Sudden Drop in Ground Support Produces Force-Related Unload Response in Human Overground Walking

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af Klint R, Nielsen JB, Sinkjaer T, Grey MJ. Sudden drop in ground support produces force-related unload response in human overground walking. J Neurophysiol 101: 1705–1712, 2009. First published January 21, 2009; doi:10.1152/jn.91175.2008. Humans maneuver easily over uneven terrain. To maintain smooth and efficient gait the motor system needs to adapt the locomotor output to the walking environment. In the present study we investigate the role of sensory feedback in adjusting the soleus muscle activity during overground walking in 19 healthy volunteers. Subjects walked unrestrained over a hydraulically actuated platform. On random trials the platform was accelerated downward at 0.8 g, unloading the plantar flexor muscles in midstance or late stance. The drop of the platform resulted in a significant depression of the soleus muscle activity of −17.9% (SD 2) and −21.4% (SD 2), with an onset latency of 49 ms (SD 1) and 45 ms (SD 1) in midstance and late stance, respectively. Input to the vestibular apparatus (i.e., the head acceleration) occurred at a latency 10.0 ms (SD 2.4) following the drop and ankle dorsiflexion velocity was decreased starting 22 ms (SD 15) after the drop. To investigate the role of length- and velocity-sensitive afferents on the depression in soleus muscle activity, the ankle rotation was arrested by using an ankle foot orthotic as the platform was dropped. Preventing the ankle movement did not significantly change the soleus depression in late stance [−18.2% (SD 15)], whereas the depression in midstance was removed [+4.9% (SD 13)]. It is concluded that force feedback from ankle extensors increases the locomotor output through positive feedback in late stance. In midstance the effect of force feedback was not observed, suggesting that spindle afferents may have a more significant effect on the output during this phase of the step cycle.

INTRODUCTION

Sensory feedback assists the transition between the locomotor phases, mediates corrective responses to external perturbations, and reinforces locomotor muscle activity (e.g., Donelan and Pearson 2004a; Pearson 2004). In this study we focus on the contribution of afferent feedback to the ongoing muscle activity in human overground walking.

We have argued that the afferent-mediated feedback component of the locomotor electromyograph (EMG) is best investigated through removal of, rather than enhancing, the afferent influx to the spinal network (Nielsen and Sinkjaer 2002; Sinkjaer et al. 2000). Instead of evoking triceps surae stretch reflexes with dorsiflexion perturbations (Dietz et al. 1984; Sinkjaer et al. 1996; Yang et al. 1991), Sinkjaer et al. (2000) imposed rapid plantar flexions in stance and showed a substantial decrease of soleus (SOL) activity in relation to the imposed ankle perturbations in human treadmill walking. This was termed the “unload response” and was suggested to arise from unloading of the muscle–tendon complex, thereby reducing proprioceptor firing rates (Sinkjaer et al. 2000). These results were extended by excluding cutaneous as well as the largest of the group I afferent fibers (Grey et al. 2004) and by showing a correlation between Achilles tendon force and the magnitude of the unload response (Grey et al. 2007).

Similar to the unload response in human, Donelan et al. (2004b) investigated the influence of ground support on the extensor muscles in intact cats and observed a close relation between ground reaction force and ankle extensor activity. In human treadmill walking, several studies have indicated that ground reaction forces influence the locomotor activity of the leg (Faist et al. 2006; Harkema et al. 1997; Stephens and Yang 1999). Recently, within-step plantar flexor activity was modulated by rapidly altering body-weight support (Bachmann et al. 2008). In overground walking, triceps surae activity was demonstrated to covary with Achilles tendon force when subjects walked on inclined or declined surfaces (af Klint et al. 2008). These studies have shown that load feedback may modulate the triceps surae locomotor activity; however, it is still unclear how peripheral afferent feedback contributes to the background locomotor activity during normal overground human walking.

The current study was designed to investigate afferent feedback-mediated activity in the soleus muscle during overground human walking. We used a paradigm whereby subjects walked unrestrained over a movable platform that was dropped when the subject was in single support phase, thereby unloading the plantar flexor muscle–tendon complex and, in effect, reproducing the “unload response” in a more natural setting. We hypothesized that if sensory force feedback contributes to the plantar flexor muscle activity during overground human walking, then the rapid decrease in ground support would elicit a depression in the muscle activity. Also, to investigate whether the muscle–tendon length change influences the unload response the ankle movement was restricted using an ankle foot orthotic (AFO). Here, we hypothesized that if the spindle afferents contribute to the response then restricting the ankle movement would reduce the response.

