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RESEARCH ARTICLE

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A task dependent change in the medium latency component of the soleus stretch reflex

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Abstract In comparison to the H-reflex, the task dependency of the human stretch reflex during locomotive and postural tasks has not received a great deal of attention in the literature. The few studies on reflex task dependency that have been performed to date have concentrated on either the group Ia mediated H-reflex or the short latency stretch reflex. In the present study the medium latency component of a mechanically evoked stretch reflex is investigated during walking, pedalling, and sitting. Stretch reflexes were evoked in the soleus muscle using dorsiflexion perturbations generated with a portable stretching device. Perturbations of equal amplitude and velocity (8 deg, 300 deg/s) were presented to 16 healthy subjects while they walked on a treadmill and pedalled a cycle ergometer. For eight of these subjects, an additional set of data was collected as they sat on the ergometer holding a steady posture. Perturbations were presented in the early to mid stance phase of walking and the downstroke of the pedal cycle. During all three conditions, the background soleus muscle activity was matched. The short (SLR) and medium (MLR) components of the soleus reflex responses were quantified by calculating the area of each burst in a 15-ms window centred on the peak of the respective burst. In addition, the stretch velocity-stretch reflex input-output curve was examined for the two locomotion tasks over a range of velocities from 100 to 400 deg/s. Peak latencies for the two reflex responses were observed at 52±5/77±6 ms (SLR/MLR) for walking, 51±3/76±6 ms (SLR/MLR) for pedalling, and 50±3/76±7 ms for sitting. A statistically significant increase in the magnitude of the MLR was observed during walking compared with pedalling and sitting (P=0.007), whereas no difference in magnitude was observed between the three tasks for the SLR (P=0.616). Furthermore, no difference was observed in the stretch velocity-stretch reflex input-output relationship between walking and pedalling. It is suggested that the medium component of the stretch reflex response is modulated to provide increased control for the postural demands of walking.

Keywords Afferent feedback · Human · Walking · Pedalling · Sitting

Introduction

Reflex activity is used by the central nervous system in the control of posture and locomotion. When performing any task, the activity in the sensorimotor pathways is modulated to facilitate the specific demands of the task (Prochazka 1989). The stretch reflex can be modulated during postural control tasks (reviewed in Horak and Macpherson 1996) and locomotive tasks such as walking and pedalling (reviewed in Zehr and Stein 1999). In the present study we focus on the modulation of the stretch reflex between three different tasks: walking, pedalling, and sitting.

The first studies during which the task dependency of the group Ia afferent mediated response was investigated used the H-reflex to compare walking with standing (Capaday and Stein 1986; Morin et al. 1982), walking with stepping (Crenna and Frigo 1987), and walking with running (Capaday and Stein 1987). These studies showed that the H-reflex magnitude is largest during standing; that it decreases during walking; and that it is smallest during running. Later, the investigation of task dependency was extended to pedalling and sitting where, again, the H-reflex was shown to be phase modulated during pedalling (Boorman et al. 1992) and depressed compared with sitting (Brooke et al. 1992). It is notable that Ferris et al. (2001) have recently challenged the idea that the H-reflex gain is modulated from walking to running. They suggested that the difference between their study and earlier studies was in the analysis methods used in the data processing. To our knowledge, a similar study has

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not been reported in the literature for pedalling and sitting. Cutaneous reflexes have also been shown to be phase and task modulated (e.g. Brooke et al. 1997; Duysens et al. 1993) although the cutaneous reflex is modulated differently than the H-reflex (Brooke et al. 1999; Zehr et al. 2001).

While the H-reflex technique is often used to probe the spinal mediation of reflex function, it has recently become possible to investigate the behaviour of the intact stretch reflex for locomotion tasks in a more natural manner. Stretch reflexes elicited by a mechanical perturbation have been produced during walking (Sinkjaer et al. 1996; Yang et al. 1991) and pedalling (Grey et al. 2001b). For both walking and pedalling, the phase modulation of the stretch reflex is similar to that of the H-reflex. However, the task dependent modulation that exists in the H-reflex does not seem to occur for a mechanically produced stretch reflex when walking is compared with standing (Andersen and Sinkjaer 1999) and pedalling is compared to sitting (Grey et al. 2001b).

