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RESEARCH ARTICLE

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Modulation of the biceps femoris tendon jerk reflex during human locomotion

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Abstract During gait it is generally accepted that there is a reduction in amplitude of H-reflexes as compared to standing. For short-latency stretch reflexes, however, it is less clear whether a similar reduction in reflex gain is present during locomotion. Stretches of constant amplitude are hard to produce under these circumstances and for this reason some previous studies on the biceps femoris (BF) have used "reduced gait" in which the stimulated leg is stepping on the spot while the contralateral leg is walking on a treadmill. With this method it was possible to show that BF tendon jerk reflexes are larger at end swing and therefore are likely to contribute to the EMG burst normally occurring in that part of the step cycle when the BF is rapidly stretched. In the present study two questions were addressed: first, whether the reflex is different in size during gait compared to standing and, second, whether it is modulated in size during the gait cycle not only during reduced but also during normal gait. It was found that during both types of gait there was a general reflex depression with regard to the respective control values obtained during standing at similar EMG activity levels. In previous studies on soleus and quadriceps, discrepancies between EMG activity and reflex amplitude have been ascribed to changes in presynaptic inhibition of Ia terminals mediating the afferent volley of the reflex. Based on the data presented, this may also be true for the BF. In both normal and reduced gait the reflex was similarly modulated in size, showing a maximum at the end of swing. This similarity implies that reduced gait may be useful as an acceptable alternative for normal gait in studies on phase-dependent reflex modulation during locomotion.

Key words Tendon reflexes · Biceps femoris · Gait · Ia afferents · Human

Introduction

Many studies have indicated that H-reflexes of leg extensors are depressed during gait as compared to standing (Brooke et al. 1991; Capaday and Stein 1986; Crenna and Frigo 1987; Dietz et al. 1990b; Morin et al. 1982). H-reflex stimuli allow for precise control but they have the disadvantage that they are artificial and that they bypass the sensitivity of the receptors involved. Therefore, several attempts have been made to introduce more natural muscle stimulations during gait. Most authors found that the short-latency reflexes induced by muscle stretch or tendon tap were also somewhat depressed during gait as compared to standing although to a different extent in different phases of the step cycle (Dietz et al. 1990a; Llewellyn et al. 1987; Sinkjaer et al. 1996). However, data were obtained on only a limited number of antigravity muscles such as quadriceps and soleus and it is not known what happens in the antagonistic muscles such as the biceps femoris (BF) and tibialis anterior. In one study (Van de Crommert et al. 1996) it was demonstrated that short-latency BF tendon jerk reflexes are present during reduced gait, but no comparison was made with standing. This reduced gait was introduced to minimize the variability of the stretches during locomotion. It was found that the amplitude of the reflexes increased at the end of the swing phase and that this increase was larger than expected on the basis of the level of EMG background activity. The question remains whether a similar phase-dependent modulation is present during normal gait. During reduced gait the joint angles are kept as constant as possible while the rhythmical loading of the leg is preserved. Therefore, one may expect that movement-related feedback is substantially reduced. Several studies have shown that such movement feedback is important for phase-dependent modulation of reflexes during cyclical locomotion-like movements (Misiaszek et al. 1995;

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for review see Brooke et al. 1997). In this view, it is possible that the previously described modulation during reduced gait is different from the one that could be found during normal gait.

The aim of the present study was therefore to assess the modulation pattern of the BF tendon jerk reflex during the normal step cycle against the background of the modulation found during reduced gait. The second question we addressed is whether the general reflex depression during locomotion compared to standing found for soleus and quadriceps is also present in the BF.

