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Modulation of cutaneous reflexes by load receptor input during human walking

Abstract To investigate the influence of load on the modulation of cutaneous reflexes, evoked by sural nerve stimulation, electromyographic activity in different leg muscles (tibialis anterior, gastrocnemius medialis (GM), biceps femoris, and soleus muscles (SO)) was recorded in healthy humans during treadmill walking with different body loads. Sural nerve stimulation was applied at two times perception threshold during different phases of the step cycle. Reflex amplitudes increased with body unloading and decreased with body loading. The reflex responses were not a simple function of the level of background activity. For example, in GM and SO, the largest reflex responses occurred during walking with body unloading, when background activity was decreased. Hence, stable ground conditions (body loading) yielded smaller reflexes. It is proposed that load receptors are involved in the regulation of cutaneous reflex responses in order to adapt the locomotor pattern to the environmental conditions.

Key words Sural nerve reflex responses · Phase dependent modulation · Body loading · Body unloading · Walking

Introduction

Afferent input from load receptors is important for the regulation of gait in rats (Fouad and Pearson 1997), cats

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(Duysens and Pearson 1980; Pearson 1995), and in humans (Dietz 1992). For example, in the cat and rat, unloading of the leg is essential for the onset of the swing phase (Duysens and Pearson 1980; Fouad and Pearson 1997; Whelan 1996; for review, see Duysens et al. 2000; Pearson et al. 1998; Whelan et al. 1995). Recently, similar effects were observed in humans, especially under conditions when supraspinal control mechanisms were impaired or incapable to regulate reflexes, for example in newborn with immature pyramidal tracts (Yang et al. 1998) or in patients with spinal cord lesions (Harkema et al. 1997).

Load during gait has two types of effect. First, from animal studies, it is known that the load-related input, derived from proprioceptive and cutaneous afferents, can induce reflexes, some of which act directly on the central pattern generator (Conway et al. 1987; Duysens and Pearson 1980; Gossard et al. 1994; McCrea 1998; Pearson 1995; Pearson et al. 1992; Whelan 1996). Proprioceptive influences, for example body loading and unloading, have strong facilitatory effects on the electromyographic activity (EMG) of extensor muscles such as the gastrocnemius (GM) and soleus (SO), but only marginal effect on the flexor muscles both in cats (Gossard et al. 1994; Pearson et al. 1998; Whelan et al. 1995) and humans (Clement et al. 1984; Dietz and Colombo 1998; Dietz et al. 1992).

Second, input signaling load can influence transmission in various afferent pathways and thereby modulate reflex responses (Brooke et al. 1997). Such interactions have been described for postural tasks. From earlier research on cats (Whelan 1996) and humans (Clement et al. 1984; Dietz and Colombo 1998; Dietz et al. 1992; Rossi and Decchi 1994), it has been shown that postural reflexes depend on body load. Interactions between body load and cutaneous reflexes in humans were investigated during standing (Rossi and Decchi 1994). It was found that reflex responses to painful stimuli are depressed as a function of body support. Furthermore, there was a correlation between postural stability and the size of the reflex responses of the tibialis anterior muscle (TA). For

gait, the presynaptic modulation of afferent input is itself modulated during gait both in cat (Menard et al. 1999) and human (Faist et al. 1996; for review, see Stein 1995).

To investigate the effects of load on cutaneous reflex activity during standing, Duysens et al. (1993) used sural nerve stimulation. Similarly, in the present study electrical stimulation of this nerve was used. However, one has to bear in mind that during walking, there is a phase-dependent modulation of these reflex responses (Duysens et al. 1990; Zehr et al. 1998; for review, see Duysens et al. 2000). Functionally it was suggested that this modulation assists to adapt the locomotor pattern to the actual ground conditions. In the present study, the role of body load on this modulation is evaluated. Therefore, the aim of this study was to investigate the effects of body loading or unloading on reflex responses in leg muscles induced by electrical stimulation of the sural nerve during different phases of the step cycle.

Materials and methods

Experimental design

Local ethics committee approval and consent of informed subjects were obtained to perform the experiments on seven healthy subjects aged between 19–36 years (mean ± SD, 25.4±6.0 years). The stimulation electrode was positioned at the left ankle at about mid-distance between the external malleolus and the Achilles' tendon, where the sural nerve is closest to the skin surface. The electrical stimulus consisted of a train of five biphasic rectangular pulses each of 1 ms duration at a frequency of 200 Hz. To ensure that stimulus conditions remained constant throughout the experiment, the stimulating electrode was firmly attached over the nerve with surgical tape. Stimulation intensity was measured after each experimental run (see experimental protocol).

Experimental protocol

A detailed description of the methods can be found in previous studies (Duysens et al. 1990, 1991). The subjects walked on a treadmill (Woodway, Germany) with a speed and step frequency which were comfortable for the individual subject. An experiment started with several short periods of walking on the treadmill. In these periods the subject was trained to walk at a comfortable, constant pace. Between these periods, during quiet standing, the perception threshold (PT) was determined by gradually increasing (above PT) and decreasing (below PT) the stimulus intensity. This procedure was repeated between the experimental runs and at the end of the experiment to ascertain that the stimulus conditions were stable. Arguments for the constancy of stimulation have been given in detail in previous publications (Duysens et al. 1990, 1996). Therefore, it is assumed that by this approach the stimulus remains constant. When a large change (>15%) in threshold was observed following an experimental run, this run was discarded. When the change was small, the average threshold over the pre- and post-trial sessions was determined and used as a reference for that session. In general, the PT appeared to decrease slightly during the first half hour, presumably because the stimulation electrode, which was firmly attached over the nerve with surgical tape, gradually settled within the tissue and thereby changed the resistance of the skin. After this initial period, the PT was stable (as was also found in our previous studies). Habituation of responses was negligible with the stimulus-intervals chosen (see Tax et al. 1995 for more details).