Most studies comparing the task dependency of H-reflex and stretch reflex function have been restricted to an investigation of a single component of the reflex. The H-reflex preferentially stimulates the large group I afferent fibres, and most stretch reflex studies have concentrated on the short latency burst, which is also strongly mediated by the large monosynaptic group Ia pathway. The H-reflex modulation that is observed between different tasks is very likely due to the different effects of presynaptic inhibition between tasks (Capaday and Stein 1987; Edamura et al. 1991; Faist et al. 1996). However, the mechanically produced stretch reflex is less sensitive to presynaptic inhibition than is the H-reflex (Morita et al. 1998a).

The stretch reflex, however, may receive contributions from a variety of pathways including cutaneous afferents, spindle groups Ia and II afferents, and load sensitive group Ib afferents. It is commonly accepted that the short latency component of the stretch reflex is mediated by the muscle spindle group Ia afferent pathway (Matthews 1991; Taylor et al. 1985). More recently, evidence has been reported suggesting that the medium latency stretch reflex very likely receives an important contribution from the group II pathway (Grey et al. 2001a, 2001c).

The purpose of the present study is to investigate stretch reflex function during walking and pedalling – two very different locomotion tasks involving a repeatable cyclic motion of the legs. To complete the picture, a sitting task is also investigated. While previous studies have concentrated on the group Ia mediated H-reflex or the stretch-evoked group Ia mediated short latency reflex response, the present study is the first to investigate the possibility of task dependency in the group II mediated medium latency stretch reflex response. In this study we show that the short latency component of the stretch reflex is not modulated between the three tasks, and the medium latency response is increased in walking compared with pedalling and sitting.

Materials and methods

Sixteen healthy subjects (ten male, six female) between the ages of 22 and 34 years with no history of neuromuscular disorder participated in this study. All 16 subjects participated in a walking and pedalling protocol, and eight of them participated in an additional sitting protocol. For each subject, all protocols were conducted on the same day with the same electrodes. Subjects gave informed consent prior to their participation and the local ethics committee approved the experiments. The experiments were conducted in accordance with the Declaration of Helsinki.

Apparatus and instrumentation

The subjects were instrumented with bipolar surface EMG electrodes over four muscles of the left leg: soleus (SOL), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF). EMG signals were amplified and bandpass filtered from 20 Hz to 1 kHz. Perturbations were imposed using a portable stretching device capable of rotating the ankle joint while the subjects walked on a treadmill or pedalled on a cycle ergometer. Complete details regarding the mechanics of the portable stretching device are reported elsewhere (Andersen and Sinkjaer 1995). Briefly, the device consisted of a functional joint attached to the subject's left ankle joint with a polypropylene plaster cast and connected to a powerful AC servomotor via flexible Bowden cables.

When pedalling, subjects were seated on a standard cycle ergometer modified so that the crank angle could be measured with an optical encoder. The handlebar and seat were adjusted to positions of comfort for each subject prior to the beginning of the experiment. Standard full shank cycling shoes were worn and fixed securely to the crank arms with clipless pedals. A larger shoe was used on the left foot to accommodate the boot of the portable stretcher. The ankle angle was measured with an optical encoder incorporated within the portable stretcher. All data were sampled at 2 kHz. The ankle and crank angular velocity was determined offline by differentiation of the respective angular position records.

