indicated by its begin and end phase in the top left of each figure. For proper visualization the data have been normalized with respect to the absolute maximum in each row. An asterisk is plotted when the increase in stimulus intensity (0–1.5 PT, 1.5–2.0 PT, 2.0–2.5 PT) is accompanied by a significant change (Wilcoxon signed-rank test: \( P < 0.05 \)) in response magnitude.

1.5 PT are compared and when 1.5 PT and 2.0 PT are compared. When going from 2.0 PT to 2.5 PT, there is on average a small response increase in the iRF and iST and a small decrease in iBF. These are not statistically significant. The intensity dependence of the iTA responses agrees with the picture of the other muscles, but both subgroups are too small for statistical testing.

Contralaterally, the intensity dependence in the concerning periods is also similar to that of the step-cycle averages. The magnitude increase for increasing stimulus intensity does not reach statistical significance in all cases.

Habituation analysis

It is possible that a certain amount of habituation occurred because of the many stimulations in an experimental run. This habituation would be expressed as a decrease in both the facilitatory and suppressive responses during the course of the experiment. In other words, any habituation would cause a decrease in the absolute response magnitude during the course of the experiment. Because for small responses any habituation cannot be measured accurately, responses are only taken into account for this analysis if the
The magnitude of habituation (i.e., the relative decrease of response magnitude) reveals a correlation coefficient of —0.92. Habituation effects persist throughout the experiment. Linear regression analysis yields a correlation coefficient of —0.92.

average was at least 5% of the maximum control activity in the step cycle. The habituation analysis is carried out on the subtracted responses as a function of the trial number (1 up to 10).

In individual subjects, linear regression analysis does not show a statistically significant correlation between the subtracted responses and the trial number. However, 10 out of 11 subjects show a tendency toward habituation. Therefore the habituation effect is statistically significant as far as the whole population is concerned (Wilcoxon signed-rank test: \( P < 0.02 \)). The latter is indicated in Fig. 6, which is constructed as follows. First, for each individual subject, all corresponding subtraction trials are averaged over all stimulus conditions (i.e., all 1st responses are averaged together, all 2nd responses, etc.). This blunt averaging leads to one set of 10 numbers per subject, containing information on the time dependence of the habituation. Second, we have normalized the corresponding responses of the sets of all subjects with respect to their average and then averaged them across subjects. The approximately linear relation in Fig. 6 between response magnitude and the order of appearance of the response during the experiment indicates that habituation effects persist throughout the experiment. Linear regression analysis reveals a correlation coefficient of —0.92. The magnitude of habituation (i.e., the relative decrease of the response from the 1st trial to the response at the 10th trial, as predicted by the regression line) appears to be 25%.

**DISCUSSION**

One of the main conclusions of this study is that low-intensity stimulation of the sural nerve during human running is sufficient to elicit large, widespread, and statistically significant reflex responses with an average latency and duration of ~80 and 30 ms, respectively. These reflex responses seem to be an elementary property of human locomotion. This is indicated by the occurrence of the responses in all subjects, the consistency of most of the reflex patterns across the subjects, and, apart from a small amount of habituation, the reproducibility of the responses during the course of the experiment.

The simultaneity of the responses in both legs supports the notion of a coordinated cutaneous interlimb reflex. This (tactile) reflex coordination appears to be largely independent of stimulus intensity, because of the similarity in intensity dependence for all muscles. The observed (muscle-specific) response modulation indicates that this cutaneous reflex changes continuously throughout the step cycle, independent of the background locomotor activities. In other words, the cutaneous reflex synergy appears to be basically different from the locomotor synergy. The possible functional role of this reflex synergy will be discussed at the end of this section.

**GENERAL CHARACTERISTICS**

**TIMING OF THE RESPONSES.** After electrical stimulation of the sural nerve, responses with three latencies are found. This is in agreement with other studies on humans concerning cutaneous stimulation at the foot (Aniss et al. 1992; Burke et al. 1991; Yang and Stein 1990). Aniss et al. (1992) observed the evoked responses as a "damped" or as a "spindle-shaped" oscillation. Although the different background activities of the muscles in the latter study (constant background activation) and our study (phase-dependent background activation) make a direct comparison difficult, the results of the two studies seem to agree. When, in this study, the middle-latency response is facilitatory, often no or only small low-latency responses are found (damped oscillation, see, for example, Fig. 1). In contrast, when the middle-latency response is suppressive, a large rebound facilitation is generally found (spindle-shaped oscillation, see, for example, Fig. 3B).