Materials and methods

All experiments were carried out on 13 healthy subjects, aged 21–33 years, all of whom gave informed consent to the procedure, which was approved by the local ethics committee. Biceps tendon jerk reflexes were obtained from the left leg during level walking on a treadmill (with separate belts for right and left feet) at a comfortable speed (3 km/h). Tendon reflexes were elicited by a hammer with a moment arm of 11 cm (weight 90 g) as described previously (Dietz et al. 1990a). The hammer was driven by a revolving field magnetic motor (weight of the whole apparatus 950 g; power 120 W) fixed to the posterior part of the calf (Van de Crommert et al. 1996). The hammer was accelerated by the motor to a constant angular velocity of 800°/s. A potentiometer located at the motor axis of rotation indicated the movement of the hammer and also allowed assessment of the moment of impact of the hammer at the tendon. Throughout all experiments, care was taken to evaluate the constancy of the stimulation by checking these potentiometer traces (Fig. 1; see also Van de Crommert et al. 1996). In additional experiments during standing we checked the variations of the reflex responses depending on the location of the impact of the hammer at the tendon. Within a range of 3 cm, reflexes varied about 10% in size. Within a range of 9 cm the reflexes declined to 20% of the value obtained at the optimum position. Therefore care was taken that during gait variations of the location of impact were below 3 cm on the biceps femoris tendon.

Force-measuring platforms under each belt of the treadmill were connected to a triggering circuit and allowed to trigger the hammer motor at a given delay after heel contact. At least 20 tendon reflexes were elicited during 16 equal phases of the step cycle using an interstimulus interval of 4 s. As a control condition the subjects performed isometric tonic voluntary contractions of the BF producing various levels of controlled EMG activity at different knee joint angles during standing by putting different amounts of body weight on the leg examined and activating voluntarily the BF. To achieve a constant EMG activity of the BF a visual feedback of the ongoing integrated EMG activity was given to the subject. EMG activity of the BF was recorded with surface electrodes, and knee and hip joint movements were measured using goniometers (for details see Van de Crommert et al. 1996). Reflex responses were measured as the rectified and averaged EMG activity. To obtain the pure reflex response the respective rectified and averaged background EMG measured in the step cycles between the stimuli was subtracted. Windows were set around the earliest reflex responses occurring 18–24 ms after the moment of impact of the hammer at the BF tendon. The responses typically lasted for 20 ms. Reflex normalization was performed by scaling the integral with respect to the maximum mean reflex response obtained during gait. To assess the influence of EMG background activity, reflexes elicited during walking were compared with control re-