Experimental protocol – walking

The subjects began the experiment with 5 min of treadmill walking to accommodate to the portable stretcher. During this period they chose a comfortable cadence and speed between 3.5 and 4 km/h that were maintained for the remainder of the walking phase of the session. Dorsiflexion perturbations of 8 deg were generated by the portable stretching device during the early to mid stance phase at approximately 200 ms from heel strike. Perturbations were applied pseudo-randomly every three to five step cycles. A 500-ms data record was collected starting 100 ms before the perturbation. A control step was recorded immediately prior to each perturbed step. Perturbations were applied until 20–25 records were acquired. The perturbation velocity was then changed and the protocol was repeated. Each subject was presented with 10–12 perturbation velocities in a range between 100 and 400 deg/s.

Experimental protocol – pedalling

Following the walking protocol, each subject was seated on the cycle ergometer and asked to perform easy pedalling at 60 rpm. The pedalling load was adjusted so that, at a crank angle of approximately 90 deg (downstroke), the soleus EMG matched that during walking at approximately 200 ms after heel strike. This phase of the crank cycle corresponds to a knee angle ranging from 105 to 120 deg of flexion. After an appropriate load was determined, the subject then pedalled for a 5-min adaptation period while the background EMG was monitored. While pedalling, visual (speedometer) and audible (metronome) feedback was provided to the subject to assist them in maintaining the correct cadence. Following the adaptation period, dorsiflexion perturbations of 8 deg were generated by the portable stretching device at a crank angle of approximately 90 deg (when the soleus EMG was matched). The perturbations were presented, and the data were collected in the same manner as for the walking protocol until 20–25 records were obtained for each of 10–12 perturbation velocities in a range between 100 and 400 deg/s.

Experimental protocol – sitting

After the pedalling protocol, an additional sitting protocol was performed with eight of the subjects. In this case, perturbations of approximately 300 deg/s were presented while the subject held the crank ankle at 90 deg and maintained the same level of background soleus EMG that was observed during walking and pedalling.

Data analysis

Signal processing and analysis were carried out offline. The EMG records were rectified and filtered with a 40-Hz first order low pass filter to extract an amplitude envelope. The individual records for a particular trial were ensemble averaged to produce a single record for each perturbation velocity and task.

The background level of soleus EMG in the control record was determined by calculating a mean rectified value over a 30-ms window immediately prior to the onset of the perturbation, as determined from the perturbed step. The peak and onset latencies of the soleus stretch reflex were determined by visual inspection using a cursor on the display. The onset latency was defined as the first major deflection in the EMG record following the perturbation. Unlike the short latency response, the onset of the medium latency response is not always easily defined. Because the EMG does not always drop to the level of the background EMG, the beginning of this response is often difficult to determine. Consequently we did not attempt to measure the onset latency of the medium latency response. In contrast, the peaks of the short and medium latency bursts were readily definable.

The short and medium components of the soleus reflex responses were quantified by calculating the area of each burst. The area for each response was defined by centring a 15-ms window over the peak of the response and subtracting the area under the control curve from that under the perturbed curve.

Statistical analysis

The magnitudes of the reflex responses were compared across the three task conditions using a repeated measures analysis of variance test (rmANOVA) with factors reflex component × task condition. To compare the effectiveness of the matched SOL background EMG and perturbation velocity, one-way ANOVA tests were performed for both factors against the task conditions.

A linear regression analysis was carried out to determine the relationship between the area increments and the perturbation velocities for all subjects. The slopes were then pooled and compared using a two-way rmANOVA with factors: slope × task condition. For all statistical tests, the 0.05 level of significance was chosen to indicate a significant difference. Results are shown throughout this report as means (± SD).

Results

A typical set of averaged data for one subject is shown in Fig. 1. A 300-ms section of data, starting 100 ms prior to the stretch onset, are shown for the walking, pedalling, and sitting tasks. Unperturbed control records (thin lines) are shown for the walking and pedalling tasks. After relatively little pedalling practice, all subjects were able to maintain the required cadence with the aid of the speedometer and/or metronome (some subjects did not require the use of the metronome). During walking, the SOL EMG (Fig. 1A) gradually increased throughout the stance phase. The burst of SOL EMG during pedalling was typically bell shaped and of shorter duration than that seen during the stance phase of walking. TA activity was minimal during both tasks when the stretches were applied (Fig. 1B). For all three tasks, the ankle angle was close to 90 deg (i.e. within 5–10 deg) when the stretch was imposed. In Fig. 1C the ankle record in this figure has been set to zero at the stretch onset to highlight the similarity of the stretch trajectory during walking and