The middle-latency cutaneous reflex responses have a somewhat larger latency in this study than in the literature. This may have two causes. First, the latency difference may be due to the different conduction velocities of the various nerves used. Yang and Stein (1990) demonstrated, in one single walking subject, suppressive responses in the iTA at ~68 ms for tibial nerve and 78 ms for sural nerve stimulation. A second cause can be the different conduction velocities of the various excitatory and inhibitory pathways that are assumed to participate in the reflex (see further): inspection of EMG data often reveals a combination of a suppression and a facilitation that begins slightly later (see Fig. 3B) (Aniss et al. 1992; Kanda and Sato 1983; Yang and Stein 1990). During nonlocomotor tasks, such as standing, mainly suppressive responses are elicited within the first 100 ms (Burke et al. 1991), whereas, with increasing speed of locomotion, the contribution of facilitatory pathways increases (Duyens et al. 1993). This might explain the somewhat larger latencies observed in this study.

During cat locomotion the earliest ipsilateral responses [the 1st peak (P1)] generally have a latency of ~10 ms followed by P2 responses with a latency of ~25 ms (Abrahmam et al. 1985; Duyens and Loeb 1980; Forsberg 1979; Pratt et al. 1991). The earliest contralateral responses found in the cat are facilitatory responses with a (P2) latency of 20–25 ms (Duyens and Loeb 1980). The human short-latency (~50 ms) and middle-latency (~80 ms) responses described in this paper may thus, in this respect, correspond to the P1 and P2 responses in cats.

**MAGNITUDE OF THE RESPONSES.** Tactile cutaneous stimulation is responsible for a strong reflex activation, which can be larger than the maximum background locomotor activity, even in phases of locomotion when the muscles are normally
inactivé (voir Figs. 2 et 4). En moyenne, le contre-latéral correspond à des réponses à la modalité des muscles flexeurs et estompées de l'ordre de 2,5 fois plus petite que la réponse de modalité ipsilatérale. En accord avec ce résultat, dans l'étude de Burke et al. (1991), les réponses contre-latérales ont été deux à quatre fois plus faibles que les réponses ipsilatérales après stimulation superficielle de l'OFR et de l'OST dans la phase d'oscillation. Néanmoins, contre-latérales peuvent être très grandes. Les résultats de cBF et cST montrent de grandes réponses, surtout pendant la phase contralatérale à la position (Fig. 4), ce qui souligne l'importance fonctionnelle de ces réponses de reflexe pendant la locomotion humaine.

La fonction importante de ces réponses de reflexe contre-latérales pendant la locomotion a également été indiquée en cas de stimulation mécanique. Les réponses (latérité ~ 70 ms) apparaissent de manière prédominante dans le muscle ipsilatéral lorsque la perturbation est appliquée pendant la phase de soutien (Berger et al. 1984). En conséquence, lorsque la perturbation est appliquée pendant le cycle d'oscillation, les réponses sont plus prononcées dans le contre-latéral, standing leg (Dietz et al. 1986). La différence est expliquée par le fait que “lors du gait, la compensation pour une perturbation à maintenir le corps en équilibre est réalisée par le standing leg, quelle que soit la position ou le swing leg était perturbé.” En accord avec ce résultat, après perturbation unilatérale, les réponses de muscles similaires sont de même amplitude dans les deux jambes pendant le balancement sur deux jambes (Dietz et Berger 1982) et sur deux jambes (Dietz et al. 1989).

Il ne peut être déterminé si l'effet d'habituation observé se produira après la durée de l'expérience (480 stimulations en ~ 37 min.) ou s'il satura. Sur le plan théorique, il est connu que les réponses de reflexes touchent peut-être disparaître ou même disparaître complètement (Desmedt et Godaux 1976; Dimitrijević et al. 1970; Fuhrer 1976; Hagbarth et Kugelberg 1958), indiquant que le système nerveux peut reconnaître un stimulant inoffensif, et que ce qui s'adapte à (ou apprend à ignorer) il. Sur le contraire, l'effet d'habituation pourrait être aussi importé un rôle: une habitude réapparaît après présentation de another (généralement, mais pas nécessairement plus fort) stimulant (Hagbarth et Kugelberg 1958; Spencer et al. 1966; Thompson et Spencer 1966). Ce qui peut avoir eu lieu dans cette expérience est que les trois différents types de stimulations utilisées et le continu après l'afférent input pendant la phase normale de running pattern. Cela signifie que la saturation de l'habitation se produira à un certain niveau, indiquant que les habitudes de réponse sont indissolublement présentes en locomotion humaine.