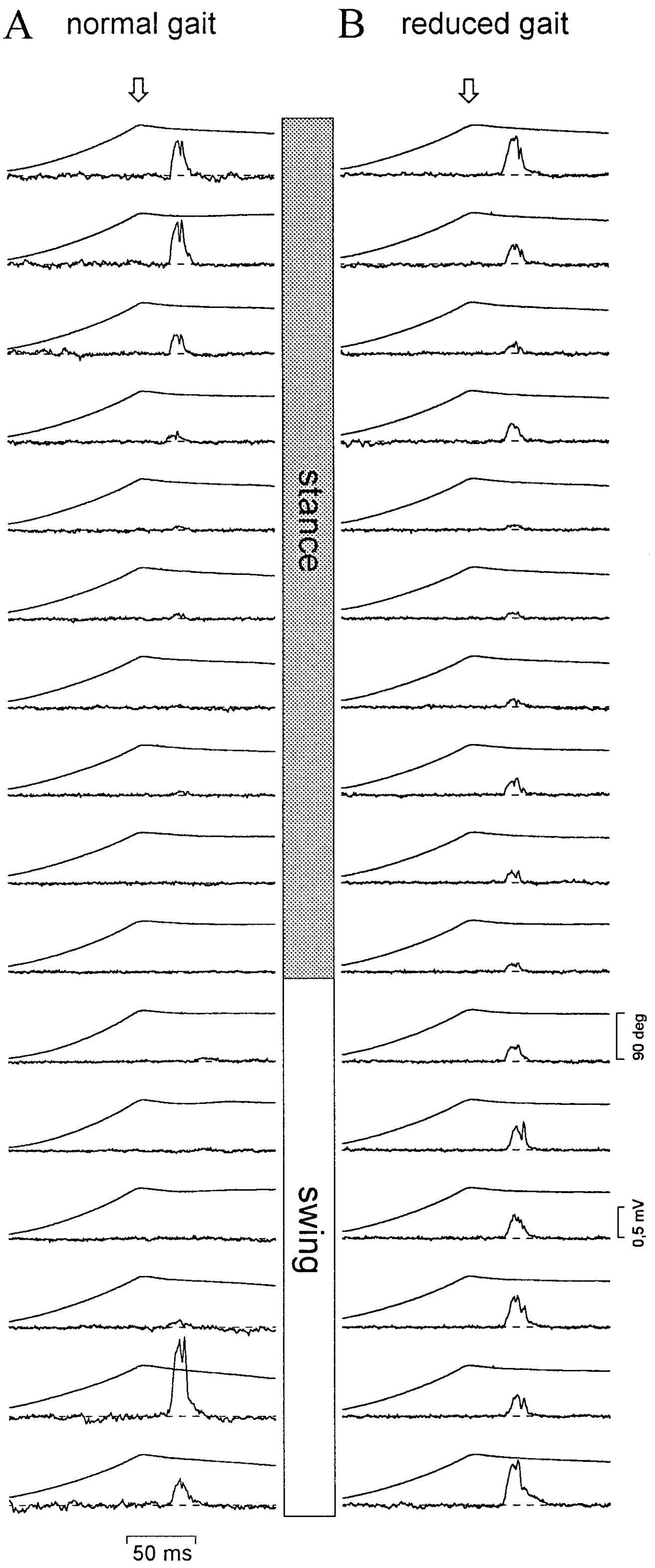

Fig. 1A, B Individual examples of biceps femoris reflex responses during gait. Rectified and averaged (n=20) net reflex responses, i.e., with background EMG subtracted, at 16 phases throughout the step cycle for normal gait **(A)** and reduced gait **(B)**. Along with the EMG of the biceps femoris, the signal of the hammer's potentiometer can be judged from the constancy of the ascending slope of the hammer position signal (potentiometer) over the different phases. For phase 1 the moment of impact of the hammer at the tendon is indicated by *an arrow*. *The hatched and open vertical bars* indicate the stance and swing phases, respectively (y-axis calibration: EMG 0.5 mV, potentiometer 90°)

sponses obtained at a similar level of EMG activity (±10%) and similar joint angles during standing (±10° difference). As the EMG activity in the m. rectus femoris was generally lower than in the BF, care was taken that only slight activation of the rectus femoris was present during the control conditions.

In five subjects the experiment was repeated and in the same session the reflexes were additionally measured during the reduced gait paradigm with only one belt of the split-belt treadmill moving (cf. Van de Crommert et al. 1996). The examined leg was lifted periodically on the non-moving belt (stepping on the spot) and was kept as rigid as possible whereas the contralateral leg was walking on the moving belt. The alternating rhythmic EMG activation pattern was also preserved in the examined leg. By minimizing knee joint movements to about 5°, this locomotion pattern permitted the stimulation conditions to be maintained at a stable level more easily than during normal gait.

To illustrate the degree of modulation during the step cycle in individual subjects, a modulation index (MI) was calculated using the formula suggested by Yang et al. (1991a): *MI=(max. reflex–min. reflex)×100/max. reflex,* where “max. reflex” and “min. reflex” are the maximum and minimum mean reflex sizes obtained throughout the step cycle. To illustrate the general depression of the reflexes during gait, the mean reflex size during the whole of the gait cycle was compared with the mean reflex size during standing. To assess the significance levels of differences between the reflex size obtained during gait and the respective controls during standing, an analysis of variance and Bonferroni corrected *t*-tests were performed. Modulation of the reflex size during walking was investigated by analysis of variance using the different phases as factor.

