

Vibration-Induced Changes in EMG During Human Locomotion

SABINE M. P. VERSCHUEREN,¹ STEPHAN P. SWINNEN,¹ KAAT DESLLOOVERE,² AND JACQUES DUYSSENS^{3,4}

¹Motor Control Laboratory, Department of Kinesiology, Faculteit Lichamelijke Opvoeding en Kinesitherapie, Katholieke Universiteit, 3001 Leuven, Belgium; ²Gait Laboratory, University Hospital UZ Pellenberg, Belgium; ³Department of Medical Physics and Biophysics, K.U. Nijmegen; ⁴Sint Maartensclinic Research, 6500 Nijmegen, The Netherlands

Submitted 28 February 2002; accepted in final form 26 October 2002

Verschueren, Sabine M. P., Stephan P. Swinnen, Kaat Deslloovere, and Jacques Duysens. Vibration induced changes in EMG during human locomotion. *J Neurophysiol* 89: 1299–1307, 2003; 10.1152/jn.00863.2002. The present study was set up to examine the contribution of Ia afferent input in the generation of electromyographic (EMG) activity. Subjects walked blindfolded along a walkway while tendon vibration was applied continuously to a leg muscle. The effects of vibration were measured on mean EMG activity in stance and swing phase. The results show that vibration of the quadriceps femoris (Q) at the knee and of biceps femoris (BF) at the knee enhanced the EMG activity of these muscles and this occurred mainly in the stance phase of walking. These results suggest involvement of Ia afferent input of Q and BF in EMG activation during stance. In contrast, vibration of muscles at the ankle and hip had no significant effect on burst amplitude. Additionally, the onset time of tibialis anterior was measured to look at timing of phase transitions. Only vibration of quadriceps femoris resulted in an earlier onset of tibialis anterior within the gait cycle, suggesting involvement of these Ia afferents in the triggering of phase transitions. In conclusion, the results of the present study suggest involvement of Ia afferent input in the control of muscle activity during locomotion in humans. A limited role in timing of phase transitions is proposed as well.

INTRODUCTION

In the cat, it is now generally accepted that the spinal cord is able to produce the rhythmic alternation of flexor and extensor activity necessary for locomotion in the absence of motion-dependent afferent feedback (Grillner and Zangger 1984). Also, in man there is growing evidence that a central pattern generator (CPG) exists (Calancie et al. 1994; Dimitrijevic et al. 1998; Duysens and Van de Crommert 1998). However, afferent feedback has been shown to modulate the locomotor pattern in different ways to adapt it to external demands. For proprioceptive afferents, two major roles have been put forward. First, afferent input may play an important role in the generation of parts of the muscular activity seen during the step cycle (amplitude effects). Second, the activity from spindles and Golgi tendon organs is thought to be involved in the regulation of phase transitions (timing effects). The amplitude effects can be independent of the timing effects, whereby the former may be regulated by pathways not influencing the CPG (Guertin et al. 1995; Hiebert and Pearson 1999; McCrea et al. 1995).

For the *amplitude effects*, a contribution of *Ia afferents* has

been put forward in the cat to explain the bursts of activity in the *hamstrings* at end swing and for *quadriceps* at onset stance. The hamstrings are rapidly stretched at end swing through the combined action of knee extension and hip flexion. This stretch is known to evoke a brisk discharge in spindle afferents (Loeb and Duysens 1979; Prochazka et al. 1976) and it has been suggested that these discharges elicit reflex activations of the hamstrings (Prochazka et al. 1976; Wisleder et al. 1990). Indirect evidence that this may also be true in humans has been obtained from studies using biceps femoris (BF) tendon taps during gait (Faist et al. 1999; Van de Crommert et al. 1996). Similar earlier experiments on the quadriceps tendon provided support for the idea that, for this muscle, the stretch reflexes contribute to the electromyographic (EMG) activity in the early stance phase in humans (Dietz et al. 1990).

For *triceps surae* activity, a contribution of Ia or Ib afferents has been suggested by several authors (e.g., Akazawa et al. 1982; Gorassini et al. 1994; Pearson and Collins 1993). For humans, the first suggestion that triceps EMG during gait may be partly reflex in origin was provided by a study of Dietz and co-workers (Dietz et al. 1979). They found a sudden increase in ankle extensor EMG just after footfall in human running and they attributed this to stretch reflex activity. Whether this is also true for regular walking is still a matter of debate. Yang and co-workers applied brief ankle rotations during walking in humans and estimated that the stretch reflex could provide ≤ 30 –60% of the activation of soleus during walking (Yang et al. 1991). Similarly, Sinkjaer and co-workers used a semiportable stretch device to study soleus stretches in various phases of the step cycle. They found that loading (unloading) of subjects during the stance phase, respectively, increased or decreased soleus EMG (Sinkjaer et al. 2000), suggesting a role of afferent feedback in the generation of soleus EMG activity.

In the experiments mentioned above, however, it is difficult to differentiate between the contribution of Ia and Ib afferents in the activation of the muscles. It has been claimed that extensor Ib load feedback provides reinforcing feedback to these muscles, especially in triceps surae (Conway et al. 1987; Duysens et al. 2000; Gossard et al. 1994; Pearson et al. 1998). Model studies have supported this claim (Prochazka and Gorassini 1998).

Accordingly, the present study was intended to evaluate the specific contribution of Ia afferents in human EMG activation.

Address for reprint requests: S. Verschueren, Department of Kinesiology, FLOK, Tervuursevest 101, B-3001 Heverlee, Belgium (E-mail: sabine.verschueren@flok.kuleuven.ac.be).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

Tendon vibration is known to activate Ia afferents more effectively than other afferents (Roll and Vedel 1982). When applied during gait, tendon vibration should selectively enhance muscle activity that critically depends on Ia stretch reflexes. To test this, subjects walked along a walkway while particular tendons of leg muscles were vibrated. The first question addressed was the effect of vibration on EMG activity of the parent muscle. Based on the studies cited above, one would expect vibration to increase quadriceps activity in early stance and hamstrings activity at end swing. Triceps surae activity during stance should be enhanced when Ia reflex pathways to that muscle are opened during this phase.

For the *timing* effects in which proprioception might be involved during locomotion, both load- and position-dependent triggering of phase transitions have been proposed in cat studies. Unloading of the extensor muscles appears critical to stop the stance and initiate the swing (Conway et al. 1987; Duysens and Pearson 1980; Gossard et al. 1994; Pearson et al. 1992; Whelan et al. 1995) and hereby the Ib afferent input is most likely involved. A particular hip extension value must also be reached before lift off of the leg is initiated (Andersson and Grillner 1983; Grillner and Rossignol 1978). This position-dependent triggering found in the cat is most likely controlled by the length-sensitive Ia afferent input. Accordingly, the second question addressed in this study concerned the contribution of the Ia afferents to locomotor-phase transitions in humans. Tendon vibration applied during gait to flexor muscles might facilitate the stance to swing transition. However, only small effects are expected since it has been shown that phase switching depends on multiple factors and is difficult to influence by a selective afferent input either in the intact cat (Duysens and Stein 1978) or in human (Stephens and Yang 1999). The main effect to be expected is from vibration of flexors at the hip since Ia input from these muscles has been shown to help induce the swing phase in the cat (Andersson and Grillner 1983; Hiebert et al. 1996).