**Phase-dependent reflex modulation**

L'une des caractéristiques les plus saisissantes concernant la modulation du reflexe de modalité tactile est la dissociation fonctionnelle entre l'OFR et l'OST: ces muscles longs de jambes provoquent l'effet de reflexe antagoniste qui apparaît pendant les périodes de synergie de la locomotion dans le step cycle. Ce reflexe antagoniste action de l'OFR et l'OST n'a pas été précédemment rapporté dans la littérature. Cependant, des actions antagonistes pour close anatomie des synergistes ne se produisent pas au cours de cette situation. Par exemple, la stimulation des nerfs cutanés provoquera une dissociation comparable dans les muscles de la jambe (Pratt et al. 1991). Les différents muscles de la jambe et muscles de la cheville sont également rapportés pour l'effet de reflexe des muscles flexeurs et des muscles extenseurs de la jambe.

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For example, the occurrence of statistically significant facilitatory cRF responses during phases with low background locomotor activity (during contralateral midswing) indicates the existence of strong facilitatory sural nerve connections with this contralateral muscle. In this light the absence of cRF responses in periods with considerable background locomotor activity can be interpreted as an instance of premotoneuronal gating.

One should bear in mind that, during normal unperturbed locomotion, various cutaneous afferents of different parts of the foot are stimulated, both by pressure during stance and by movement of the skin during swing. In this natural case the integrated effect of the sural, tibial, and peroneal afferents might well agree with the concept of automatic gain compensation, whereas the effect of either one of these nerves stimulated in isolation (as in this study) might not.

In principle it is possible that a task group mechanism (Loeb 1985; Yang and Stein 1990) is the only premotoneuronal modulating factor. Within a single muscle different background locomotor activity bursts could be provided for by different groups of motoneurons. This could be the case when the two periods of activity are related to two different kinematic demands. A reflex reversal is then explained by excitatory pathways to one task group and by inhibitory pathways to another task group. In that case there would have to be a strict correlation between background activity and reflex magnitude within each activity burst. However, such a strict correlation is not observed (Figs. 2 and 4).

Reflex reversals are demonstrated in iST, iTA, and cTA. In addition to the general, large facilitation in iRF (see also Yang and Stein 1990) and iBF, instances of suppressive effects are found as well in some subjects. This means that stimulation of low-threshold cutaneous afferents can simultaneously activate both excitatory and inhibitory pathways to single muscles. It is therefore suggested that both facilitatory and suppressive responses are the net result of a balanced input of both (partly) opened excitatory and inhibitory pathways. For example, the amplitude decrease of the facilitatory iBF responses around phase 14 (Fig. 2) can then be regulated by two parameters: partly by closing the facilitatory pathway and partly by opening the inhibitory pathway. This would agree with the notion of a premotoneuronal modulation (switching) of both parallel excitatory and inhibitory pathways to single motoneurons (Yang and Stein 1990).

Potential sources of premotoneuronal modulation include the interaction of cutaneous afferent activity with afferent input related to limb position or movement, descending input, the spinal central pattern generator (CPG) for locomotion, or a combination of these elements. There is now general agreement that for the cat the main modulation of reflexes is exerted by the spinal CPG for locomotion (Pearson 1993; Sillar 1991). However, fine tuning of reflexes by interaction with other afferent input seems to play a role as well (Grillner and Rossignol 1978; Rossignol and Drew 1986; Rossignol and Gauthier 1980).

In general, the reflex responses are different for the homologous muscles in the two legs. For example, during the two active periods of the ST, suppressions are observed ipsilaterally (Fig. 2) and facilitations contralaterally (Fig. 4). Common features are observed as well. These are observed primarily with respect to the phase of the leg in which the responses occur, and not with respect to the phase of the stimulated leg. Examples are given in Fig. 7. The iTA shows suppressions at ipsilateral end swing, whereas the cTA shows suppressions at contralateral end swing. Perhaps, the intersubject variability of the iTA during early to midswing may be observed in the iTA during contralateral early to midswing as well. Another example is the gain reduction of reflexes during phases 13 and 14 in the iBF, which is also observed in the cBF (and cST) during phases 5 and 6. Both periods correspond to the same part of (end) swing of the two respective legs (Fig. 7).