Results

Because of the rigid fixation of the hammer device, it was possible to obtain near constant tendon taps even during normal gait but the exact location of the impact on the tendon varied slightly (estimated range 3 cm). In

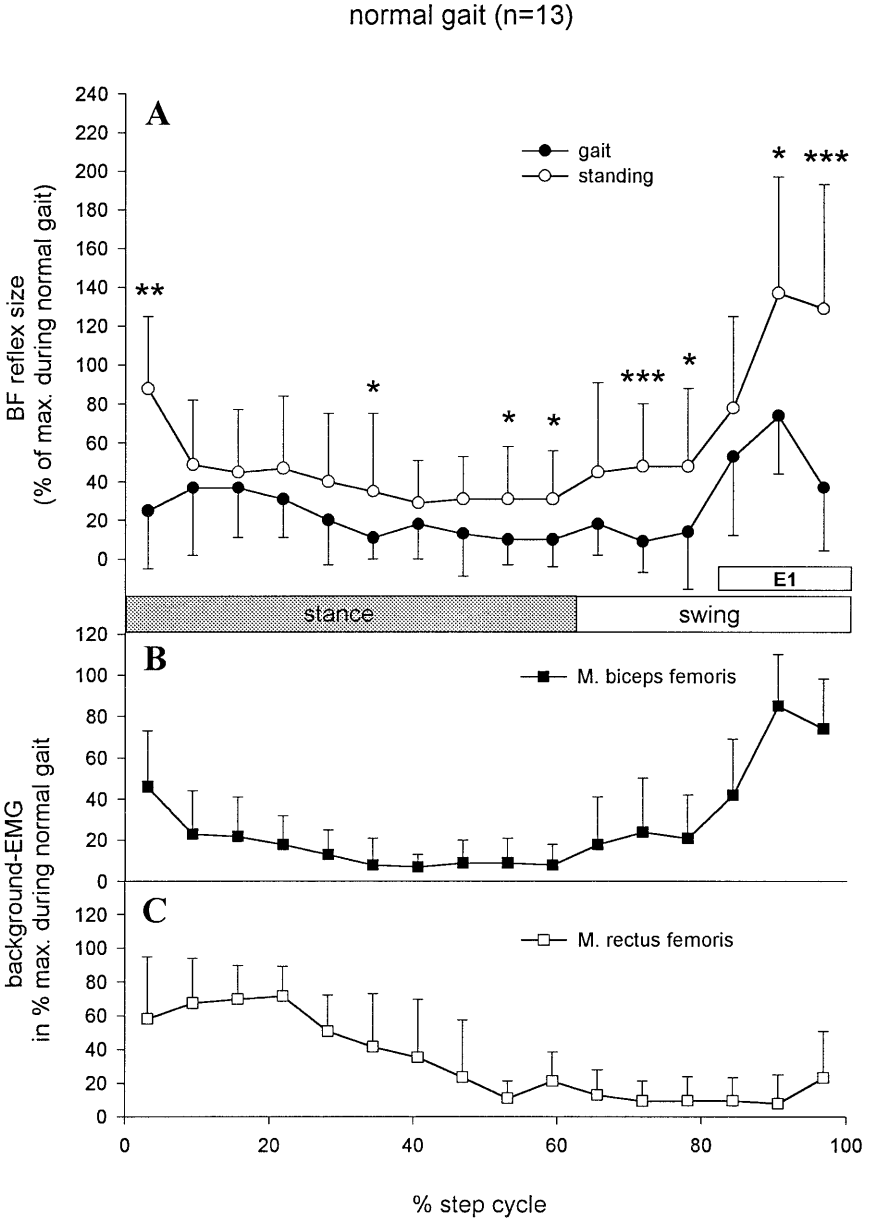

Fig. 2 **A** Quantified values of the subtracted normalized biceps femoris tendon reflex during gait and standing (control) at corresponding knee angles and voluntary EMG activity. To allow intersubject comparison the reflex integrals (*n*=20) were expressed as the percentage of the maximum reflex observed during gait. *Each symbol* represents the mean reflex integral of 13 subjects. *Vertical bars* indicate 1 SD. **B, C** The integrated background EMG values of biceps femoris **(B)** and rectus femoris **(C)** were normalized to the maximum EMG value obtained during gait. The percentage of the step cycle at the time of the hammer impact was calculated from heel contact. The E1 phase is indicated by *a horizontal bar*. The