Preliminary results have been presented in abstract form (Verschuereen et al. 1999).

METHODS

Subjects

Nine undergraduate students (age: 20–29, mean: 23.1) with no known neuromuscular deficits volunteered for the experiment. Each subject provided written consent for participation. The experiment was approved by the local Ethics Committee of Biomedical Research at the Katholieke Universiteit Leuven, according to the Declaration of Helsinki. Subjects were naive about the purpose of the experiment.

Apparatus and task

The experiments were performed in the gait laboratory of the University Hospital Katholieke Universiteit Leuven, Pellenberg.

The subjects walked blindfolded along a walkway 8 m long at their preferred speed. Gait kinematics were recorded with a six-camera Vicon 370 motion analysis system at a sampling rate of 50 Hz. Six reflective surface markers were placed in precise anatomical positions bilaterally on the body: anterior superior iliac spines (SISA), lateral thigh, lateral epicondyl, lateral shank, lateral malleolus, and forefoot between second and third metatarsal. One marker was placed on the sacrum, midway between the posterior superior iliac spines (PSIS).

In some trials, continuous tendon vibration (75 Hz–1 mm) was

applied transversally to the tendon or on the muscle belly as close as possible to the tendon of one of the following muscles of the right limb: rectus femoris at hip and quadriceps femoris (Q) at knee, BF (at hip and knee), tibialis anterior (TA)/extensor digitorum longus, and triceps surae. In the case of rectus femoris vibration at the hip, the vibrator was positioned on the proximal tendon about 2 cm under the SISA. For quadriceps vibration at the knee, the vibrator was fixed to the patella tendon. In the case of BF vibration at the hip, the vibrator was placed on the muscle belly just underneath the buttock line; for the knee the vibrator was positioned on the distal tendon about 3 cm above the knee joint. In the case of TA/extensor digitorum vibration, the vibrator was fixed on the tendon about 5 cm above the ankle joint. In the case of triceps surae vibration, the vibrator was fixed to the Achilles tendon at ankle joint level. Vibration was produced by cylindrical vibrators (Dynatronic, *vibrateurs proprioceptives*) attached to a tendon by means of a rubber band (3.5 cm wide). The rubber band ensured good fixation of the vibrator on the tendon during the whole gait cycle. This method of fixation results in vibration parameters (frequency and amplitude) that do not change more than 10% throughout the gait cycle (Ivanenko et al. 2000a). The pressure of the rubber band did not cause any discomfort nor paresthesia to the subjects, meaning that blood circulation was unaffected. The vibrators weighted 100 g, were 7 cm long, and had a diameter of 3 cm. The dimensions and the positioning of the vibrators did not disrupt locomotion.

Recordings of EMG activity (K-Lab, Biometrics Europe) were obtained with surface electrodes from six muscles of each leg: rectus femoris, vastus lateralis, medial and lateral hamstrings, TA, and the lateral gastrocnemius (LG). The preamplified signal (100*, CMR > 115 dB @ 50 Hz) was band-pass filtered (20–1,500 Hz) prior to digitization at 2,500 Hz.

Procedure

Prior to data collection, the following physical measurements of the subjects were recorded: height, weight, right and left leg length, right and left knee width, right and left ankle width. The EMG surface electrodes and reflective markers were placed on the subject.

After static and dynamic calibration of the data analysis system, a number of static trials of the subject were recorded to calibrate certain internal axes of limb segments.

In the test protocol, subjects walked along the platform under several proprioceptive conditions, as follows: 1) no vibration (control trial), 2) TA vibration, 3) BF vibration at knee, and 4) rectus femoris vibration at the hip in one half of the session; and 1) no vibration (control condition), 2) triceps surae vibration (Achilles tendon), 3) Q at knee (patella tendon), 4) BF vibration at the hip in the other half of the session. There were four trials per condition, resulting in 32 trials in total. The entire sequence was randomized with respect to the vibration condition. Recordings were only made in one walking direction. Subjects walked back to the start position without vibration applied. This allowed dissipation of the potential after effects of tendon vibration (Rogers et al. 1985).

Data analysis

The hip, knee, and ankle joint angles were calculated with Vicon Clinical Manager software, using standard marker placements and established biomechanical algorithms (Verschuereen et al. 2002).

The raw EMG data were rectified and then normalized with respect to the gait cycle to share a common time base with the joint angle data. The gait cycle started at heel contact and ended at the following heel contact. Mean EMG activity per gait cycle was calculated for each trial and averaged across trials of the same proprioceptive condition. The activity during unperturbed walking was taken to be 100% and the level of EMG activity during vibration was calculated as a percentage of the control condition. Group means [standard deviation

(SD)] were calculated for all subjects. In addition, the onset of TA activity prior to swing was defined using custom written software. Mean onset times were calculated across trials of the same condition. In addition, mean EMG was calculated during the swing and stance phase separately. The transition between stance and swing was arbitrarily taken at the time of onset of TA EMG.

Statistical analysis

The effect of vibration was assessed by comparing the data in trials with and without vibration. Analysis of variance (ANOVA) with repeated measures was used to test for differences among the proprioceptive conditions. Significant effects were defined as those at the $P < 0.05$ probability level. When significant effects were found, post hoc testing (i.e., contrast analysis) was conducted to identify the source of the differences. As we were primarily interested in differences between a particular vibration condition and the corresponding control condition, RESULTS will focus mainly on the results of those post hoc analyses.

RESULTS

Figure 1 displays the mean EMG of the vibrated muscle in the different vibration conditions. The EMG is expressed in percentage of the EMG during the control condition. Per group of three bars, the black bars represent the mean EMG across the complete gait cycle; the stippled bars represent the stance phase, and the hatched bars represent the swing phase. As can be seen, vibration applied around the knee did affect the mean EMG during gait substantially, whereas the other vibration conditions had virtually no effect on mean EMG.

At the knee (Fig. 1, middle 2 groups of bars), vibration of the Q (patella tendon) resulted in an increase of the EMG of rectus femoris to 169% of control values [$F(1,8) = 8.59$, $P < 0.05$] and of vastus lateralis to 165% [not shown, $F(1,8) = 6.48$, $P < 0.05$]. Further analysis whereby the gait cycle was divided in stance and swing phase showed that the increase in EMG was significant both during the stance

phase (to 173%), and during the swing phase (to 158%). In vastus lateralis, the increase in EMG was significant in the stance phase, but not in the swing phase. Figure 2A represents the mean rectus femoris EMG of a representative subject with and without vibration at the patella tendon and shows the increase in EMG during stance. Vibration of BF at the knee increased EMG activity of the mother muscle to 129% [$F(1,8) = 5.79$, $P < 0.05$]. This increase was due to a significant EMG increase during the stance phase (to 148%), while there was no significant change during the swing phase (102%). Figure 2B, displaying BF EMG of a representative subject with and without vibration at the knee, illustrates this EMG increase during the stance phase.