The step cycle was divided into ten periods of equal length (0–90% of the step cycle in 10% increments) in order to obtain temporal resolution of changes in the reflex activity in leg muscles throughout the step cycle. The sural nerve was stimulated with an intensity of twice PT.

One experiment consisted of six task periods (i.e., walking with a loading or unloading), each with a duration of 12 min. During every task period the body load was altered. Following each task period, except the first (baseline condition), a resting period of 2 min was permitted followed on request by a 1-min period of walking with normal body load (NBL), to return to baseline conditions.

During the first task period, the subjects were walking on the treadmill with NBL. After this period, the body was either unloaded or loaded. During unloading, the body was supported by 20%, 40%, or 60% of body weight. Unloading was achieved by suspending the subjects from a parachute harness connected to an overhead crane. The degree of unloading was provided by a counterweight and was varied randomly for each subject. Subsequently, a fifth and sixth task period were performed with an added body load (BL) of 10% or 30%. Body loading was achieved by wearing a vest with different lead weights. To randomize these events, half the experiments began with the body load task followed by body unloading (BU), and vice versa with the remaining experiments. The influence of BU and BL on reflex responses during standing was tested in three subjects.

Recordings

During all task periods, EMG activity of the biceps femoris (BF), TA, SO, and GM of both legs was recorded using surface electrodes. Force sensors (located underneath the treadmill belts) provided a record of the force exerted by the legs on the treadmill. The force signal indicating left heel strike, and thus the onset of left stance, was used as a trigger. Individual step cycles were normalized to a relative time scale of one step cycle starting and ending with the left heel strike.

Triggering of the stimulator and randomization of trials were performed by a PC-based stimulation program. All signals were sampled at a frequency of 1000 Hz. The EMG of the muscles and the reflex effects of the electrical stimulus were recorded by an EMG amplifier (Madaus Schwarzer, Germany). The force signals from the sensors (Kistler K-SHEAR Piezotron acceleration sensor; Kistler, Switzerland) were used to determine heel strike, subsequently were fed to an amplifier (Kistler Multichannel Charge Amplifier), and were converted into a computer. The EMG recordings were amplified, band-pass filtered (30–300 Hz), full-wave rectified, and transferred together with the force plate recordings to a computer, where they were analyzed using Soleasy (ALEA Solutions, Switzerland).

For each of the ten phases of the step cycle, ten electrical stimuli were randomly applied in one experimental session. Stimuli were given at the beginning of any one of the ten periods. Stimulated steps were mixed with steps without stimulation (control stimuli, i.e., a "zero" pulse). The stimulus trains were given with an average interval of 3.5 s. For an average speed of 4 km/h, this corresponded to stimulation in about every third step. After sampling ten responses and ten controls for each stimulus condition (ten phases), the treadmill was stopped. The overall effects of nerve stimulation on leg muscle EMG activity was obtained by averaging ten trials for all 20 conditions (ten phases with and ten control phases without nerve stimulation) and subsequently by subtracting the resulting control data from the corresponding stimulus data ("pure" responses, see Fig. 1). Hence, for each experiment (i.e., loading condition) and for each muscle ten subtraction traces were obtained, corresponding to the ten phases in the step cycle.

Statistical analysis

The EMG responses were quantified by calculating the mean amplitude over the period in which the response occurred. Therefore, for each muscle, one fixed time window was set around the responses for all ten phases in the step cycle. The window was chosen in such a way that the whole response could be sampled within the window limits.

The response peaks appeared 70–80 ms after the stimulus and lasted for 30–40 ms. Therefore, the time window was set at 70–110 ms after the stimulus over all muscles in all subjects (Fig. 1B).

To allow comparison of leg muscle activity as a function of phases of the step cycle between the subjects, individual mean amplitudes of the averaged reflex responses for each condition were normalized to the maximum control amplitude (i.e., largest background activity of each subject) obtained during the walking condition with normal body load. To determine the reflex responses during body (un)loading, individual mean amplitudes were related to the maximum control amplitude obtained during each condi-

tion. To determine the influence of loading on the reflex responses and the influence of different phases on the mean amplitude, statistical significance (of the whole population) was determined with an analysis of covariance (ANCOVA, significance at $P<0.05$), with background activity as the covariance. Sometimes, the individual responses were tested to see how many subjects showed significant changes in reflex responses (ANCOVA, significance at $P<0.0033$, Bonferoni correction).