statistical significance of the differences between gait and standing was assessed by analysis of variance and Bonferroni corrected *t*-tests (**P*<0.05; ***P*<0.0l; ****P*<0.001)

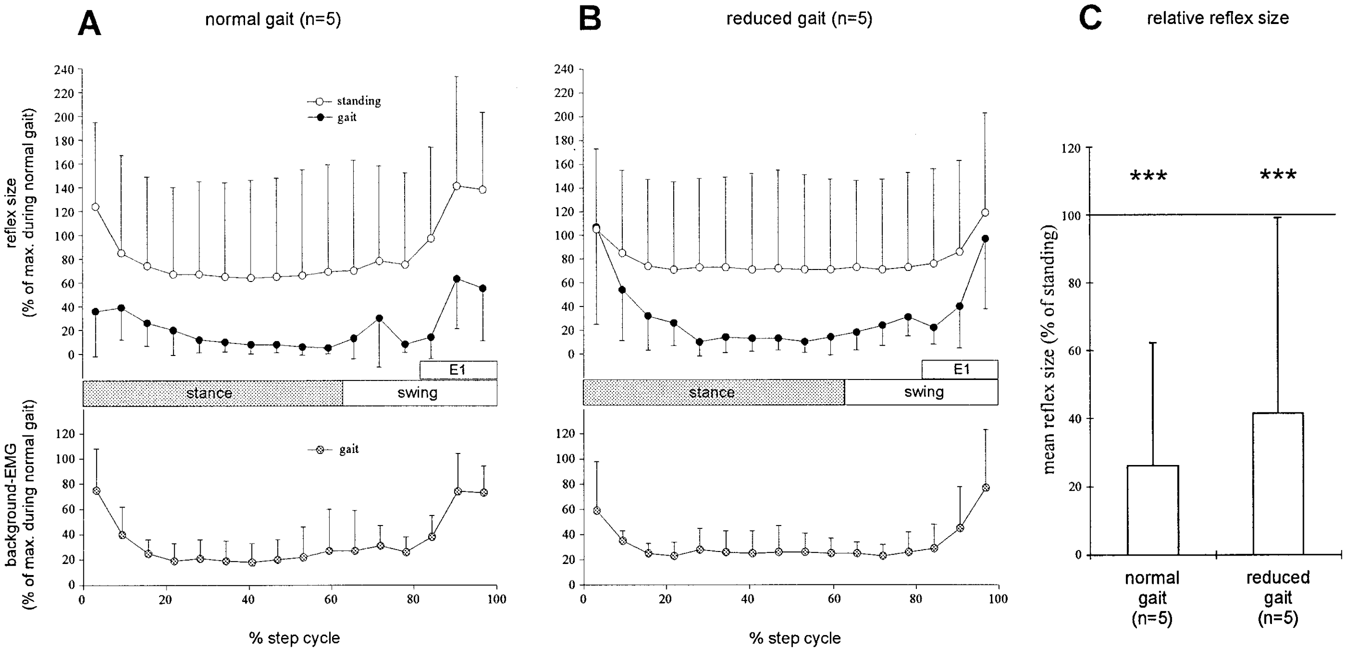

Fig. 3 Modulation of the biceps femoris tendon jerk reflex in five subjects investigated during both normal **(A)** and reduced gait **(B)**. All data on single subjects were obtained within one experimental session. The E1 phase is indicated by *a horizontal bar.* Reflexes and background EMG in **A** and **B** were normalized with respect to the maximum values obtained during normal gait. Symbols as in Fig. 2. **C** Mean reflexes during normal and reduced gait (i.e., average of reflex size over the 16 phases of the step cycle). The reflex size during gait is normalized with respect to the value of the reflex size obtained in the standing condition. Significance levels of differences between gait and standing were calculated by analysis of variance (***$P<0.001$)