Some of these data were previously reported in a brief abstract (af Klint et al. 2006).

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METHODS

Twenty healthy volunteers (7 female and 13 male, mean age: 27 yr, range: 22–39 yr) with no known history of neuromuscular disorder participated in this experiment. The study conformed to the Declaration of Helsinki and was approved by the local ethics committee (VN 2004/24). All subjects provided informed written consent.

The experimental setup is illustrated in Fig. 1. All subjects walked barefoot at a self-selected speed ($\sim$4–5 km·h$^{-1}$) on a 10-m path over a robotic platform mounted flush in the floor of the laboratory. The robotic platform has 4 degrees of freedom and is composed of a force plate (OR6-5, Advanced Mechanical Technology, Watertown, MA) mounted on hydraulically actuated pistons (van Doornik and Sinkjaer 2004). After an initial training period the subjects’ right foot touched down approximately centered on the platform. On random trials the platform was dropped vertically by 8 cm with a constant acceleration and deceleration of 0.8 g. The movement of the platform was initiated at a preset latency after heel touchdown corresponding to midstance and late stance ($\sim$40 and $\sim$60% of stance, respectively) as determined by the force plate. Similarly, on some trials the platform was also moved upward (6 cm) in late stance with the same acceleration profile of 0.8 g. The perturbations were presented randomly with a ratio of 3:5 between perturbed and nonperturbed (control) trials to prevent subject anticipation. Data were acquired until 20 trials of each perturbation were recorded.

The right ankle excursion was recorded using goniometry (model SG150; Biometrics, Gwent, UK). Muscle activity was recorded from the soleus (SOL) and tibialis anterior (TA) using surface EMG (surface electrodes, interelectrode distance 2 cm; NeuroLine 720, Ambu A/S, Ballerup, Denmark). The EMG signals were amplified and band-pass filtered (10–1 kHz) using custom-built amplifiers. All signals were sampled at 2 kHz and stored for further processing.

Additionally, in six subjects an accelerometer was placed on the head to reveal the timing of the input to the vestibular organs during the platform movements. A highly sensitive two-directional accelerometer (ADXL-301; Analogue Devices, Norwood, MA) was taped to the forehead of the subjects and the vertical component of the acceleration was recorded while the subjects followed the protocol.

Ankle foot orthotic

Ten subjects followed an extended protocol to determine the influence of ankle movement on the response in the muscle activity. After having finished the first recordings, the subjects were seated semireclined while the ankle foot orthotic (AFO) was custom molded on the foot and shank. The AFO was constructed from two pieces of double-layered 3.4-mm thermoplastic material placed on the dorsal and ventral sides of the foot and leg. It was secured and reinforced with high-strength duct tape for a tight fit. The AFO extended from approximately the first metatarsal, to enable toe movement, to three quarters up the shank. Safety, a thin rubber pad was placed under the heel to prevent slipping. When the thermoplastic had hardened the ankle goniometer was repositioned on the AFO around the ankle and the subjects were asked to continue walking. After an accommodation period of 2–3 min the subjects could touch down with the right foot approximately centered on the platform and the experiment continued. Trials were collected until 20 records of each condition were acquired.

Analysis and statistics

Data analysis was conducted off-line. The EMG records were rectified and low-pass filtered (40 Hz, first-order Butterworth) to extract an amplitude envelope. All records were ensemble-averaged to create a single set of records for each subject and condition.

Trials were manually inspected for each subject. Any step that was not completely on the platform, as evidenced from the force records, was excluded from the analysis. Similarly, records with movement artifact in the EMG prior to the platform movement were also excluded from further analysis. In all cases, ensemble averages were calculated from no less than 15 data records for each condition.