The influence of body load on the step cycle duration was determined with Scheffe's t-test (significance at level $P<0.05$).
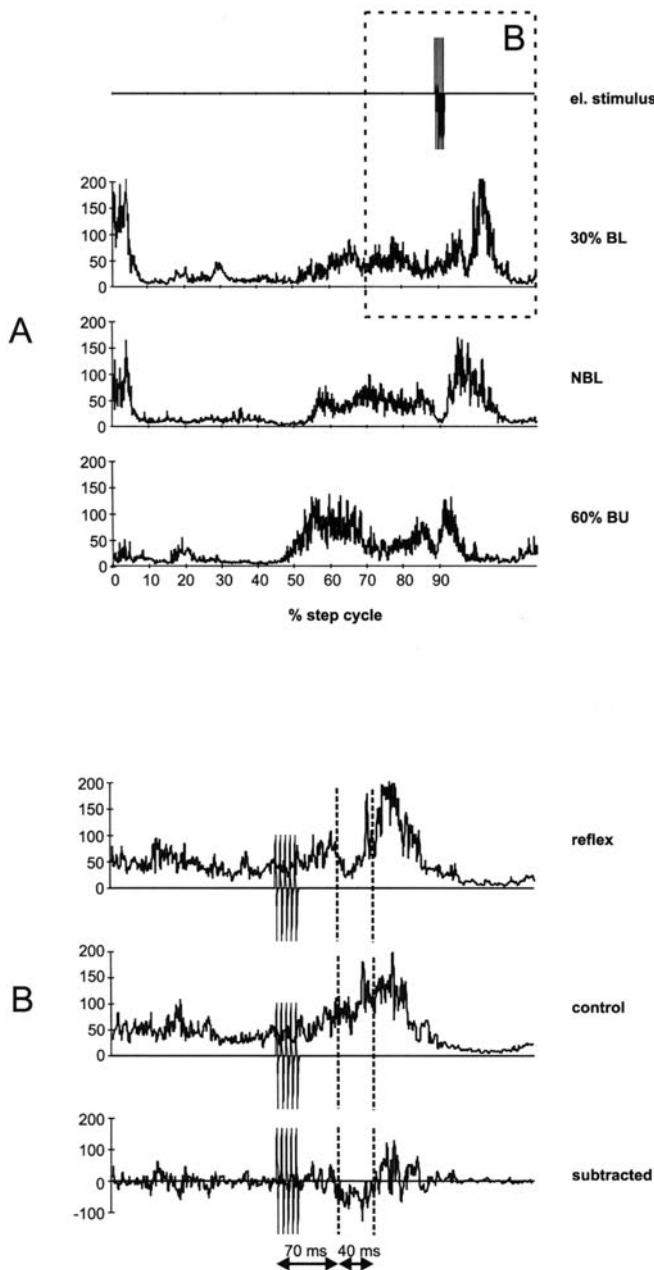
Results

Influence of body load on step cycle timing

The influence of body load in three loading conditions on the duration of the step cycle is summarized in Fig. 2. During the different loading conditions, the duration of the step cycle changed significantly (Scheffe's t-test, $P\leq0.05$). In three out of six subjects, the step cycle became longer during walking with BU (mean ± SD, 1252±18 ms for 60% BU) in comparison with walking with NBL (mean ± SD, 1163±9 ms; see also Table 1).

Fig. 1A,B Example of electromyographic (EMG) responses of the tibialis anterior muscle of the ipsilateral leg. **A** Reflex data (i.e., reflexes with background activity) during walking with different loading conditions. **B** Pure responses (subtracted data, i.e., reflex data minus control data) and time window settings (*vertical dotted lines*). *BU* = Body unloading, *NBL* = normal body load, *BL* = body loading
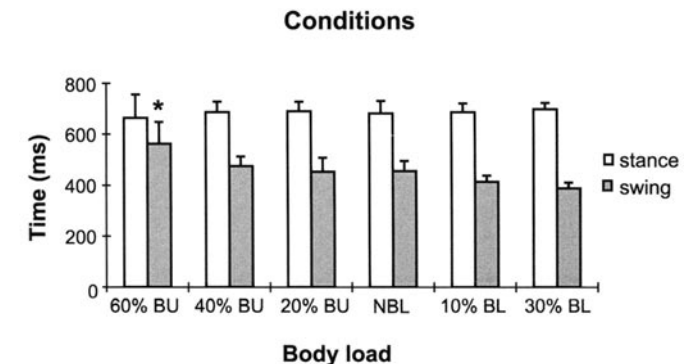
Table 1 Mean values and standard deviations of the stance and swing phases during walking with different body loads ($P<0.05$). Mean values and standard deviations of the stance phase, swing phase, and total step duration during walking with different body loads. These data are the mean durations of six subjects (one subject walked with metronome to walk stable and, therefore, is not included here). (*BU* = Body unloading, *NBL* = normal body load, *BL* = body loading)

Condition (%)	Stance		Swing		Total step	
	Mean (s)	SD (s)	Mean (s)	SD (s)	Mean (s)	SD (s)
–60 BU	0.66	0.09	0.56*	0.09	1.26*	0.20
–40 BU	0.69	0.04	0.48	0.04	1.18	0.07
–20 BU	0.69	0.04	0.45	0.06	1.17	0.08
NBL	0.68	0.05	0.46	0.04	1.16	0.09
+10 BL	0.69	0.04	0.41	0.02	1.12	0.05
+30 BL	0.70	0.03	0.39	0.02	1.10	0.04

*Significant difference ($P\leq0.05$)

Fig. 2 Duration of the stance phase, swing phase, and total step during walking with different body loadings. Data are the average over all subjects. *Asterisk* Significant difference ($P\leq0.05$)