At the ankle (Fig. 1, leftmost 2 groups of bars), vibration of the TA and vibration of the triceps surae changed neither the overall mean EMG of the vibrated muscle nor the mean EMG during stance or swing ($P > 0.05$). Figure 3A shows the TA EMG of a representative subject in the control condition (dark trace) and with vibration of the TA (dashed line), and no differences can be observed. Figure 3B shows a similar plot of the lateral gastrocnemius EMG with and without vibration of the triceps surae (Achilles tendon). Again no EMG modulation due to vibration can be observed.

At the hip (Fig. 1, rightmost 2 groups of bars), rectus femoris vibration had no effect on mean EMG values (see also Fig. 4A). BF vibration led to a decrease in activation of the BF to 93% of control values [$F(1,8) = 5.98$, $P < 0.05$]. This effect was due to a decreased activation during swing as can be seen on Fig. 4B representing the BF EMG trace with and without vibration at the hip.

Some vibration conditions did provoke EMG changes in remote muscles (not illustrated). TA vibration led to an increased EMG in vastus lateralis but this was only significant during the stance phase [128% of control value; $F(1,8) = 5.74$, $P < 0.05$]. Vibration of triceps surae resulted in a decrease of

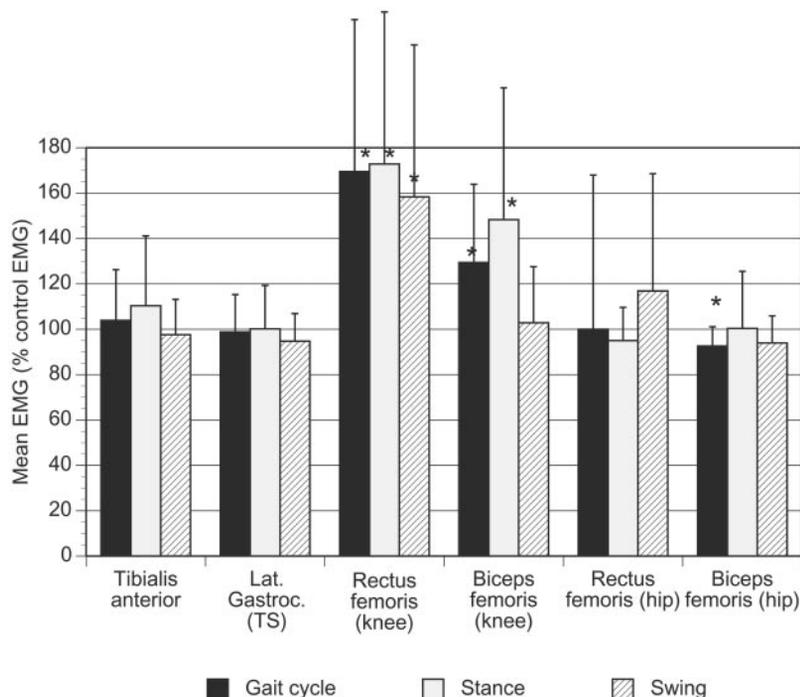


FIG. 1. Mean electromyographic (EMG) activity of the vibrated muscle for the different proprioceptive conditions in percentage of EMG activity in the control condition. The black bar represents the mean EMG of the complete gait cycle; the stippled bar represents the stance phase, and the hatched bar represents the swing phase. Asterisks indicate statistical significance ($P < 0.05$).

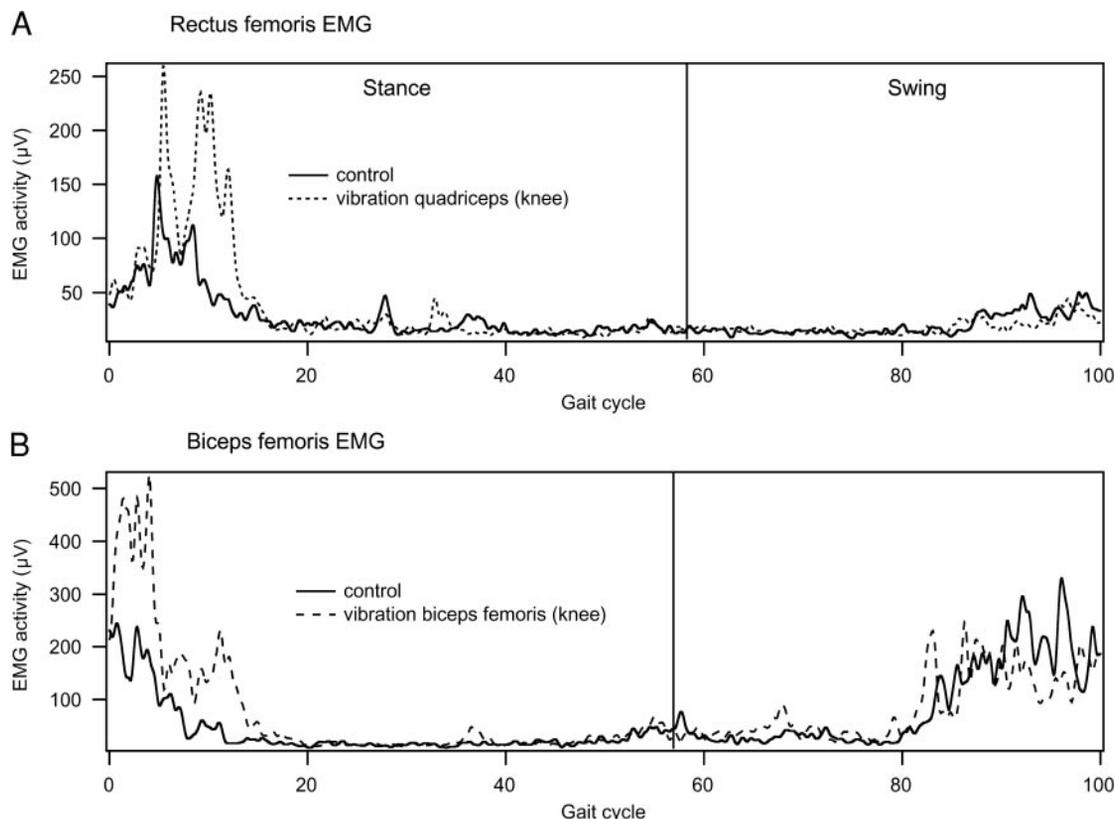


FIG. 2. EMG activity during the gait cycle of a representative subject in the control condition (*dark trace*) and with vibration at the knee of the muscle shown (*dashed trace*). In *A*, the rectus femoris is illustrated, and in *B*, the biceps femoris (BF) is illustrated. The zero point represents the foot contact and the 100% point represents the following foot contact. The vertical line is the dividing line between the stance phase and the swing phase, based on the onset of tibialis anterior (TA) EMG in the control condition.