The onset of the platform movement was determined on the basis of the vertical component of the ground reaction force. The responses in the muscle activity to the perturbations were analyzed on the basis of the difference between the ensemble average of the control and the perturbed trials. The latency of the response was assessed through visual inspection determining when the perturbed trial’s EMG significantly deviated from the control within a window of 35 to 70 ms immediately after the perturbation onset. If the perturbed trials did not deviate when wearing the AFO the latencies recorded in the trials without AFO were used. To quantify the response, the relative difference of the area under the curve for the perturbed trials and the control was used.

One-way repeated-measures ANOVA (rmANOVA) was used to determine the effect of perturbing in midstance or late stance without wearing the AFO on the amount of depression in soleus EMG and on the latency of the response. A two-way rmANOVA with factors time in stance (Mid, Late) × AFO (With, Without) was used to determine the effect of the AFO on the muscle activation of the perturbed trials. When significant effects were found the post hoc Tukey–Kramer multiple comparison was used to determine the differences between levels. All statistical tests were conducted with a significance level of 0.05 and all results are shown as mean (SD) according to guidelines in Curran-Everett and Benos (2007).

RESULTS

In 4 of 20 subjects, the drop of the platform did not produce soleus activity that deviated significantly from the control EMG within the 35- to 70-ms window following the midstance perturbation. So as not to bias the data the experiment was terminated for these subjects despite the fact that all had a clear depression in the late stance.

Nonconstrained ankle movement

A typical set of ensemble-averaged data from a single subject is presented in Fig. 2. The subject was walking at about

FIG. 1. Subjects walk at a self-selected speed on a 10-m walkway, stepping on a hydraulically activated platform (I) with the right leg. Joint rotation of the ankle was recorded throughout the step using goniometry (II). A surface electromyogram (EMG) was recorded from the soleus (SOL) and tibialis anterior (TA) muscles (III). On random trials the platform was accelerated downward with 0.8 g at a preset timing in stance.
4.5 km·h⁻¹ and the traces of the perturbed trials (thin lines) are shown together with the control trace (thick line). The platform was rapidly lowered (dropped) at a preset latency (207 and 338 ms) to heel strike (0 ms) in mid- to late stance. This caused a reduction in SOL EMG activity followed by a strong facilitation. No change was observed in TA. The onset of the movement was determined by the vertical ground reaction force (dashed line) and latencies were calculated with respect to this time.

In all subjects, a depression in the soleus muscle activation was seen at latencies ranging from 40 to 62 ms, measured from the onset of the platform drop. The latencies between the perturbations occurring in midstance [49 ms (SD 1), range 40–62 ms] and late stance [45 ms (SD 1), range 40–56 ms] were significantly different [one-way rmANOVA, F(1,15) = 12.57, P < 0.003, Tukey–Kramer, P < 0.003]. The amplitude of the soleus EMG stayed below the level of the control step for 30 ms (SD 8) (range 20–54 ms). To quantify the depression in EMG, the area under the curve was calculated for a window of the ankle movement, which faded away before the depression in the muscle activity. This was not the case for the late perturbation. The latency of the depression in the muscle activation (47 and 42 ms for mid- and late stances, respectively) and in the ankle excursion (14 and 9 ms for mid- and late stances, respectively) is measured with respect to the drop in ground reaction force (middle column). No significantly increased muscle activity in TA was seen prior to the depression in soleus activity, indicating that reciprocal inhibition is unlikely to contribute to this depression.

During the normal unperturbed step the ankle dorsiflexes during the stance phase. However, when the ground support is decreased by the drop of the platform, the dorsiflexion is stopped and, in some cases, the ankle undergoes a small plantar flexion. Across all subjects and time of perturbation, the relative change in area under the curve of the soleus EMG for the perturbed trials was −19.6% (SD 9). No significant difference was found in the amount of depression irrespective of whether the perturbation was performed in midstance or late stance [one-way rmANOVA, F(1,15) = 1.15, P > 0.3, −17.9% (SD 2) and −21.4% (SD 2) for mid and late, respectively].