Fig. 3 Loading/unloading effects on the EMG activity of the different muscles of the ipsilateral leg during walking without stimulation. Tibialis anterior (*TA*), soleus (*SO*), and gastrocnemius medialis (*GM*) EMGs are the averages from all subjects. Biceps femoris (*BF*) EMGs are the averages from the four subjects who had the extra EMG burst during walking with 60% BU
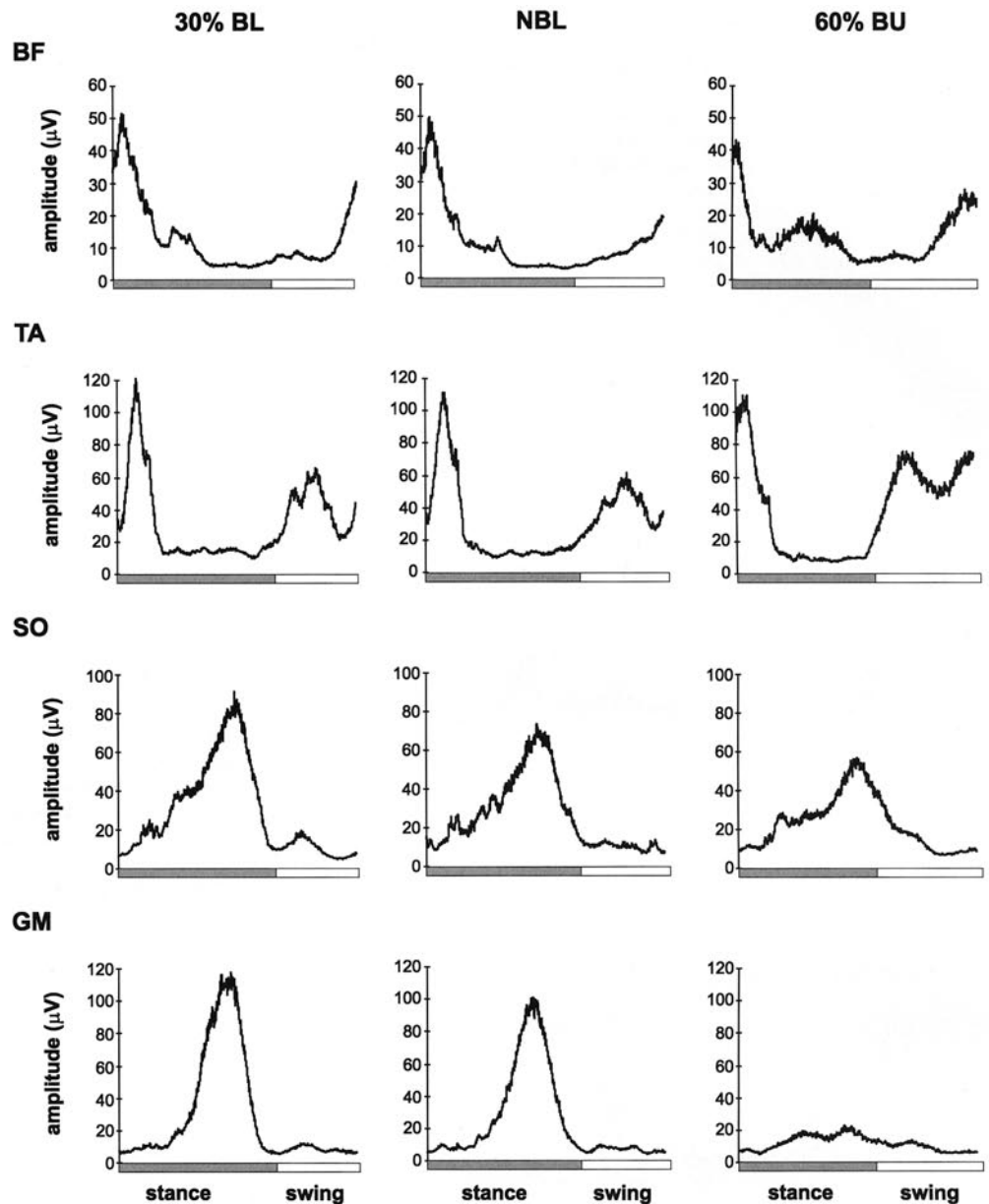
Walking with BL shortened the step cycle (mean ± SD, 1098±4 ms for 30% BL).

When the stance and swing phases were analyzed separately, as shown in Table 1, there was no significant difference in stance duration phase between the loading conditions (see also Fig. 2). In contrast, the duration of swing phase was load dependent. The more loading applied, the shorter the swing phase. Thus, the difference in step cycle length was primarily due to change in duration of the swing phase.

Influence of body load on background activity

During standing, there were no changes in reflex responses. Figure 3 shows the loading/unloading effects on the background EMG activity of the BF, TA, SO, and

GM of the left (ipsilateral) leg during walking. Three walking conditions are shown: NBL, 30% BL, and 60% BU. In all subjects, there was a strong effect of BU on the GM EMG activity in both legs compared with NBL walking. This activity was significantly reduced with less body weight (ANCOVA $P \leq 0.05$). During BL the amplitude of GM EMG activity increased slightly (difference not significant). The SO reacted similarly, but during unloading the activity did not decline as much as the GM activity.

In contrast to the GM and SO, the TA was more activated at unloading than during loading. The difference in EMG amplitude between the different loads was significant (ANCOVA $P \leq 0.05$). The difference in activity was not only present in the form of larger amplitudes but also in the form of longer bursts in all subjects. This means the TA was active longer during the step cycle (Fig. 3)

Fig. 4 Reflex reversal of the tibialis anterior muscle (*TAL*) of the ipsilateral leg in different loading conditions. Data are from one person. During walking with 60% BU, the reflex reversal disappears
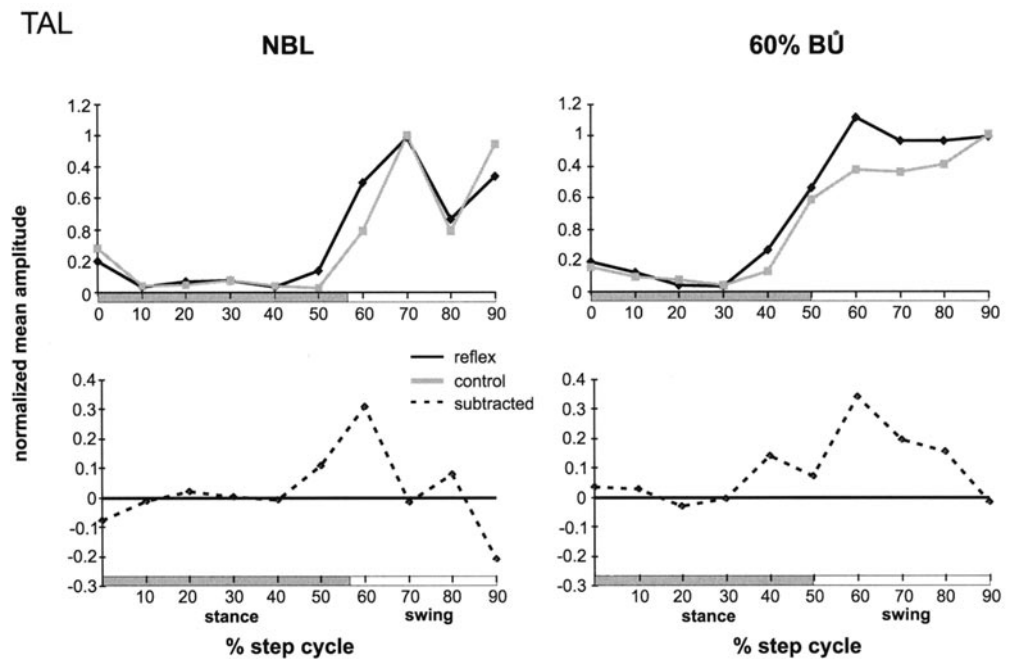
and was accompanied by a coactivation of the SO during unloading.