TA EMG during swing [91% of control value, $F(1,7) = 6.41$, $P < 0.05$], but not overall or during stance.

Vibration of rectus femoris at the knee (patella tendon) did increase the EMG activity of the TA to 110% [$F(1,7) = 5.25$, $P = 0.05$]. BF vibration at the hip led to an overall decreased activation of gastrocnemius EMG [$F(1,8) = 7.43$, $P < 0.05$] and of medial hamstrings EMG [$F(1,8) = 5.87$, $P < 0.05$]. This decrease in EMG in both muscles was mainly present during the stance phase.

Effect of vibration on stance-to-swing transition

The onset of TA activity at the beginning of swing was measured to determine whether vibration affected the transition from stance to swing. In Fig. 5, *A* and *B*, a representative example is given of the EMG activity of TA in the control condition (*A*) and with vibration at the patella tendon (*B*). Onset of TA at the end of stance is marked by the vertical lines. As can be seen, vibration of the patella tendon resulted in an earlier onset of TA in the gait cycle.

Figure 6 shows the mean onset times of TA in the different proprioceptive conditions. As can be seen, none of the vibration conditions delayed the onset of TA. There was a general tendency toward an earlier onset of TA due to vibration, but this was only significant for patella tendon vibration [$F(1,8) = 12.19$, $P < 0.01$] and marginally significant for TA vibration [$F(1,8) = 4.72$, $P = 0.06$] and rectus femoris vibration [$F(1,8) = 4.69$, $P = 0.06$].

DISCUSSION

The main results of the present study are that vibration of the BF (at the knee) and QF (at the knee) selectively enhances the EMG bursts of these muscles in the stance phase of walking, suggesting involvement of Ia afferent input of those muscles in EMG activation. In contrast, vibration of ankle muscles had no significant effects on burst amplitude. Compared with previous cat literature, the effects of afferent stimulation on EMG activity found here in humans are relatively weak, which is consistent with what similar studies in humans have found recently (Courtine et al. 2001; Ivanenko et al. 2000).

The effects of vibration on locomotion found in the present study are assumed to be provoked by stimulation of the Ia afferents. Microneurographic studies have shown that the other muscular afferents (group II muscle spindles and the Golgi tendon organs) are much less sensitive to vibration (Brown et al. 1967; Roll and Vedel 1982; Roll et al. 1989). Both slowly and fast adapting cutaneous afferents do respond to the kind of vibration stimulus used here (Ribot-Ciscar et al. 1989) and can therefore not be ruled out totally as possible mediators of the effects observed. On the other hand, it is not very likely that cutaneous input played an important role since it is mainly the cutaneous afferents from the foot and ankle that can cause large reflex effects while more proximal skin locations are less effective (Duysens and Loeb 1980).

If one assumes that Ia input was the primary source of the vibration effects, then the present results on enhanced EMG

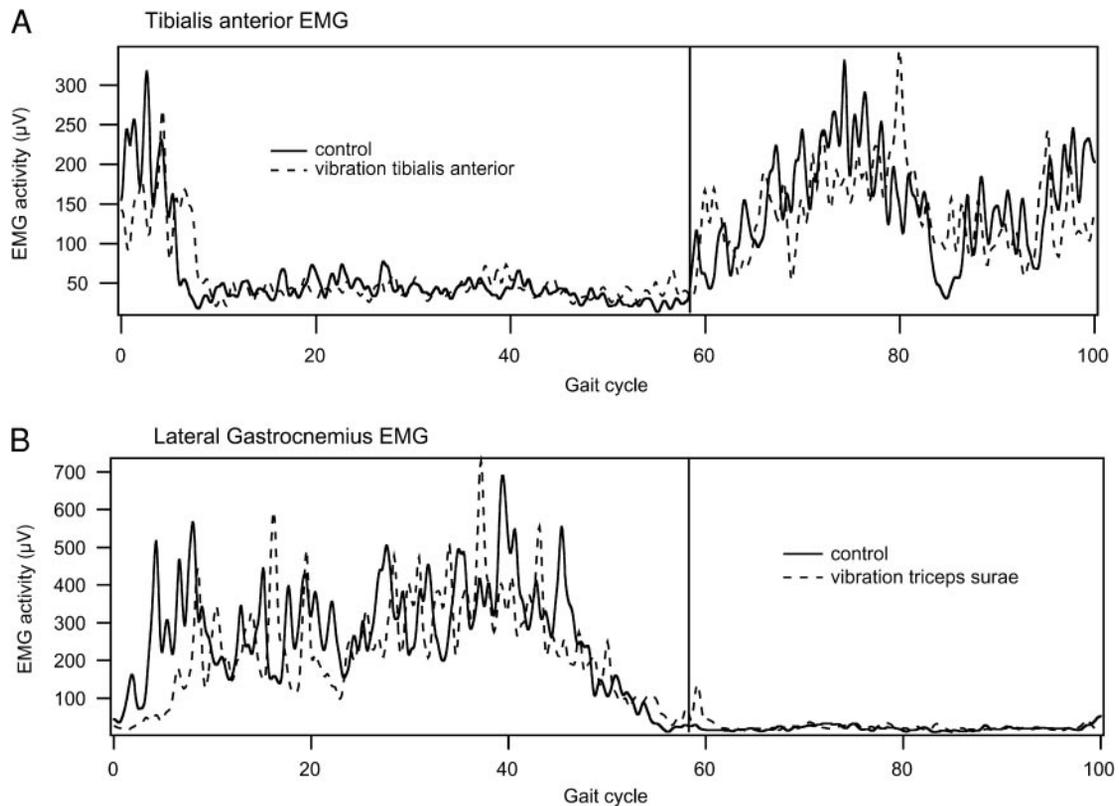


FIG. 3. EMG activity during the gait cycle of a representative subject in the control condition (*dark trace*) and with vibration at the ankle of the muscle shown (*dashed trace*). In A, the tibialis anterior is illustrated, and in B, the gastrocnemius is illustrated.

activity during vibration can most likely be explained by Ia reflex activations. There have been numerous suggestions that during normal gait, some of the normally occurring EMG activity is caused by stretch reflexes (see INTRODUCTION). The present data confirm that this is likely to be true for some muscles but not for others, and furthermore, it confirms that these contributions are phase-dependent.