![Diagram](http://jn.physiology.org/)

**FIG. 2.** Ensemble-averaged trials from typical subject for control steps (thick gray curve, n = 116) and perturbed midstance (thin dotted curve, n = 16) and late-stance (thin curve, n = 16) steps. The left column shows the whole stance phase and the middle and the right columns show the portion of stance surrounding the mid- and late-stance perturbation (dashed vertical lines). In the perturbed trials, at a preset latency (207 and 338 ms, respectively) after heel strike (0 ms), the platform is rapidly lowered (dashed line) at a constant acceleration and deceleration of 0.8 g. The effect of the reduction of ground support is shown in the vertical ground reaction force (Fz), ankle trajectories (Ank), and in the SOL and TA muscle activation (40 Hz, low-pass filtered). The drop of the platform produces a depression of the soleus muscle activity (filled gray area) and reduces the dorsiflexion of the ankle. In this subject, the perturbation in midstance induced an artifact in the SOL EMG at the time of the ankle movement, which was seen prior to the depression in soleus activity, indicating that reciprocal inhibition is unlikely to contribute to this depression.
could produce an increased activity in the tibialis anterior (TA) muscle that through reciprocal inhibition would reduce the SOL muscle activity, the muscle activity of TA was monitored throughout the perturbation. However, in treadmill experiments where a forced plantar flexion produced clear stretch reflexes in the TA, the depression in SOL was still present after common peroneal nerve block (Sinkjaer et al. 2000), demonstrating that the depression was not caused by reciprocal inhibition. In the present study, no significant increase in TA activity was found prior to the decrease in SOL.

In addition to the platform drops, these same subjects were also exposed to platform movements in the upward direction in late stance (Fig. 3). The platform movement induces higher forces on the plantar flexor muscles and thereby a dorsiflexion around the ankle, with a latency of ankle movement of 19 ms (SD 15). The activity of the soleus muscle was also increased with the upward movements of the platform, 18.4% (SD 12), starting at a latency of 46 ms (SD 5) (range 38–55 ms). The absolute magnitude and latency of the response was not significantly different from the drops in late stance [one-way rmANOVA, $P = 0.7$, $F_{(1,15)} = 8.16$, and $P = 0.52$, $F_{(1,15)} = 0.43$, for magnitude and latency, respectively].

**Acceleration of the head**

To investigate whether vestibular organs could contribute to the response, an accelerometer was fixed to the forehead of six subjects to reveal the onset of the input to the vestibular organs. The inherent latency of the accelerometer, 1.9 ms (SD 0.4), was measured by tapecing the device to the platform and dropping the platform. This value was subtracted from the head acceleration latencies. The subjects were dropped in both midstance and late stance (Fig. 4). The head was accelerated at a latency of 10.3 ms (SD 2.7) and 9.7 ms (SD 2.2) for mid- and late stances, respectively; average latency 10.0 ms (SD 2.4).

Values of timing between the soleus activity depression and the changes in ground reaction force and head acceleration are listed in Table 1. The latencies of the head movement are such that the vestibular apparatus cannot contribute to the response (see Discussion).

**Ankle foot orthotic**

Ten subjects were fitted with a custom-molded ankle foot orthotic (AFO). After the accommodation period, the subject had adapted to wearing the AFO. The AFO did not hinder the subject’s walking, but effectively reduced the ankle excursion measured over the whole control step by 84% (SD 10) (Fig. 5). The stance phase duration remained approximately constant: 607 (SD 40) and 614 ms (SD 49), without and with AFO, respectively.

Walking with the AFO decreased the muscle activity in soleus, although the general activation pattern remained. Reduction of the control muscle activity caused by the AFO was −46% (SD 28) and −54% (SD 14) for the mid and late analysis windows, respectively. Dropping the platform had different effects in midstance compared with late stance (Fig. 6). In late stance, the depression was still present with the AFO [−18.2% (SD 15)]. However, in midstance the effect of the drop was not clear [4.9% (SD 13)]. In some subjects the muscle activity was increased relative to the control steps and, in most subjects, no obvious drop in the activity could be seen, even though the signal-to-noise ratio of the muscle activity was >2.

The two-way rmANOVA revealed a significant interaction effect between AFO and time in stance [$F_{(1,9)} = 8.39$, $P = 0.018$] and a post hoc test showed that there was a significant difference between the drop in early stance with AFO and all other groups (Tukey–Kramer, $P < 0.005$); all other comparisons showed no significance.