The BF was more strongly activated during BL and less so during BU compared to NBL. In four subjects, a second peak activity appeared during mid-stance during 60% BU (Fig. 3). This peak did not occur during NBL or BL in these subjects.

Influence of body load on EMG reflex amplitude

In response to the sural nerve stimulation during the step cycle, all seven subjects showed a facilitatory response with a latency of 70 ms, most pronounced in the TA and BF of the ipsilateral leg. The amplitudes of these responses differed considerably. In the TA and BF the largest responses were about 3–4 times background activity, while for the GM and SO they were only 1.5–2 times background activity.

To determine the significance for the pure reflex amplitude in each phase the reflex amplitude was statistically corrected for background EMG activity by using the ANCOVA test. All reflex responses were individually observed. There was a significant difference if $P<0.0033$ (Bonferoni correction).

Generally, when compared individually with NBL, significant differences in reflex amplitudes were observed only for 60% BU, 40% BU, and 30% BL. Therefore, only the results of these loads are presented here. In all muscles, reflex responses were larger with BU and reflex responses were larger in the ipsilateral (stimulated) than in the contralateral (non-stimulated) leg. The largest differences were observed in the 60% BU condition, at mid- and end of stance of the ipsilateral leg (phases 20, 30, 50), and at mid- and end of swing (phases 70 and 80). The 30% BL resulted in significant differences in

these phases, but not so frequently as in the BU conditions.

The reflex responses to sural nerve stimulation varied as a function of the phase where the stimulus was applied. In five subjects, a reflex reversal (i.e., reversal from facilitatory to suppressive responses) occurred in the TA at the end of swing during walking with body loading. A representative example of this reflex reversal is given in Fig. 4. However, during unloading (60% BU), the suppressive responses at end swing disappeared in two subjects (see Fig. 4). In the other subjects, the suppressive responses were seen in all loading and unloading conditions. No significant differences were obtained during the onset of stance and mid-stance (ANCOVA $P>0.05$). The data of the leg flexor muscles of all subjects are summarized in Fig. 5. The TA muscle of the ipsilateral leg showed facilitatory reflex responses that were most prominent in the stance phase (for 40% and 60% BU) and near the transition from stance to swing. This was most observed both in the 30% BL [significant differences in three subjects, $P<0.0033$ (ANCOVA)] and in the 60% BU condition (significantly different in two subjects). At the end of the swing phase, the reflex responses decreased again despite the high background activity.

The BF and TA showed the largest facilitatory reflex responses around the transition from stance to swing and the onset of the swing phase (phase 50–60). The reflex responses of both muscles decreased in mid-swing (phase 70 and 80) and the TA decreased again at end swing (phase 90; see Fig. 5). The BF increased at end swing. At onset stance (phase 0), the BF was decreased again in six out of seven subjects.

In the BF muscles most pronounced reflex responses were present during the unloading conditions. More unloading resulted in stronger reflex response amplitudes.