The finding that Ia afferent activation by Q vibration contributes to the generation of EMG activity in rectus femoris and in vastus lateralis during stance is entirely consistent with earlier suggestions that this Ia path is facilitated during that period of the step cycle (Dietz et al. 1990). Similarly the activation of BF by vibration around the swing-stance transition is consistent with previous data showing that tendon taps elicit the strongest stretch reflexes selectively in that part of the cycle, both during limping (Van de Crommert et al. 1996) and during normal gait (Faist et al. 1999). The present data show that the main facilitation was at onset stance, while in the earlier studies with tendon taps, the onset appeared to occur earlier. This difference may simply be due to differences in the way the time of occurrence of the stance-swing transition was measured (in our case the onset of TA EMG activity was used). Alternatively, it cannot be excluded at this point that the later onset of the facilitation in the present study is related to a potential problem of vibration transmission to the muscle throughout the cycle. The tensing of BF associated with its hip extensor role during weight support may increase the reliability of the vibrator-IA mechanical coupling. In contrast with our results, Ivanenko and co-workers did not find any systematic changes in mean EMG of BF due to application of vibration during treadmill walking (Ivanenko et al. 2000a). They report

an increase of 30% in BF EMG in some subjects and a decrease $\leq 60\%$ in some others. A possible explanation for this discrepancy with our results might be the location of the vibrators. In our experiment, the vibrator was positioned either on the tendon of BF at the knee or at the hip, whereas they positioned the vibrator about halfway along the muscle on the muscle belly. In our study, vibration of BF at the knee did result in an increased BF EMG, whereas vibration at the hip resulted in a small decrease, suggesting some topographical differences in muscle spindle function of this bi-articular muscle. However, it cannot be excluded that the transmission of the vibration at the hip was less effective than at the knee due to fat tissue for instance. Quadriceps vibration also had a remote effect on the TA EMG, which was not unexpected as stretch of the quadriceps is known to affect the control of muscles in the lower leg (see for the cat Eccles et al. 1957 and Misiaszek and Pearson 1997 and for humans Brooke et al. 1993). Finally, it is noteworthy that in the cat also it is thought that knee extensor afferents contribute significantly to the activation of knee extensor muscles (Hiebert and Pearson 1999).

In contrast to our results of Q and BF vibration, there was no increase in EMG amplitude with vibration of the Achilles tendon (AT). This is an important result since there has been a lot of speculation as to the contribution of reflexes to locomotor activity in triceps surae muscles. Indeed, several studies in humans have shown that the afferent input of the soleus muscle is very important in the generation of soleus EMG activity (Sinkjaer et al. 2000; Stephens and Yang 1999). In contrast, we did not find an effect of AT vibration on mean gastrocnemius EMG. Can this reflect a soleus-LG difference or are there other possible explanations? One might consider the possibility that

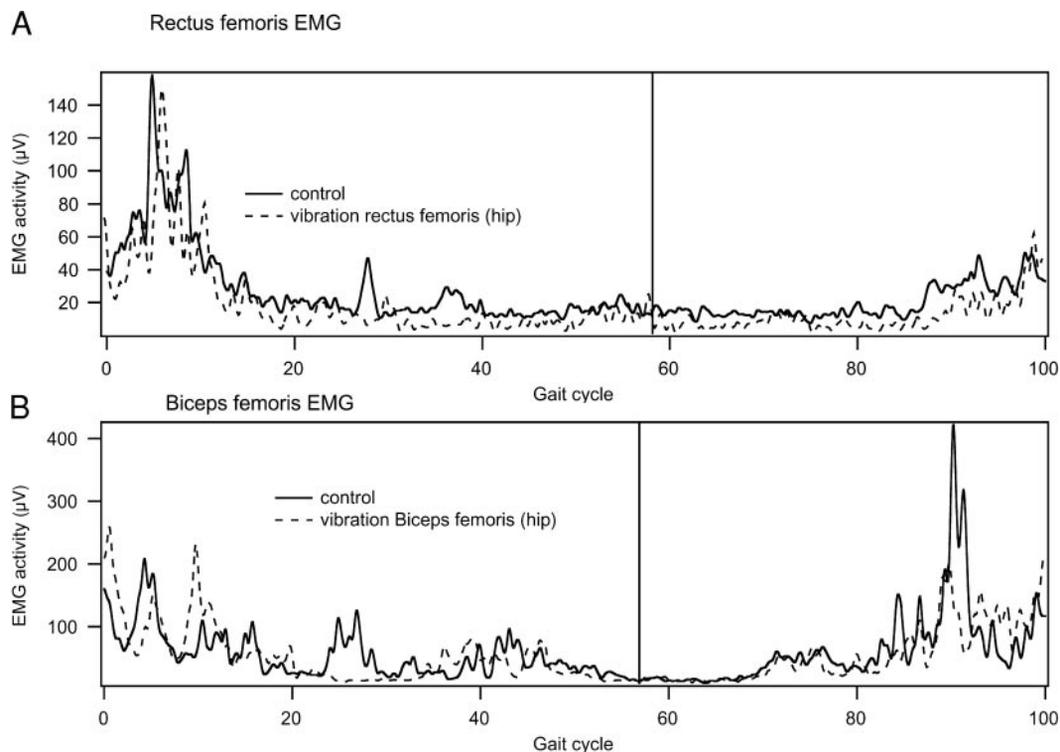


FIG. 4. EMG activity during the gait cycle of a representative subject in the control condition (*dark trace*) and with vibration at the hip of the muscle shown (*dashed trace*). In *A*, the rectus femoris is illustrated, and in *B*, the BF is illustrated.

the vibration of the AT was inadequate to activate the Ia afferents. We consider this as very unlikely for several reasons. First, the AT vibration did provoke movement illusions in the resting condition consistent with what would be expected due to Ia afferent activation. Second, AT vibration lead to changes in ankle and knee kinematics during locomotion (Verschuere et al. 2002). Third, AT vibration has been used extensively and proven to be effective in a number of studies on presynaptic inhibition (Milanov 2000) or on postural perturbation (Ivanenko et al. 2000b). In the previous studies, loading and unloading was used as a technique to show the contribution of afferent activity in extensor EMG, but it is hard to distinguish the contribution of Ia and Ib afferents in this paradigm. Using tendon vibration, our study focused primarily on the contribution of Ia afferents. Thus our study suggests that the ankle extensor Ia afferents in humans do not contribute very much to the production of EMG activity in these muscles during walking. In running, however, the Ia afferents appear to contribute to the triceps surae EMG by a short-latency reflex elicited by ground contact (Dietz et al. 1979). The relative absence of Ia effects does not exclude that other types of afferent input from ankle extensors play a role in the generation of EMG activity during walking, as previously described in the cat (Guertin et al. 1995; McCrea et al. 1995; Pearson and Collins 1993; Whelan et al. 1995). Gorassini and co-workers (Gorassini et al. 1994) found a decrease in LG EMG activity in the absence of ground support. Recently, Hiebert and Pearson (1999) addressed the same issue by studying the EMG amplitudes in the absence of ground support and following deafferentation of a leg. They found that afferent feedback contributes to about 50% in the generation of extensor activity during the stance phase of walking. Both muscle spindles (group Ia and group II afferents) and Golgi tendon organs (group Ib afferents) have

been put forward as mediators of this excitatory feedback effect. The present data suggest that the largest contribution is likely to be provided by afferents other than the Ia afferents.