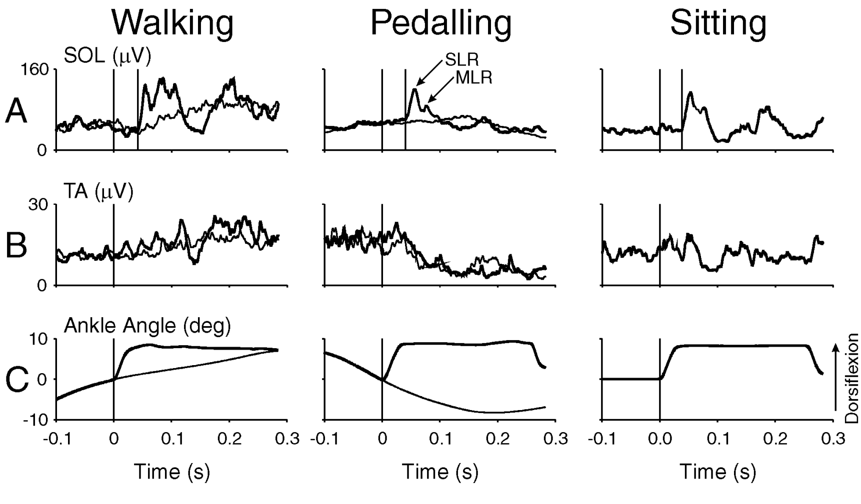

Fig. 1A–C Example data from one subject during walking, pedalling, and sitting. These data represent an ensemble average of 20 records. Perturbed traces (*bold*) are shown superimposed over control traces (*thin*) for the locomotor tasks. The time scale is offset so that time zero occurs at the start of the perturbation and is indicated with a *vertical line* through each panel. **A** The short (*SLR*) and medium (*MLR*) latency components of the stretch reflex can be seen in each of the soleus EMG records. A *second vertical line in each panel* indicates the onset of the SLR. **B** The perturbation had no effect on tibialis anterior EMG. **C** The ankle angular position is offset so that zero corresponds with the start of the stretch. In this case a dorsiflexion perturbation of 8 deg and 325 deg/s was presented at time zero

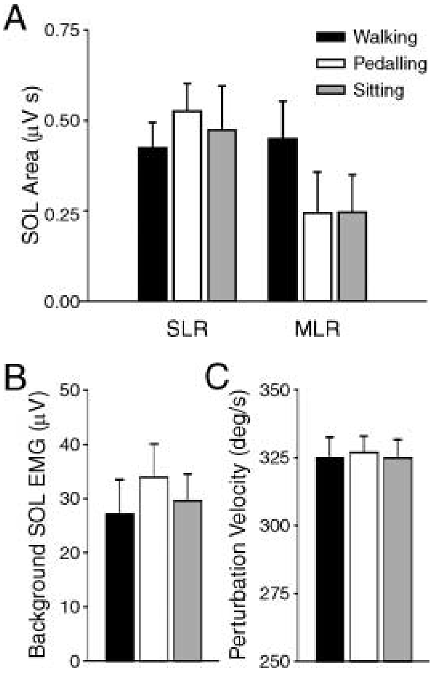

Fig. 2 **A** Area increments across all subjects for the short (*SLR*) and medium (*MLR*) latency components of the soleus stretch reflex in response to a perturbation during the early to mid stance phase of walking (n=16), the downstroke phase of pedalling (n=16), and sitting (n=8). SLR was not different between the three tasks (P=0.616). MLR during walking was different from MLR during pedalling and sitting (P=0.007). **B** Background soleus EMG and **C** perturbation velocity were not different between the three tasks (P=0.478 and P=0.959 respectively). The eight subjects who participated in the sitting protocol were a subset of the 16 who participated in the walking and pedalling protocols. *Error bars* represent 1 SD