Fig. 5 Normalized mean amplitudes of the tibialis anterior (*TAL*) and biceps femoris muscle (*BFL*) of the ipsilateral leg during walking with different loading conditions. Reflex data (*black lines*, i.e., reflex and background activity), control data (*gray lines*, i.e., only background activity), and subtracted data (*dotted lines*, i.e., reflex minus control activity) are shown. Data are the averages obtained from all subjects and are normalized to the maximum mean EMG amplitude of the control step, obtained during walking with NBL
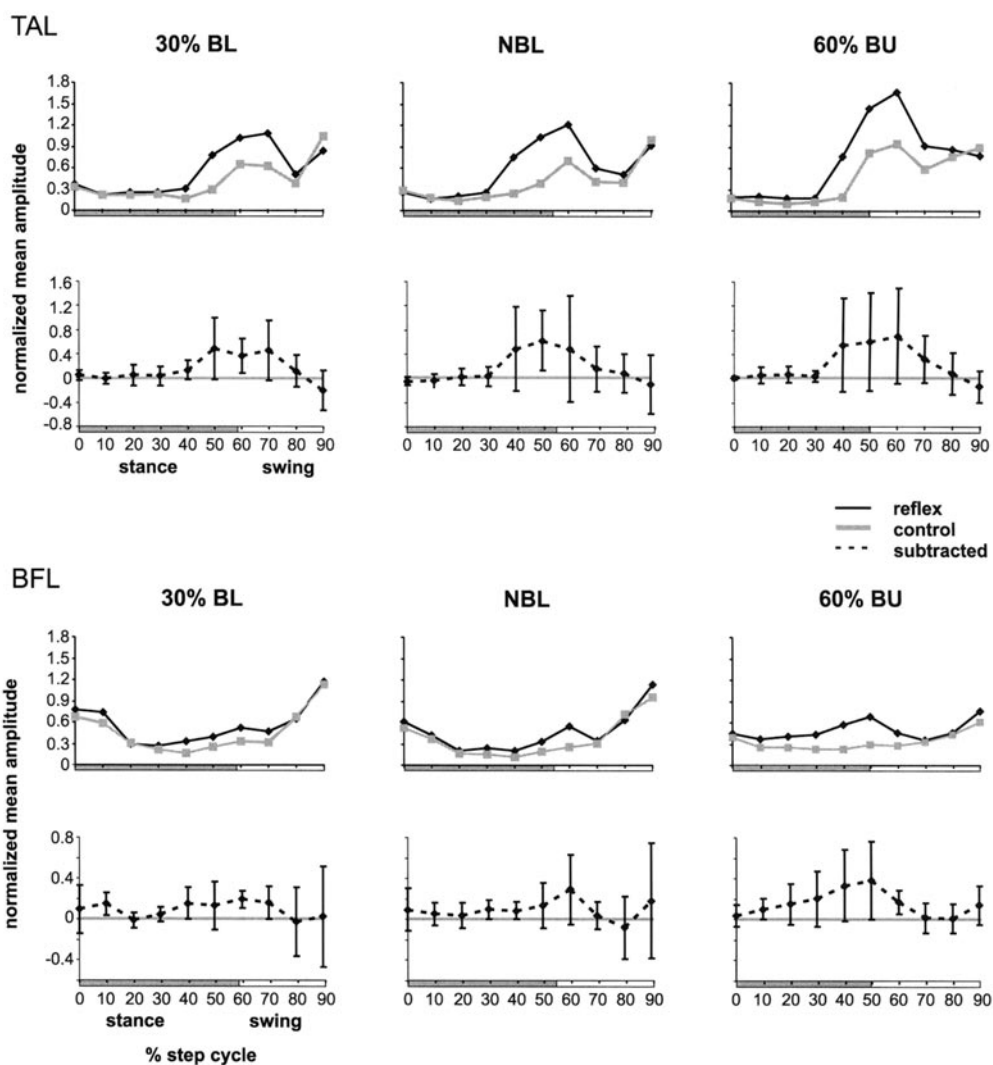

The difference between 60% BU and NBL was significant (ANCOVA $P<0.05$). In the ipsilateral BF, reflex responses appeared most clearly during walking with 60% BU in the transition from stance to swing (phase 50) and mid-swing (phase 80). The response amplitudes in phase 50 were significantly larger in 60% BU compared to those of NBL in three subjects. During walking with 40% BU, two subjects showed significant differences ($P<0.0033$). During BL, there was no significant difference in reflex amplitudes throughout the whole step cycle compared with the NBL condition. The BF of the right (contralateral to the stimulation) leg also showed reflex responses at the end of swing and onset of stance. However, these reflex responses were not as consistent as in the ipsilateral leg and, therefore, the data are not shown. In the ipsilateral ankle extensors, the responses were small and mostly suppressive. In the SO muscles (see Fig. 6) the largest suppressive reflex responses appeared during mid-stance. At the 20% phase the reflexes were smaller at unloaded conditions than at NBL. The difference between 40% BU and NBL was significant (ANCOVA $P<0.05$). During swing, there were no reflex

responses. The GM muscles of both legs had the most prominent suppressive reflex responses during mid-stance (phase 30, for GML for normalized and not normalized data, see Fig. 6) during walking with 30% BL. These (suppressive) reflex responses were more dominant than those of the SO muscles. Again the response amplitude decreased with BU. There was a significant difference between the unloading conditions and NBL ($P\leq 0.05$). During swing, reflex responses were absent.

Discussion

The aim of this study was to evaluate the load dependency of the cutaneous reflex responses, resulting from sural nerve stimulation. The main results obtained were: (1) a high degree of load dependency of the background EMG activity in extensor muscles (in particular the GM), (2) an increase in amplitude with BU of the large reflex responses in flexor muscles such as the BF and TA at end swing, and (3) an absence of reflex reversal during BU in some subjects.