Vibration of AT did result in a decreased EMG activity of TA and this only during the swing phase. This result is consistent with the decreased TA activity found by Courtine and co-workers (Courtine et al. 2001), which is according to them most likely due to a re-programming of the command to TA based on the provoked illusion of dorsiflexion by AT vibration and thus directed to avoid "excessive" foot dorsiflexion during swing.

In principle, vibration can also provide information with respect to involvement of Ia afferents in the timing of the transitions between stance and swing phases. The present results showing an earlier onset of TA activity following RF (and TA) vibration underscore this role of Ia afferents of the flexor muscles in initiation of swing in humans. The results are consistent with results of Hiebert and co-workers in spontaneously walking decerebrate cat (Hiebert et al. 1996). They showed that vibration of the ankle flexors [tibialis anterior and/or extensor digitorum longus (EDL)] and vibration of the iliopsoas (IP) during stance promoted an earlier onset of flexor activity. They concluded that as the flexor muscles lengthen during stance, their spindle afferents (both group Ia and II) are stimulated and act to inhibit the extensor activity and facilitate the initiation of swing. But, whereas Hiebert and colleagues found a reduction of the stance phase by 10–15%, we found only a reduction by 2%. In this respect it must be stated that Hiebert and co-workers (Hiebert et al. 1996) also found much smaller effects in a normal quadrupole locomotion situation (5%) than in the paradigm in which the studied limb was fixated. This suggests that the effects on the CGP rhythm became smaller when more proprioceptive input is provided

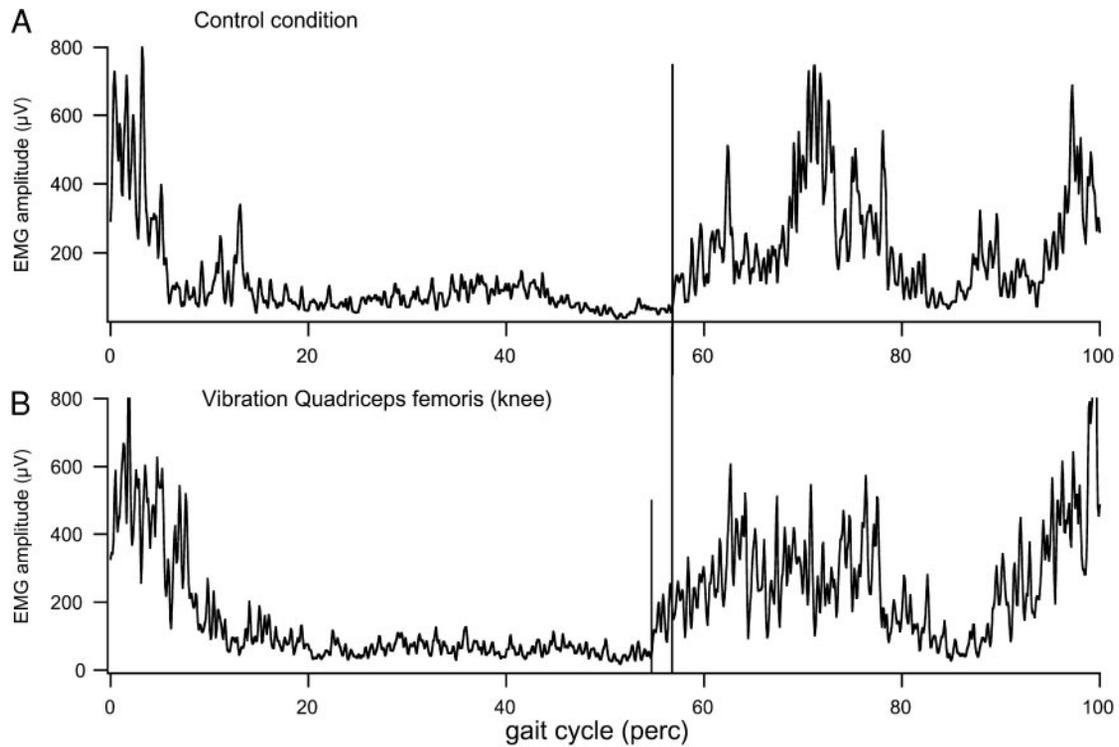


FIG. 5. Effect of vibration on the onset time of TA. The mean normalized TA EMG of a representative subject is shown in *A* (control condition) and *B* (vibration of the patella tendon). Vertical lines mark the TA onset at the end of stance. Vibration of the patella tendon resulted in an earlier onset of TA.

and when a normal locomotion situation is more closely mimicked (see also Whelan and Pearson 1997).

One might argue that the earlier onset of TA EMG in certain vibration conditions might be the indirect consequence of changes in walking velocity, i.e., an increased speed. Analysis of the walking velocity, however, revealed that there was an overall tendency for a decrease in walking velocity in all vibration conditions (Verschuere et al. 2002). As the walking velocity did definitely not increase, the effects of RF vibration on TA onset may reflect a pure change of CPG rhythm.

Alternatively, the earlier onset of TA EMG found following RF vibration might be related to the increase of TA EMG found in the same condition resulting in a more apparent onset of TA than in the other conditions.

However, it must be taken into consideration that the effects found are small, which makes additional research necessary to elucidate in detail the involvement of Ia afferents in phase transitions.

Several possibilities from both a methodological and a physiological slant can be put forward to explain the relative weak-

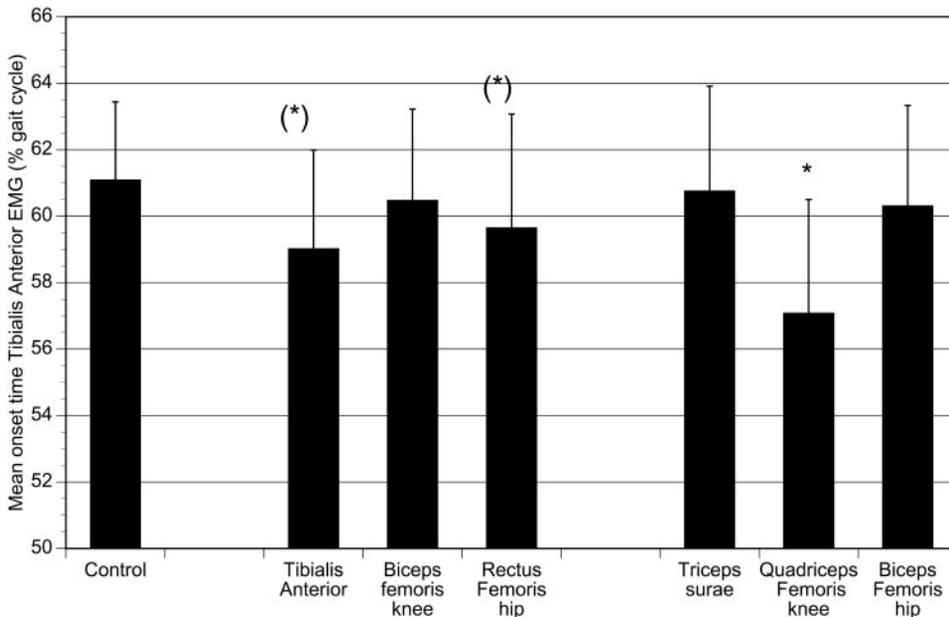


FIG. 6. Mean onset times ($n = 9$) of TA in the different proprioceptive conditions.