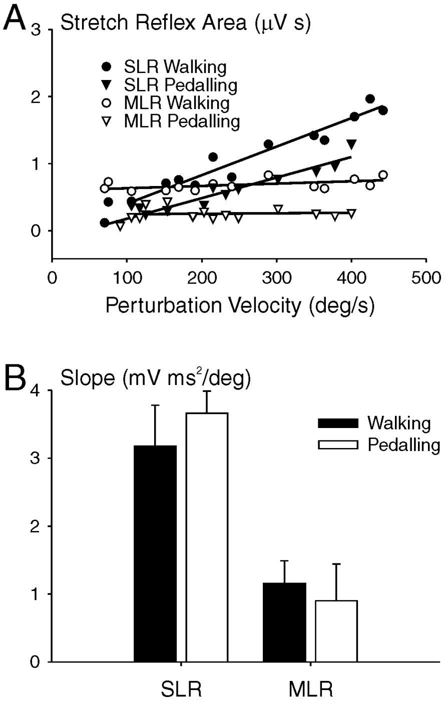

Fig. 3 **A** Example data from one subject of the stretch velocity-stretch reflex input-output curve during the early to mid stance phase of walking (n=16) and the downstroke phase of pedalling (n=16) for the short (*SLR*) and medium (*MLR*) latency components of the soleus stretch reflex. The slopes of these curves were similar between the two tasks for both SLR (walking: 4.1 mV ms2/deg; pedalling: 3.2 mV ms2/deg) and MLR (walking: 0.9 mV ms2/deg; pedalling: 0.8 mV ms2/deg). **B** Across all subjects there was no difference between the tasks for either SLR or MLR (P=0.379). *Error bars* represent 1 SD

pedalling. Across all subjects, the knee angle ranges were 5–15 deg during walking, and 105–120 deg during cycling and sitting when the perturbations were imposed.

The effects of the dorsiflexion perturbations are highlighted in Fig. 1 with bold lines superimposed over the control records. In all cases during walking, the ankle was undergoing a dorsiflexion movement when the stretch was presented. Across all subjects, the average angular velocity of the dorsiflexion movement at the time of the perturbation was 25±6 deg/s. During pedalling, however, there was much more variability in the angular velocity. Although there was very little intertrial variability within a given subject, considerable intersubject variability was observed. In most cases the ankle underwent a slow plantarflexion movement (e.g. Fig. 1C) while in other cases a slow dorsiflexion was observed. Across all subjects, the average angular velocity at the time of the perturbation was 13±7 deg/s toward plantarflexion. Prior to the stretch, the soleus EMGs for the control and perturbed steps were similar in the three task conditions (Fig. 1A). For this subject, the onset of the first component of the stretch reflex can be seen at 42 ms for walking, 41 ms for pedalling, and 39 ms for sitting. In this case, the onset of the medium latency response is also evident at approximately 64 ms for walking while for pedalling and sitting it is not clearly defined. Whereas the onset latency of the SLR was always clearly defined, the MLR onset was not always well defined for all subjects and all tasks. In contrast, peak latencies for the different components of the reflex are more easily defined. In Fig. 1A, for example, peaks can be seen at 56/80 ms (SLR/MLR) for walking, 55/78 ms (SLR/MLR) for pedalling, and 53/74 ms for sitting. A long latency component of the stretch reflex is also present at 105 ms for the walking condition. Across all subjects, the peak latencies for the two reflex responses occurred at 52±5/77±6 ms (SLR/MLR) for walking, 51±3/76±6 ms (SLR/MLR) for pedalling, and 50±3/76±7 ms for sitting. The perturbation did not produce a change in tibialis anterior activity preceding or during the time period where the present analyses were carried out.