Fig. 6 Unnormalized (**A**) and normalized mean amplitudes of the gastrocnemius medialis muscle (*GML*; **B**) and soleus muscle (*SOL*; **C**) of the ipsilateral leg during walking with different loading conditions. Reflex data (*black lines*, i.e., reflex and background activity), control data (*gray lines*, i.e., only background activity), and subtracted data (*dotted lines*, i.e., reflex minus control activity) are shown. Unnormalized data are from one person and normalized data are the averages obtained from all subjects and are normalized to the maximum mean EMG amplitude of the control step, obtained during walking with NBL
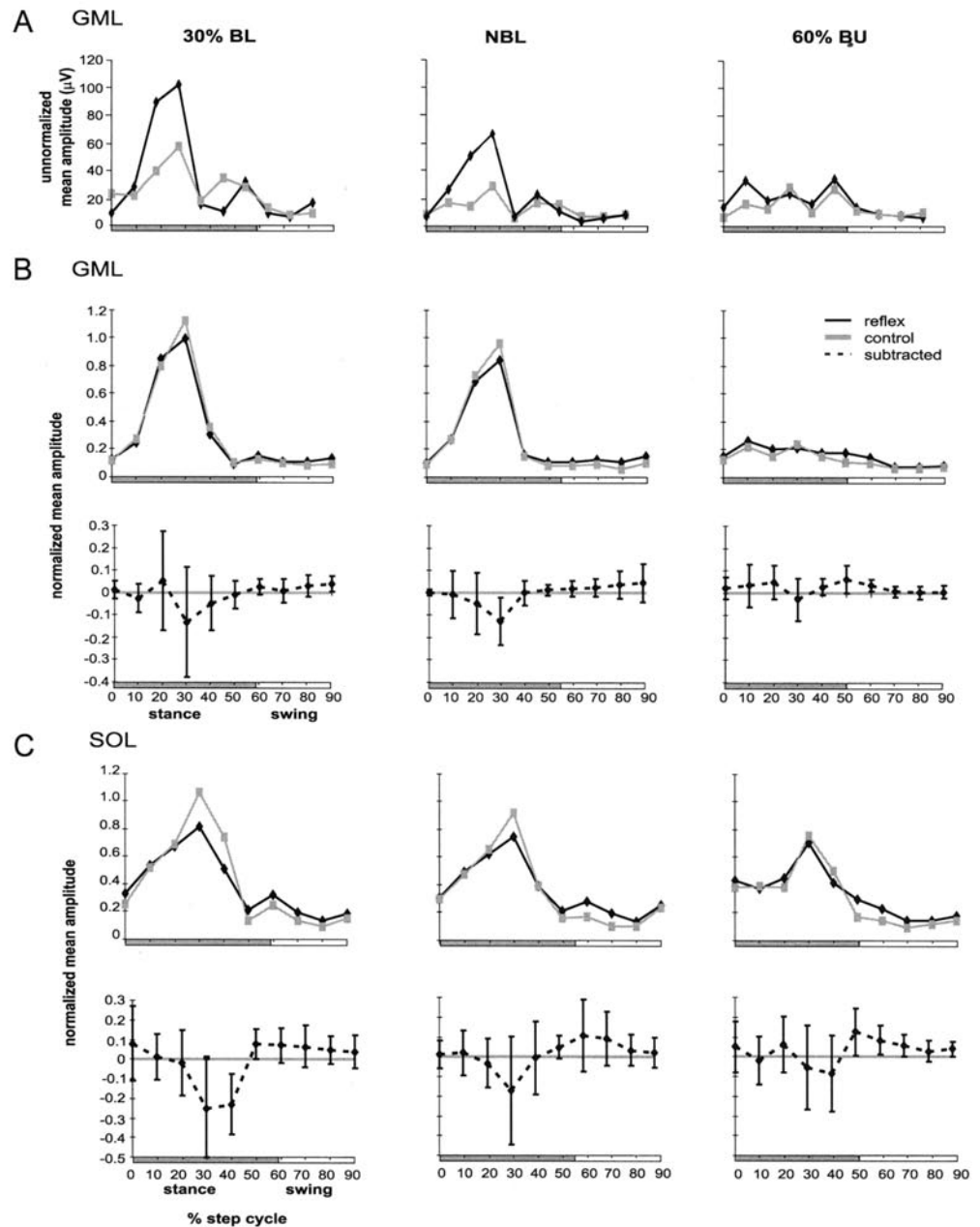
Influence of body load on step cycle timing

During the loading conditions, the step cycles were shorter in comparison with the NBL condition due to a shortening of the swing phase, which is in line with other studies (Ghori and Luckwill 1985). During walking with loading on the back, the center of gravity is raised, making the body equilibrium more unstable. The body appears to compensate for this by a shortening of the swing phase. This gives more stability of the step cycle with both feet on the ground. The fact that the stance phase did not alter is at variance with findings in children (Yang et al. 1998) and animals (Conway et al. 1987; Duysens and Pearson 1980; Fouad and Pearson 1997; Gossard et al. 1994; McCrea 1998; Pearson et al. 1992;

Whelan 1996; Whelan et al. 1995). These studies indicate that body loading results in an increase in step cycle duration as a result of prolongation of the stance phase. This seems to be the result of a prolonged loading of the extensor muscles. One has to notice that in these studies, the supraspinal control mechanisms are either not fully developed (children) or not intact (reduced animal preparations). In the present study, this control is intact, which can explain the difference. The present results are also at variance with other studies (Finch et al. 1991; Stephens and Yang 1999). However, in the latter studies (Finch et al. 1991; Stephens and Yang 1999), there were no counterweights used as in our study. The body was more or less fixed, thereby stabilizing the equilibrium. In the present study, the harness and extra weights did not sta-

bilize body equilibrium, but only produced (un)loading. The risk of falling was still given. Therefore, the control of equilibrium in the present study might affect the swing phase duration.

In fact, other studies where loading has been manipulated during gait also failed to show substantial changes in step cycle duration. Danion and co-workers (1995) used elastic cords ("penguin suit") to increase load. They showed that step cycle duration was invariant, but a slight decrease occurred in the duration of the swing phase. In a subsequent study (Danion et al. 1997) they made their subjects walk against a vertical load. Again it was shown that this could occur without changes in step cycle characteristics. The loading induced an increase in the EMG amplitude but did not affect the timing of the EMG bursts. Hence, in general, intact humans can maintain their step cycle characteristics despite different changes in load.

During unloading, however, the step cycle duration was longer than with NBL. This was due to a prolonged swing phase in BU, while the stance phase remained about constant. This observation is again at variance with earlier studies which indicated that BU does not influence the stride time duration (Stephens and Yang 1999). The discrepancy could be due to the difference in BU being smaller (30% BU; Stephens and Yang 1999).

Influence of body load on background activity

When subjects were stimulated during standing, no change in cutaneous reflex responses between BU and BL was observed. In this study, in contradiction to other studies (Rossi and Decchi 1994), no changes were found during standing. This can be due to the fact that the stimulus used here was not painful, and loading methods were different. In this study we used a vest with lead weights for loading and a parachute harness with counterweights for unloading, while in the study from Rossi and Decchi (1994) a controlled pressure was used for loading. Unloading was not performed in this study.