ness of the effects of afferent stimulation in comparison with similar studies in the cat. At this point there is no conclusive answer, however. One might question the stability of the vibration parameters (amplitude and frequency) throughout the gait cycle. Unstable parameters would lead to unpredictable, irregular spindle behavior, thereby masking the real importance of spindle input during locomotion. We do believe, however, that the parameters of vibration did not change more than 10% throughout the cycle (see Ivanenko et al. 2000a).

Further, the question arises whether a vibration frequency of 70 Hz is sufficiently different from the spindle firing rate during normal locomotion. To date, no recordings of human spindles have been made during locomotion, and thus, the firing rate can only be estimated from models mainly based on cat studies (≤ 130 Hz) (Prochazka 1999) or from human studies on sinusoidal movements (rarely > 50 Hz) (Grill and Hallet 1995; Kakuda and Nagaoka 1998). At the slow walking velocity of the present study, namely 0.85 m/s, 70-Hz vibration is thus believed to be sufficiently higher than the normal Ia firing rate to induce a significant artificial afferent input. The effectiveness is underscored by the findings that vibration clearly affected kinematics (Verschuere et al. 2002) and modified the EMG activity of some muscles (present study).

Alternatively, walking with vibration might be a task that is not challenging enough for the proprioceptive system. The latter is underscored by a very recent study of Sorensen and co-workers (Sorensen et al. 2002) that clearly shows that the effect of vibration during locomotion is context dependent. The contribution of muscle spindle input to the control of locomotion appears to increase when it is necessary to make adjustments in response to environmental demands, as for instance, stepping over an obstacle.

More physiological reasons have been proposed by Courtine and co-workers who also found only minor effects of continuous AT vibration on locomotion (Courtine et al. 2001). The central pattern generator might be able to gate unwanted Ia afferent input. Alternatively, the group II afferents that are quasi-insensitive to vibration might be more important in the regulation of antigravity muscle activity during walking than the Ia afferents.

The effects found on EMG activity in the present were thus perhaps not overriding, but they were larger than in previous studies by others (Courtine et al. 2001; Ivanenko et al. 2000a). One reason for this might be the choice of the muscle vibrated, as we also found no effects for instance due to Achilles tendon vibration, suggesting that the role of afferent input for EMG activity is different from muscle to muscle. Further, only right leg muscles were vibrated in the present study, whereas the others vibrated both legs simultaneously. The latter might facilitate the gating of (unwanted) IA input.

Overall, it is concluded that tendon vibration appears to be a useful noninvasive tool in the assessment of proprioceptive control of locomotion in humans and it might be particularly interesting for studying changes in proprioceptive control of locomotion due to pathological conditions or aging.

This work was supported by a grant from the Research Council of K.U. Leuven, Belgium awarded to S. P. Swinnen (Contract No. OT/99/39). Prof. J. Duysens was supported by a fellowship from the Research Council of K. U.

Leuven (Contract F/99/34). S.M.P. Verschuere is a postdoctoral fellow of the Fund for Scientific Research, Flanders, Belgium.

REFERENCES

- Akazawa K, Aldridge JW, Steeves JD, and Stein RB. Modulation of stretch reflexes during locomotion in the mesencephalic cat. *J Physiol* 329: 553–567, 1982.
- Andersson O and Grillner S. Peripheral control of cat's step cycle. II. Entrainment of central pattern generators for locomotion by sinusoidal hip movements during "fictive locomotion". *Acta Physiol Scand* 118: 229–239, 1983.
- Brooke JD, Misiaszek JE, and Cheng J. Locomotor-like rotation of either hip or knee inhibits soleus H reflexes in humans. *Somatosens Mot Res* 10: 357–364, 1993.
- Brown MC, Engberg I, and Matthews PBC. Relative sensitivity to vibration of muscle receptors of the cat. *J Physiol* 192: 773–800, 1967.
- Calancie B, Needham-Shropshire B, Jacobs P, Willer K, Zych G, and Green BA. Involuntary stepping after chronic spinal cord injury. Evidence for a central rhythm generator for locomotion in man. *Brain* 117: 1143–1159, 1994.
- Conway BA, Hultborn H, and Kiehn O. Proprioceptive input resets central locomotor rhythm in the spinal cat. *Exp Brain Res* 68: 643–656, 1987.
- Courtine G, Pozzo T, Lucas B, and Schieppati M. Continuous, bilateral Achilles' tendon vibration is not detrimental to human walk. *Brain Res Bull* 55: 107–115, 2001.
- Dietz V, Disher M, Faist M, and Trippel M. Amplitude modulation of the human quadriceps tendon jerk reflex during gait. *Exp Brain Res* 82: 211–213, 1990.
- Dietz V, Schmidtbleicher D, and Noth J. Neural mechanisms of human locomotion. *J Neurophysiol* 42: 1212–1222, 1979.
- Dimitrijevic MR, Gerasimenko Y, and Pinter MM. Evidence for a spinal central pattern generator in humans. *Ann NY Acad Sci* 860: 360–376, 1998.
- Duysens J, Clarac F, and Cruse H. Load-regulating mechanisms in gait and posture: comparative aspects. *Physiol Rev* 80: 83–133, 2000.
- Duysens J and Loeb GE. Modulation of ipsi- and contralateral reflex responses in unrestrained walking cats. *J Neurophysiol* 44: 1024–1037, 1980.
- Duysens J and Pearson KG. Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. *Brain Res* 187: 321–332, 1980.
- Duysens J and Stein RB. Reflexes induced by nerve stimulation in walking cats with implanted cuff electrodes. *Exp Brain Res* 32: 213–224, 1978.
- Duysens J and Van de Crommert HWAA. Neural control of locomotion; part 1. The central pattern generator from cats to humans. *Gait Posture* 7: 131–141, 1998.
- Eccles J, Eccles R, and Lundberg A. The convergence of monosynaptic excitatory afferents on to many species of alpha motor-neurons. *J Physiol* 137: 22–50, 1957.
- Faist M, Blahak C, Duysens J, and Berger W. Modulation of the biceps femoris tendon jerk reflex during human locomotion. *Exp Brain Res* 125: 265–270, 1999.
- Forssman MA, Prochazka A, Hiebert G, and Gauthier MJA. Corrective responses to loss of ground support during walking. I. Intact cats. *J Neurophysiol* 71: 603–610, 1994.
- Gossard J-P, Brownstone RM, Barajon I, and Hultborn H. Transmission in a locomotor-related group Ib pathway from hindlimb extensor muscles in the cat. *Exp Brain Res* 98: 213–228, 1994.
- Grill SE and Hallet M. Velocity sensitivity of human muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors. *J Physiol* 489: 593–602, 1995.
- Grillner S and Rossignol S. On the initiation of the swing phase of locomotion in chronic spinal cats. *Brain Res* 146: 269–277, 1978.
- Grillner S and Zangger P. The effect of dorsal root transection on the efferent motor pattern in the cat's hindlimb during locomotion. *Acta Physiol Scand* 120: 393–405, 1984.
- Guertin P, Angel MJ, Perreault M-C, and McCrea DA. Ankle extensor group I afferents excite extensors throughout the hindlimb during fictive locomotion in the cat. *J Physiol* 487: 197–209, 1995.
- Hiebert GW and Pearson KG. Contribution of sensory feedback to the generation of extensor activity during walking in the decerebrate cat. *J Neurophysiol* 81: 758–770, 1999.
- Hiebert GW, Whelan PJ, Prochazka A, and Pearson KG. Contribution of hind limb flexor muscle afferents to the timing of phase transitions in the cat step cycle. *J Neurophysiol* 75: 1126–1137, 1996.