The changes in area of the short and medium components of the soleus stretch reflex across all subjects and task conditions are presented in Fig. 2A together with the background soleus EMG (Fig. 2B) and the stretch velocity (Fig. 2C). In all cases, the background soleus EMG and the ankle perturbation velocity were very similar between the three task conditions. There was no significant difference in either the background EMG

(*P*=0.478) or perturbation velocity (*P*=0.959). There was also no statistical difference between the three task conditions in the stretch reflex responses (*P*=0.616). There was, however, a significant interaction between the reflex components and the task conditions (*P*=0.007). This interaction is evident in Fig. 2A where the MLR response during walking is greater than that of both pedalling and sitting.

The results of the input-output analysis of the stretch reflex response to perturbation velocity are summarized in Fig. 3. An example set of input-output curves from a single subject is shown in Fig. 3A. In this case the linear best-fit slopes of the SLR during walking and SLR during pedalling are similar (4.1 mV ms2/deg and 3.2 mV ms2/deg, respectively). Similarly, the slopes for the MLR response are also very close (0.9 mV ms2/deg and 0.8 mV ms2/deg, for walking and pedalling respectively). The linear best-fit slopes of the responses across all subjects are shown in Fig. 3B. The rmANOVA on the slope of the reflex responses showed that although there was a significant difference between the slopes of the short and medium reflex responses (*P*<0.001), there was no difference between the walking and pedalling tasks (*P*=0.379).

Discussion

In this study, we examined the responses of the short and medium latency components of a soleus stretch reflex to an unexpected stretch during walking, pedalling, and sitting. While there was no difference in the magnitude of the short latency response between the three tasks, the medium latency response during walking was greater than that during pedalling or sitting. There was no difference between walking and pedalling in the slope of the input-output curve of the reflex responses when the perturbation velocity was changed.

Methodological considerations

When comparing reflex modulation between different tasks, there are several factors that must be considered. Comparing walking, pedalling, and sitting, for example, it is not possible to match the kinematic and electromyographic variables at the same time because these variables are mutually dependent, and vary in a complex way. Because the reflex amplitude is strongly modulated by the level of muscle activity and the perturbation kinematics, we chose to match the level of background activity and the perturbation trajectory between tasks at the expense of ankle angular position and ankle angular velocity. Although the kinematic variables between the two locomotion tasks were similar, they were not matched. Given that the stretch reflex is known to modulate with length and velocity changes in muscle (e.g. Kearney and Hunter 1982; Matthews 1972), the interpretation of these results must be made cautiously. However, in matching the level of background activity, we have made an attempt to match the level of excitability of the motoneurone pool.

It should also be noted that the external constraints for the three conditions were not alike. Therefore, it is possible that the stiffness of the muscle was different between the three tasks at the time of the perturbation. Furthermore, the tasks involve eccentric, concentric, and isometric muscle contractions. This leads to the possibility that the muscle spindles do not receive a similar stretch during walking, pedalling, and sitting despite the fact that the amplitude and velocity of the ankle perturbations were matched.

Task dependency of the stretch reflex

The results of the present study supplement those of previous studies where task dependency of the mechanically evoked short latency stretch reflex was examined (Andersen and Sinkjaer 1999; Grey et al. 2001b; Sinkjaer et al. 1996). Combining these results with those of the present study, it appears that, in contrast to the H-reflex, the short latency component of the soleus stretch reflex does not exhibit task dependency between walking, standing, sitting, and pedalling– at least in the early to mid part of the stance phase. The present study does not rule out the possibility that there exists a task dependent modulation of the short latency reflex response in other phases of the step/pedal cycle. It should be noted that while Sinkjaer et al. (1996) did not observe a difference in the short latency component of the stretch reflex between walking and standing, such differences have been reported for stretch reflexes in response to tendon taps (Llewellyn et al. 1987; Dietz et al. 1990). However, in contrast to joint perturbations, it can be very difficult to control the stretch amplitude and velocity resulting from a tendon tap. The comparison between the joint perturbation study of Sinkjaer et al. (1996) and the tendon tap studies is further complicated by the fact that different muscles were investigated in these three studies. Llewellyn et al. (1987) measured reflex responses in the medial gastrocnemius muscle, Dietz et al. (1990) used two quadriceps muscles, and Sinkjaer et al. (1996) investigated the responses in the monoarticular soleus muscle.