The load dependency of EMG activity in the antigravity muscles (i.e., GM and SO muscles) during walking, seen in all subjects, is in line with the results from earlier studies in cats (Duysens and Pearson 1980; Hiebert and Pearson 1999; Whelan 1996) and humans (Dietz and Colombo 1998; Dietz et al. 1992; Finch et al. 1991; Harkema et al. 1997). These studies provided indirect evidence that input from extensor load receptors, presumably Golgi tendon organs, play a major role in leg extensor activation and force feedback during locomotion. During walking with unloading, these load receptors are less activated resulting in a decrease in feedback (Hiebert and Pearson 1999) and a reduction in extensor EMG activity. Also other receptors, from joint, bone, and cutaneous receptors, might influence the reflex responses. It cannot be decided from this study which receptors were involved in detail.

In the other muscles, the effect of body load was less clear. The BF showed an extra activity burst in mid-stance during unloading. This can be due to the straps, used to fix the harness, which pulled the hips in a flexed position with higher unloading. This could require more extensor activity. Although this could explain part of the extra activity burst, the burst did not disappear when subjects walked without the straps. The BF is a knee flexor and a hip extensor. This extra activity of the BF can also be due to the BF acting as a hip extensor to replace the propulsion provided normally by ankle extension (which was nearly absent in 60% BU).

During BL there was no difference of the TA EMG activity compared to walking with NBL. The increase in the TA EMG activity during unloading is in agreement with other studies (Finch et al. 1991; Rossi and Decchi 1994). It may be due to the reduced activity in the antagonistic GM, i.e., due to the reduced reciprocal inhibition of antagonistic leg muscles (Duysens et al. 1991). Another explanation might be the lack of TA inhibition. Normally, the TA is inhibited at end swing to avoid an extra ankle dorsi-flexion in the crucial period around footfall (Duysens et al. 1992, 2000). Walking with strong BU might reduce this inhibition, resulting in excitation of the TA. A possible reason for the reciprocal activation of the SO during TA activation might be the change in the relation swing-stance phase duration. SO activity was slightly larger during loading than during walking with NBL, while the activity was lower during unloading. This difference was, however, not significant. Although being a leg extensor, the SO was less load-sensitive than the GM. This can be due to the fact that the SO is a predominant postural muscle and, therefore, receives less load-related reinforcing feedback to compensate for sudden load changes. This assumption is in line with findings in the cat (Hiebert and Pearson 1999).

Influence of body load on reflex amplitude

All muscles studied showed a phase-dependent modulation of the sural nerve reflex responses. This modulation was most clearly seen in the BF and TA. In some subjects the TA also showed a reflex reversal in late swing phase, as described earlier (Duysens et al. 1990, 1996; Yang and Stein 1990; Zehr et al. 1998). In some subjects the reversal disappeared at 60% BU. This is likely to be related to a difference in function of the TA at the end of swing. Normally the TA is active in that period in order to damp the sudden plantar flexion after heel strike. However, with 60% BU there is less need for this function since the reduced reaction force at the ground no longer imposes a strong momentum at the ankle joint. This situation is similar to the one observed during imposed limping, during which subjects were asked to walk with one leg held stiff (Faist et al. 1999; Van de Crommert et al. 1996). In that case, there is a reduction in heel strike and the preliminary data with sural nerve stimulation indicate that there is also an absence of TA

suppressive responses at end swing (Hauglustaine, Berger and Duysens, personal communication).

The amplitude relationship between reflex responses and background activity during walking with different body loads was studied in the light of the principle of "automatic gain control" (larger reflex responses with stronger background activity). However, an inverse relationship was observed for most muscles (BF, SO, and GM), i.e., when body load and background EMG level increased, the reflex response decreased. Most clear reflex responses occurred in muscles with a flexor function (TA ankle flexor and BF knee flexor) at the end of the stance phase. In the TA there was a distinct enhancement of the facilitatory responses at the end of the stance phase when the body was unloaded.

Such an enhancement might be due to an opening of the so-called "flexor reflex afferents" (FRA) pathway at end stance (Hultborn and Illert 1991; for review see Duysens et al. 2000), i.e., that cutaneous reflex pathways, which can activate flexor muscles, are opened just prior to the onset of the flexor burst at end stance (presumably to facilitate the flexion phase). The circuitry involved (FRA system), is thought to be in part the same as the flexor part of the "central pattern generator" for locomotion (Jankowska 1992). It is assumed that this part is suppressed by input from load afferents from extensor muscles (Duysens and Pearson 1980; Hiebert and Pearson 1999; Whelan 1996). In the current study a reduction in the size of reflexes was observed by loading. This would fit with the idea that extensor load receptor input suppresses activity in these common circuits for the generation of flexion reflexes and the flexion phase of gait.

Only small reflex responses were present in the SO and GM (extensor) muscles. In agreement with earlier work (Duysens et al. 1991) these reflex responses were suppressive and more prominent during the stance than during the swing phase. The suppressive responses were smaller in the BU conditions, presumably because background activity was also reduced (see Fig. 3) as compared to the other conditions (suppression is better expressed in a motoneuron pool in which many neurons are active). In line with earlier reports (Brooke et al. 1997; Duysens et al. 1991), it appears that the amplitude of reflexes do not strictly covary with ongoing EMG activity, suggesting that premotoneuronal mechanisms play a role.

Conclusions

The results indicate that afferent input from load receptors is involved in the modulation of cutaneous reflex responses. With increasing body load, a reduction in reflex response amplitudes became prominent, most clearly seen in the flexor muscles, such as TA and BF. It is proposed that higher body load improves stability of upright stance with the consequence that less reflex activity is required.

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