additional experiments we were able to show that within this range only minor changes occurred in reflex size (see “Materials and methods”). In all subjects a clear modulation of the BF reflex response during the step cycle was observed. Figure 1 shows the EMG recordings taken from a single subject where experiments were performed during normal and reduced gait. It illustrates the net reflexes after subtraction of the background EMG activity during the 16 phases of the step cycle. A clear modulation of the reflex size can be seen in both locomotion paradigms. The quantitative values during normal gait of 13 subjects are shown in Fig. 2A, which demonstrates the modulation of the reflex response during gait and the respective responses obtained in a control condition with a similar EMG activity and knee joint angles during standing. The reflex responses of the control condition were clearly increased with increasing background EMG activity (Fig. 2B). The reflex modulation pattern during gait, however, was not simply related to that of the BF background EMG. The ongoing EMG activity of the rectus femoris during gait did not have an obvious effect on the BF reflex size (Fig. 2C). A reflex maximum can be seen towards the end of the swing phase. During normal gait, this maximum is followed in most subjects by a slight decrease in reflex size around heel contact (during the transition from swing to stance), both in terms of absolute values and with respect to the control condition. In several subjects the reflexes slightly increased again at the beginning of the stance phase.

During most phases of the step cycle the reflex level was below the control condition and the size of the gait reflex at the end of swing was larger than in all other phases. A two-factorial analysis of variance with the 16 phases as one factor and standing vs. gait as a second factor showed significant differences between standing and gait ($P<0.0001$) and also between phases ($P<0.0001$). Furthermore the interaction was significant, reflecting that there is modulation during gait different from the EMG-matched control condition ($P<0.05$).

The quantitative values of the five subjects tested during both locomotion paradigms are presented in Fig. 3A,B. During normal gait the pattern of phase-dependent modulation was quite similar to the one found during reduced gait. In particular the amplitudes were especially large in the first extension (E1) period of the swing phase (as also observed in a previous study; see Van de Crommert et al. 1996). The main difference was that in normal gait the reflexes were slightly smaller near foot contact than during reduced gait. In fact at that point of the step cycle the size of the reflexes was similar for standing controls and for reduced gait while for normal gait there was still a sizeable difference. It is noteworthy that during reduced gait at that time of the step cycle, joint movements are smaller than during normal gait. The reflexes during standing for Fig. 3A,B were different since they were matched, for each phase, to the corresponding EMG levels and knee joint angles as observed during gait. Figure 3C represents the mean relative reflex size of the entire step cycle (i.e., average of the 16 phases shown in Fig. 3A,B as a percentage of standing) of the five subjects tested during normal and reduced gait. During both locomotion paradigms a significant reflex depression was found compared to the respective control values obtained during standing at similar EMG activity levels (*P*<0.001), and in both paradigms a significant reflex change was seen during the step cycle (*P*<0.0001, analysis of variance). However, the mean reflex size during normal gait was not significantly different from the one obtained during reduced gait. Furthermore, the rhythmic activation pattern of the background EMG activity in BF was preserved (Fig. 3A,B, bottom trace).

The mean modulation index (MI) of the BF reflex of the five subjects shown in Fig. 3 was 97.0(±4.2)% and 94.5(±4.4)% for normal and reduced gait, respectively. The modulation index of the background EMG was 91.9(±7.0)% and 67.7(±14.4)% for normal and reduced gait, respectively, this difference being statistically significant (*P*<0.05, Scheffé test). Hence, reflex modulation depth, as expressed by MI, was relatively independent of the modulation range of the background activity for these two locomotor tasks.