There is a strong task dependent modulation of the H-reflex between walking and standing (Capaday and Stein 1986), and between pedalling and sitting (Boorman et al. 1992; Brooke et al. 1992). Capaday and Stein (1986) reported that the H-reflex during standing was up to 3.5 times as large as that during walking compared with standing in some phases of the step cycle. Similarly, Brooke et al. (1992) reported that the H-reflex was significantly depressed during pedalling compared with sitting. The depression in the H-reflex during these dynamic tasks is thought to be the result of presynaptic inhibition of the muscle spindle group Ia pathway (for review see Stein 1995). The lack of depression in the mechanically evoked stretch reflex is possibly explained by the observation that the stretch reflex is less susceptible to presynaptic inhibition than is the H-reflex, probably due to the comparatively greater temporal dispersion in the mechanically evoked response (Morita et al. 1998b). Presynaptic inhibition could gate the afferent inflow of the group Ia activity during unperturbed walking, but the more rapid Ia discharge that results in response to a mechanical perturbation might overcome the inhibition, thus allowing the stretch reflex to exert its full corrective response.

In contrast to the short latency component of the stretch reflex response, the medium latency component increases, on average, to the level of the short latency component during walking while it is smaller during pedalling and sitting. A major difference between the walking task and the seated tasks is that the body weight is supported and the plantarflexors do not play a role in the control of balance during pedalling and sitting. It is possible that the increase in the MLR during walking occurs as a result of the need for a better controlled stretch reflex response when balance must also be controlled. Although not analysed in the present study, we also noted a distinct trend for a moderate to large long latency response during walking. In contrast, this response was typically smaller or absent during the pedalling and sitting tasks. The long latency component of the stretch reflex most probably reflects a transcortical pathway from the large diameter group Ia afferents (e.g. Petersen et al. 1998; Sinkjaer et al. 1999). The medium latency response is very likely contributed to by group II afferents (Grey et al. 2001a, 2001c) probably via a polysynaptic pathway (reviewed in Jankowska 1992). It is possible that the group II pathway is depressed by either presynaptic or postsynaptic mechanisms during pedalling and sitting, and that these inhibitory effects are weak during walking.

It might be argued that our balance control proposal suggests that load receptors might have a role in regulating the corrective reflex response to a perturbation. There exists evidence from cat experiments to show that load receptors contribute importantly to the magnitude (Duysens and Pearson 1980) and timing (Duysens and Pearson 1980; Pearson and Collins 1993; Whelan et al. 1995) of the reflex response during walking. Recently, it has been shown in human experiments that load receptors contribute to the regulation of stance phase timing (Stephens and Yang 1999). Based on animal studies and human postural studies, it has been suggested that load receptors contribute strongly to the magnitude of the reflex response during the stance phase of walking (Dietz 1997, 1998; Dietz and Duysens 2000; Dietz et al. 1992; Duysens et al. 2000); however, conclusive evidence for such a contribution has not yet been established. In contrast, we have recently investigated reflex responses during whole body loading and unloading and found that load receptors do not contribute strongly to the compensatory action of either the short or medium latency components of the response (Grey et al. 2001c).

Examining the input-output relationship between the perturbation velocity and the stretch reflex is an indirect method of probing the mechanisms underlying the stretch reflex (Kernell and Hultborn 1990). Our observation that the slope of the stretch velocity-stretch reflex relationship does not change appreciably between the downstroke phase of pedalling and the early to mid stance phase of walking suggests that the spinal cord controls the two locomotor tasks in a similar manner. The higher slope observed for the SLR compared with the MLR is simply an indication of the greater velocity sensitivity of the group Ia pathway compared with the group II pathway.

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