- Ivanenko YP, Grasso R, and Lacquaniti F.** Influence of leg muscle vibration on human walking. *J Neurophysiol* 84: 1737–1747, 2000a.
- Ivanenko YP, Solopova IA, and Levik YS.** The direction of postural instability affects postural reactions to ankle muscle vibration in humans. *Neurosci Lett* 292: 103–106, 2000b.
- Kakuda N and Nagaoka M.** Dynamic response of human muscle spindle afferents to stretch during voluntary contraction. *J Physiol* 513: 621–628, 1998.
- Loeb GE and Duysens J.** Activity patterns in individual hindlimb primary and secondary muscle spindle afferents during normal movements in unrestrained cats. *J Neurophysiol* 42: 420–440, 1979.
- McCrea DA, Shefchyk SJ, Stephens MJ, and Pearson KG.** Disynaptic group I excitation of synergist ankle extensor motoneurons during fictive locomotion in the cat. *J Physiol* 487: 527–539, 1995.
- Milanov IG.** Evaluation of the presynaptic inhibition by comparing the amplitudes of H reflexes and F waves. Is it possible? *Electromyogr Clin Neurophysiol* 40: 491–495, 2000.
- Misiaszek JE and Pearson KG.** Stretch of quadriceps inhibits the soleus H reflex during locomotion in decerebrate cats. *J Neurophysiol* 78: 2975–2984, 1997.
- Pearson KG and Collins DF.** Reversal of the influence of group Ib afferents from plantaris on activity in medial gastrocnemius muscle during locomotor activity. *J Neurophysiol* 70: 1009–1017, 1993.
- Pearson KG, Misiaszek JE, and Fouad K.** Enhancement and resetting of locomotor activity by muscle afferents. *Ann NY Acad Sci* 860: 203–215, 1998.
- Pearson KG, Ramirez JM, and Jiang W.** Entrainment of the locomotor rhythm by group Ib afferents from ankle extensor muscles in spinal cats. *Exp Brain Res* 90: 557–566, 1992.
- Prochazka A.** Quantifying proprioception. *Prog Brain Res* 123: 133–142, 1999.
- Prochazka A and Gorassini M.** Models of ensemble firing of muscle spindle afferents recorded during normal locomotion in cats. *J Physiol* 507: 277–291, 1998.
- Prochazka A, Westerman RA, and Ziccone SP.** Discharges of single hindlimb afferents in the freely moving cat. *J Neurophysiol* 1090–1104, 1976.
- Ribot-Ciscar E, Vedel JP, and Roll JP.** Vibration sensitivity of slowly and rapidly adapting cutaneous mechanoreceptors in the human foot and leg. *Neurosci Lett* 104: 130–135, 1989.
- Rogers DK, Bendrups AP, and Lewis MM.** Disturbed proprioception following a period of muscle vibration in humans. *Neurosci Lett* 57: 147–152, 1985.
- Roll JP and Vedel JP.** Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. *Exp Brain Res* 47: 177–190, 1982.
- Roll JP, Vedel JP, and Ribot E.** Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. *Exp Brain Res* 76: 213–222, 1989.
- Sinkjaer T, Andersen JB, Ladouceur M, Christensen LOD, and Nielsen JB.** Major role for sensory feedback in soleus EMG activity in the stance phase of walking in man. *J Physiol* 523: 817–827, 2000.
- Sorensen KL, Hollands MA, and Patla E.** The effects of human ankle muscle vibration on posture and balance during adaptive locomotion. *Exp Brain Res* 143: 24–34, 2002.
- Stephens MJ and Yang JF.** Loading during the stance phase of walking in humans increases the extensor EMG amplitude but does not change the duration of the stepcycle. *Exp Brain Res* 214: 363–370, 1999.
- Van de Crommert HWAA, Faist M, Berger W, and Duysens J.** Biceps femoris tendon jerk reflexes are enhanced at the end of the swing phase in humans. *Brain Res* 734: 341–344, 1996.
- Verschuere SMP, Desloovere K, and Swinnen SP.** Effect of tendon vibration on gait patterns in humans. *Gait Posture* 9, S 1:S31, 1999.
- Verschuere SMP, Swinnen SP, Desloovere K, and Duysens J.** Effects of tendon vibration on the spatiotemporal characteristics of human locomotion. *Exp Brain Res* 143: 231–239, 2002.
- Whelan PJ, Hiebert GW, and Pearson KG.** Stimulation of the group I extensor afferents prolongs the stance phase in walking cats. *Exp Brain Res* 103: 20–30, 1995.
- Whelan PJ and Pearson KG.** Comparison of the effects of stimulating extensor group I afferents on cycle period during walking in conscious and decerebrate cats. *Exp Brain Res* 117: 444–452, 1997.
- Wisleder D, Zernicke RF, and Smith JL.** Speed-related changes in hindlimb intersegmental dynamics during the swing phase of cat locomotion. *Exp Brain Res* 79: 651–660, 1990.
- Yang JF, Stein RB, and James KB.** Contribution of peripheral afferents to the activation of the soleus muscle during walking in humans. *Exp Brain Res* 87: 679–687, 1991.