Discussion

Two main results were found in the present study: (1) short-latency reflexes of the BF evoked by a tendon tap are generally smaller during locomotion than during a standing condition with equivalent voluntary EMG activity and (2) the reflexes are modulated in a phase-dependent fashion during normal treadmill walking similar to that found during reduced gait.

The finding of the overall reduction in size of tendon jerk reflexes in BF during gait illustrates that such reductions are not restricted to typical antigravity muscles such as soleus and quadriceps (Dietz et al. 1990a; Llewellyn et al. 1987; Sinkjaer et al. 1996). The depression cannot be explained by a lowering in general background EMG activity during gait as compared to standing since these levels were carefully matched for each phase of the step cycle. It has been speculated that a mismatch in EMG activity and reflex level may be due to changes in presynaptic inhibition of Ia afferents (Capaday and Stein 1986; Dietz et al. 1990a, 1990b; Morin et al. 1982; for review see Stein 1995).

Recently, for Ia terminals projecting onto soleus, evidence was provided for changes in presynaptic inhibition during different periods of the step cycle (Faist et al. 1996). These changes may be of peripheral or central origin and may be responsible at least partly for a functionally meaningful modulation pattern of short-latency reflexes. However, as recently shown (Morita et al. 1997), it has to be noted that the sensitivity of H-reflexes, tendon taps and stretch reflexes to presynaptic inhibition are very different. Thus conclusions about one of these reflexes based on results from the others have to be drawn with caution. Modulation of these different short-latency reflexes during the step cycle has been reported for both soleus (Capaday and Stein 1986; Crenna and Frigo 1987; Llewellyn et al. 1987; Sinkjaer et al. 1996; Yang et al. 1991b) and quadriceps muscles (Dietz et al. 1990a, 1990b). For the BF only data during reduced gait were available, showing a maximum of the tendon jerk reflex at the end of swing (Van de Crommert et al. 1996).

The question arises whether data obtained during reduced gait can be extrapolated to normal gait. For the soleus H-reflex a similar phase-dependent modulation has been reported during reduced gait (single-limb treadmill walking), normal treadmill walking and single-limb stepping on one spot (Crenna and Frigo 1987). The results described here for BF tendon jerk reflexes during reduced gait confirm the pattern described by Van de Crommert et al. (1996). In agreement with Crenna and Frigo (1987), it was found that the modulation pattern was similar during reduced and normal gait. One minor difference is the relatively larger reflex response around foot contact during reduced gait as compared to normal gait. A possible reason for this difference could be a less constant hammer impact during normal gait in that period of the step cycle. However, this is unlikely since no difference in reflex size was observed in the remaining phases of the step cycle including mid-swing when one might expect much greater instability. In the latter phase the knee is maximally flexed during normal gait as compared to reduced gait, where the knee joint is kept as stiff as possible. Hence, although there must have been more variability in the exact locus of impact of the hammer on the tendon during normal gait as compared to reduced gait, this did not have a pronounced effect on the amplitude of the responses. A more plausible reason for the differences between reduced and normal gait at this stage is related to the difference in movement-induced peripheral feedback (for review see Brooke et al. 1997). During reduced gait, movements before and around heel contact are reduced at the knee and ankle joint compared to normal gait. However, the basic modulation pattern is similar in both locomotion paradigms.

Functional considerations

Based on suggestions from cat experiments (Prochazka et al. 1976), it was hypothesized that activation of the BF at end swing is at least partly generated through stretch reflexes. Irrespective of the mechanisms discussed, the results show that there is a modulation of Ia afferent input effectiveness onto BF motoneurones during human locomotion. Finally the overall suppression of different short-latency reflexes in a variety of muscles, including BF, during gait is consistent with a general decrease in reliance on these potent automated reflexes during gait except for some specific parts of the step cycle.

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