Even though the AFO prevented most of the ankle movement, it was not completely rigid. Therefore the ankle rotation deviated from the control steps as a result of the decreased ground reaction forces associated with dropping the platform. The amplitude of the deviation from control was decreased by −39% (SD 22) compared with the nonconstrained condition. Nevertheless, the depression in SOL activation in late stance was not significantly different when wearing the AFO (Tukey–Kramer, $P = 0.833$).

**DISCUSSION**

The aim of this study was to investigate afferent-mediated background muscle activity in the soleus muscle during the stance phase of overground human walking. Our experimental paradigm was designed to decrease proprioceptive afferent influx by rapidly decreasing the ground support in the mid- and late-stance phases. This perturbation is in many ways similar to the rapid plantar flexor rotations investigated during treadmill walking (Grey et al. 2004, 2007; Sinkjaer et al. 2000). The effect of reducing the tension on the extensor muscle–tendon units resulted in a depression of the soleus activity, termed the unload response (Sinkjaer et al. 2000). Similarly in this study, the drop of the supporting surface consistently produced a reduction in the soleus muscle activity at spinal onset latencies, suggesting an afferent-mediated nature of the response. In addition, the subjects’ ankle rotation was blocked to decrease the impact of velocity- and length-sensitive spindle afferents on the reduced soleus activity. In midstance the depression was
not detectable during the blocked ankle rotation. Firm conclusions cannot be drawn from this observation (see following text). However, the decrease in soleus activity was present in late stance, while the ankle rotation was blocked, suggesting that neither velocity- nor length-sensitive afferents contribute substantially to the depression in activity.

It should be noted that the midstance response is less consistent than is the late-stance response. In the present study, 4 of the 20 subjects did not show a consistent depression in midstance following a drop of the platform. In these 4 subjects no onset latency for the response could be measured; they were removed from the subsequent analysis so as not to bias the results. On the other hand, the analysis window was chosen to make the response as consistent as possible so that a fair comparison could be made between walking with and without the AFO. Using a longer analysis window would increase the potential for reflex-generated muscle activity to occlude the effect of the platform drop, as can be noted by the variability of the extent of the depression induced by the sharp increase in muscle activity following the depressions (see Fig. 2).

The effect of rapidly dropping the platform, in the single support stance phase, has a major impact on the biomechanics of walking. This is different from foot-in-hole experiments, where ground support is removed prior to (van der Linden et al. 2007) or immediately after heel contact (Nakazawa et al. 2004). As the platform is accelerated downward the ground reaction forces (GRFs) are significantly decreased. This reduction of GRF would have a direct impact on the ankle moment and thereby the forces on the plantar flexor muscles. In the specific parts of stance where these perturbations were performed, the major component of the GRF is in the vertical direction and thus we would expect a significant decrease in moment when the platform is accelerated downward. Similarly, the unload response is mediated by imposing a rapid and sustained plantar-flexion rotation around the ankle using a functional joint. This rotation decreases the load on the monarticular muscles around the ankle and also removes the naturally occurring eccentric contraction of the soleus muscle–tendon unit during stance. The response was preserved following an anesthetic block of the common peroneal nerve, demonstrating the unload response was not simply the result of reciprocal inhibition from the stretched TA muscle (Sinkjaer et al. 2000). The magnitude and extent of the unload response found during treadmill walking (Grey et al. 2004, 2007; Sinkjaer et al. 2000) were both greater and longer than those found in the current findings performed during unconstrained walking. These discrepancies are at least partly likely to be attributed to the active rotation of the ankle joint used to produce the unload response.

The tendency for subjects to adapt to or anticipate the next perturbation can significantly alter responses, as for example in slip experiments (e.g., Marigold and Patla 2002). To prevent subjects from anticipating the platform movements in the

TABLE 1. Latency of EMG depression

<table>
<thead>
<tr>
<th>Time in Stance</th>
<th>GRF/Platform movement</th>
<th>Acceleration at the head</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mid</td>
<td>46.6 ms (SD 4.0)</td>
<td>32.1 ms (SD 5.5)</td>
</tr>
<tr>
<td>Late</td>
<td>43.5 ms (SD 4.8)</td>
<td>29.9 ms (SD 5.5)</td>
</tr>
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</table>
Neural mechanism of the response in locomotor EMG