Similarities of ipsi- and contralateral responses with respect to the phase of the corresponding leg are also observed in cats. For example, Duyens and Loeb (1980) have found that there is a sharp increase in facilitatory P2 responses in TA just near the onset of it’s control activity burst at the end of stance, both on the ipsilateral and on the contralateral side of stimulation. These observations suggest that, both in cats and humans, there are separate premotoneuronal modulating mechanisms for both legs.

Cutaneous reflex coordination: function and strategy

At this stage, the observed tactile reflex responses will have to be interpreted with caution because of the shortcomings in the kinesiological data and because of the lack of additional reflex data from other (monarticular) upper leg muscles. Nevertheless, this study still allows some interesting conclusions to be made regarding their functional significance. The subtracted data of Figs. 2B, 3A, and 4B are averaged for the three intensities used and redrawn in Fig. 8 to emphasize the coordination of the different muscles at each of the 16 phases in the step cycle. Several important periods in the step cycle will be discussed. In between these periods the different reflex coordinations gradually merge into each other. One should bear in mind that, in all phases of the step cycle, the observed tactile reflex coordination can be expected to disappear and be replaced by a protective reflex coordination when the range of noxious stimulation is entered (Duyens et al. 1992).

Ipsilateral stance. The most striking phenomenon in this period is the functional reflex dissociation within the ipsilateral hamstring muscles. During midstance (phases 3–5) this dissociation is even expressed by an antagonistic reflex action: the iBF shows facilitatory whereas the iTA shows suppressive responses. The effect of this reflex coordination is thought to be an exorotation of the lower leg. The lower leg is fixed on the ground, however, so in this period pressure will increase (positive feedback) on the lateral side of the foot. This increase is considered by Hugon (1973) as a ‘‘placing’’ strategy. As a consequence the upper leg will endorotate and cause the body to be directed toward the other (unperturbed) leg.

In the latter, swinging leg the reflex coordination seems to aim at an early placement (starting in phase 2, largest in phases 6 and 7): facilitatory cBF and cST responses (i.e., a deceleration of the forward movement of the contralateral leg), together with suppressive cTA responses (i.e., plantar flexion of the foot). This bipedal reflex can be interpreted as a nice example of a reflex being integrated into the background locomotor pattern such that postural stability and stable running cadence are assured. One could view this reflex coordination as some sort of early safety reaction (“early” with respect to perturbation severeness).
FIG. 7. For BF and TA, population averages of the contralateral control and mean (of the 3 intensities used) reflex data are plotted, starting with contralateral footfall (phase 9), and compared with the corresponding mean ipsilateral data, starting with ipsilateral footfall. Note that in this format, the black bar indicates the ipsilateral as well as the contralateral stance phase (±SD). Same format as in Fig. 2.

FIG. 8. Mean subtracted responses, determined from the top figures in Figs. 2, 3A, and 4, are redrawn to emphasize the reflex coordination in each of the 16 phases in the step cycle. The large vertical bars indicate ipsilateral and contralateral stance. The calibration bar indicates 0.5 of the maximum background locomotor activity.

One should keep in mind that, especially during stance, adjustments in EMG patterns need not be accompanied by kinesiological changes. For example, the EMG variability may reflect various "balance synergies" for the trunk during normal locomotion that are not reflected in different limb kinematics (Winter 1984). This may explain the fact that during the stance phase appreciable kinesiological changes were not observed after low-intensity cutaneous stimulation during human locomotion (Duysens et al. 1992) and not (Abraham et al. 1985) or only moderately (Drew and Rossignol 1987; Duysens and Loeb 1980; Forssberg 1979) during cat locomotion.