Several afferent and central pathways may contribute to the plantar flexor activity in overground walking. One such central pathway would be the vestibulospinal tract that has been shown to influence soleus activity during standing (Fitzpatrick et al. 1994). The output of the vestibular apparatus changes in response to the acceleration of the head as the body accelerates vertically from the decrease in GRF. However, we believe that it is unlikely that this vestibular input contributes to the depression in locomotor EMG for the following reasons. First, it is unlikely that a vestibular reflex would be directional in the present paradigm. The platform perturbation is more likely to be interpreted as a destabilizing event; therefore it would be more likely that a vestibular response would increase muscle activity to stabilize balance rather than decrease muscle activity. We have noted that the soleus activity is briefly decreased when the subject loses ground support. This reaction would lower the stiffness of the ankle when dropped, leaving the ankle in a more vulnerable state at the inevitable touchdown. Second, the very short latency of the response in soleus with respect to the recorded acceleration of the head (32.2 and 29.9 ms for midstance and late stance, respectively) makes a vestibular response unlikely. Latencies for mechanical vestibular perturbations in gastrocnemius and tibialis anterior are about 50 and 60 ms, respectively (Horstmann and Dietz 1988). Thus the latency for the soleus muscle can be assumed to be around 50 to 60 ms because the innervations zone of the soleus is at a similar distance from the CNS. Latencies for galvanic vestibular perturbations in the soleus range from 56 ms (Fitzpatrick et al. 1994) to 62 ms (Britton et al. 1993). Therefore we conclude that it is very unlikely that the depression in soleus activity stems from descending vestibular influence.

Cutaneous afferents from the sole of the foot have been shown to play an important role in regulating locomotor activity during walking (Duyssens et al. 2000; Zehr and Stein 1999). The rapid decrease in GRF would invariably impose changes to the load distribution of the foot and thereby also the cutaneous and proprioceptive afferent firing rates from the foot and ankle. However, depressing cutaneous afferents from the foot and ankle during rapid plantar-flexion perturbations did not have an effect on the depression in soleus activity (Grey et al. 2004). Therefore it is unlikely that cutaneous afferents

![Graph of ankle dorsiflexion, ground reaction force (Fz), and soleus muscle activity.](image)

**FIG. 5.** Ensemble averages of ankle excursion, vertical ground reaction force, and soleus muscle activity shown for a typical subject perturbed in mid- and late stances (200 and 350 ms, respectively). The traces of control (thick gray lines) and perturbed trials (thin black lines) are shown for the nonconstrained ankle movements (continuous lines) and for the steps where the ankle movements were constrained by an ankle foot orthotic (AFO, dotted lines). The stance duration remained approximately the same for the two conditions with and without AFO. Both the measured range of ankle excursion during the nonperturbed steps and the ankle movement in response to the perturbations were significantly decreased by the AFO (~84% and ~39%, respectively). The overall activity in the soleus muscle was also reduced by the AFO but the activation pattern was still present when the subjects’ ankle movement was constrained. The effect in the muscle activity of dropping the platform is a reduction in muscle activity (gray filled area). In late stance, this response is still present when the ankle movement is constrained, indicating that afferents sensitive to modalities other than length and velocity contribute to the response. However, in midstance no decrease in EMG can be found, possibly suggesting a greater importance of spindle afferents in this part of the stance phase.

Current investigation the perturbations and control trials were randomly presented throughout the experiment. Furthermore, to investigate adaptation, the mean of the first three, the middle three, and the last three responses to each perturbation was determined in all subjects. The rmANOVA with factors perturbation type (mid drop, late drop, and late up) × time in the experiment (first, middle, and last) did show significance between the groups for the main factor perturbation type [F(2,30) = 41.57, Pperturbation < 0.0001], as expected from the sign difference between the upward perturbations and the drops. However, no time [F(2,30) = 0.27, Ptime = 0.70] or interaction effects [F(4,60) = 1.49, Ptime×perturbation = 0.24] could be found. This indicates that the response in the locomotor EMG to the mechanical perturbations was not significantly altered during the course of the experiment.

**Neural mechanism of the response in locomotor EMG**

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would have a significant impact on the soleus depression reported in this study.

The contribution of proprioceptive sensory output in generating the locomotor output has spiked interest over the years. Velocity- and length-sensitive spindle-mediated Ia- and II-afferent pathways have a significant role in corrective responses to rapid dorsiflexions (Dietz et al. 1984; Sinkjaer et al. 1996; Yang et al. 1991). Unlike previous studies in treadmill walking (Bachmann et al. 2008; Grey et al. 2007) the experimental paradigm used in this investigation ensured that forces on the plantar flexor muscles could be changed with minimal ankle movement. Using the AFO constricted the ankle movement and, subsequently, the muscle–tendon length and lengthening velocity of the monoarticular soleus muscle. However, it should be noted that the absolute muscle-fiber lengths can be different from the muscle–tendon lengths (Loram et al. 2004) and further studies will have to characterize the specific muscle-fiber changes. Ideally, the afferent input to the CNS would best be recorded using microneurography during walking. With the current recording techniques this is impossible. To the best of our knowledge, microneurographs have not yet been recorded with large-amplitude rapid-velocity unloading similar to the paradigm used in the present study. However, spindle microneurographs have been recorded from the common peroneal nerve during small voluntary dorsiflexion and plantarflexion movements and these recordings demonstrate that such movements do modulate the spindle firing rates, although the modulation decreases as the muscle is loaded (Burke et al. 1978). In the present study the triceps surae was decreased but not fully removed as the platform dropped and, furthermore, the ankle movement prior to the response was decreased by 34% using the AFO. Therefore it is still likely that preventing the muscle–tendon movement would minimize the effects on muscle fascicles and thereby the input to the velocity- and length-sensitive group Ia- and II-afferents. Unloading the muscle–tendon complex may initially distribute the length/velocity changes differently between tendon and muscle fibers. Preliminary data of soleus muscle fascicle ultrasonography during platform drops with unrestricted ankle movement show a delayed muscle fascicle shortening of about 18 ms (af Klint et al., unpublished observation). The drop of the platform in late stance produced a depression in soleus EMG while the ankle was arrested. This suggests that force-sensitive afferents, presumably stemming from Golgi tendon organs, contribute to the locomotor activity in the soleus muscle in late stance. This is in line with the results of Grey et al. (2007) showing a correlation between Achilles tendon force and the unload response in late stance. Other force-sensitive afferents as group III joint receptors are unlikely to contribute due to the relatively short latency of the response. However, both afferent activity from joint receptors and cutaneous receptors may be integrated at longer latencies and thus influence the locomotor activity.

In stance the Achilles tendon force progressively increases (Komi et al. 1992) and with it the output of Golgi tendon organs (Prochazka and Wand 1980) and other force-sensitive afferents. Consequently, in midstance the force and force-sensitive afferent feedback would be lowered compared with that later in stance. This could be one of the contributing factors that in four of the subjects no response was shown in midstance. Furthermore, in the remaining subjects that showed a consistent depression in midstance, the lack of a depression while wearing the AFO for the midstance perturbations could indicate that load-sensitive afferent pathways have a relatively lower contribution in midstance than that in late stance. Additionally, the slightly longer latency of the midstance response could indicate that other pathways are involved, e.g., group II afferents (Sinkjaer et al. 2000). Another cause for the lack of depression in soleus activity could be that the lowered EMG levels prevent detection of a depression in activity. However, the EMG level for the unperturbed condition was significantly decreased in the midstance condition, although the level was still detectable (signal-to-noise ratio ≥ 2). A third possibility could be that as less proprioception is reaching the spinal cord a greater proportion of the signal is mediated by central drive. Therefore a firm conclusion cannot be drawn from the lack of depression in midstance soleus EMG.

In overground walking the modulation of afferent feedback has been studied using an irregular surface setup (af Klint et al. 2008). It was shown that the locomotor output of the triceps surae covaries with the Achilles tendon load and muscle–tendon length. Similarly, in this study we found that the increased GRF produced an increase in the soleus activity with latencies similar to those of the depressions. This indicates that the same pathways may be responsible for the increases and the decreases in soleus activity and would imply that the human soleus muscle in walking is modulated through positive force feedback. Further studies will have to investigate whether this contribution stems from autogenic or heterogenic positive feedback.

G R A N T S

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R E F E R E N C E S


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