First half of ipsilateral swing. In this period (phases 8–12) both ipsilateral hamstring muscles show facilitatory responses, although smaller in iST than in iBF, whereas hardly any background locomotor activity is present. On the basis of this synergistic iBF/iST reflex coordination, the response would be directed mainly toward knee flexion and/or hip extension (an additional exorotatory component may be integrated in the reflex movement as well because of the larger responses in iBF). In contrast, the facilitatory iRF response in this period indicates an increased knee extension and/or hip flexion. This cocontraction of iBF, iST, and iRF might indicate a locking of the forward swinging leg or, according to the dominant extensor role for both biceps femoris and rectus femoris in humans (Lombard 1903), an earlier placement of the foot. However, the same hamstring/quadriceps synergy is observed during the beginning of swing for increasing
relatively low. Because precisely this coordination is found during the swing phase, whereas at the same time the contralateral, swing phase), whereas at the same time the contralateral, standing leg provides for an extra propulsive force. Generally the reflex coordination points at the “withdrawal” hypothesis (Hagbarth 1960; Sherrington 1910), although instances of it, only as far as the resulting movements are concerned, may be compatible with the so-called “assistance” hypothesis (Duysens et al. 1992).

ipsilateral end swing. The iBF/iST reflex coordination is similar as in midstance: iBF facilitation and iST suppression. As far as the iTA is concerned, the response pattern shows a general increasing influence of suppression during this period, in contrast to the facilitation found in the ipsilateral medial gastrocnemius (iGM) (Duysens et al. 1991, their Fig. 7B and compare Figs. 8, B and D). In fact, this lower leg reflex coordination is used to explain the induced plantar flexion during end swing in several subjects (Duysens et al. 1992).

During this period of swing, the iTA shows variable responses across subjects. Facilitatory responses would agree with the notion of a flexion reflex. Duysens et al. (1992) showed that, similar in the case of the knee, facilitatory iTA responses are accompanied by an additional dorsiflexion. In contrast, suppression of iTA activity will cause a plantar flexion of the ankle. Physical contact with any obstacle against the foot (stimulated by the electrical stimulus) is enhanced by iTA suppression, perhaps to generate push-off away from the obstacle, whereas a facilitatory response will, in coordination with the additional flexion around the knee, lift the foot above the obstacle to prevent further contact.

Contralaterally, the hamstring muscles also show a facilitatory, synergistic reflex response (phases 9–14). This synergistic cBF/cST coordination during contralateral stance is quite remarkable because during ipsilateral stance the homologous muscles on the ipsilateral side are reflexively activated as antagonists. This difference can only be related to stimulus location, which is found, by definition, on the ipsilateral side. In this view, any local reflex actions with respect to the area of stimulation, such as an exorotation of the lower leg, are expected to occur mainly in the ipsilateral leg, whereas a more integral, supportive role would be reserved for the contralateral leg.

The contralateral reflex coordination is aimed at a combination of knee flexion and/or hip extension. Flexing the knee in this period seems inappropriate, because the other leg has just been perturbed, and bending the knee of the standing leg can cause instability. Therefore hip extension seems to be the primary reflex task. This may have two possible functions. First, the system provides an anticipatory action for more stability: the ipsilateral leg is perturbed during its swing phase and the contralateral supporting leg reacts with an extension force to reduce the chance of a possible fall. The lack of any response in the cRF during this period, however, does not agree with this idea, because this muscle seems well suited to provide an additional extension force around the knee. A second explanation, which is not mutually exclusive from the first one, is that the facilitatory response is used to produce an additional propulsive force for the ongoing background locomotor task. In fact, Jacobs and Van Ingen Schenau (1992) showed that, while performing a propulsive force on the ground during standing, both BF and ST are strongly activated, whereas the RF activation is relatively low. Because precisely this coordination is found in the reflex pattern of these three contralateral muscles, it is likely that during this period the spontaneous locomotor task is reinforced with an additional propulsive force.

In summary, the ipsilateral reflex coordination points to a kind of flexion reflex (an immediate withdrawal of the ipsilateral leg does not lead to a severe loss of stability in the swing phase), whereas at the same time the contralateral,
though for transient tactile stimulation no change in swing duration is found, the locomotor program may still allow a prolonged cutaneous input from the foot to be instrumental for inducing the switch both from flexor phase to extensor phase and, in parallel, from flexor reflexes to extensor reflexes at end swing.

In conclusion, human cutaneous feedback from the sural nerve performs rather a complex role and does, as in cats (Drew and Rossignol 1987; LaBella et al. 1992; Pratt et al. 1991), not simply reflect an enhancement (i.e., assistance) of the ongoing locomotor task. It is suggested that the bipedal tactile cutaneous reflex control in humans is organized such that it promotes removal of the limb from the stimulus as quickly as possible, but only with the general constraint of preserving both the cadence and the balance at all times during the step cycle. The contralateral responses are thought to play an important, supportive role in promoting a smooth transition between these potentially conflicting requirements.

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REFERENCES


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