

## RESEARCH ARTICLE

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## Loading during the stance phase of walking in humans increases the extensor EMG amplitude but does not change the duration of the step cycle

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**Abstract** Prior work from mammals suggests that load experienced by extensor muscles of the hindlimbs (i.e. Duysens and Pearson 1980; Pearson and Collins 1993; Fouad and Pearson 1997) or cutaneous afferents from the plantar surface of the foot (Duysens and Pearson 1976; Guertin et al. 1995) enhances activity in extensor muscles during the stance phase, and delays the onset of flexor activity associated with the swing phase. The presumed functional significance of this phenomenon is that extensor activity of the supporting limb during walking can: (a) reinforce the supporting function in proportion to the load experienced, and (b) prolong the stance phase until unloading of the limb has occurred. Whether a similar functional role exists for load-sensitive afferents during walking in the human is unknown. In this study, the effect of adding or removing a substantial load (30% of body weight) at the centre of mass was studied in healthy adult human subjects. Loads were applied near the centre of mass to avoid the need for postural adjustments which might confound the interpretation of the results. Subjects walked on a treadmill with either: (a) a sustained increase or decrease in load, or (b) a sudden unexpected increase or decrease in load. In general, subjects responded to the changes in load by changing the amplitude of the extensor electromyographic (EMG) bursts. For example, with sudden unexpected additions in load, the average increase in amplitude was 40% for the soleus across the stance phase, and 134% for the quadriceps during the early part of the stance phase. Extensor EMGs increased with both sustained and sudden increases in load. Extensor EMG durations also increased (average increase in duration of 4% for soleus with sudden loading, and 7% for sustained loading). Cycle duration hardly changed (average increase

of 0.5% with both sudden and sustained loading). These results differ from those of infants subjected to a similar perturbation during supported walking. A large change in timing (i.e. an increase in the duration of the stance phase by 30% and the step cycle by 28%) was seen in the infants, with no change in the amplitude of the EMG burst (Yang et al. 1998). These results suggest that the central nervous system can control the timing and amplitude of extensor EMG activity in response to loading independently. Maturation of the two components most likely occurs independently. In the adult, independent control of the two components may provide greater flexibility of the response.

**Key words** Locomotion · Load · Human

### Introduction

Recent work in decerebrate and spinal cats has confirmed that group I sensory input from extensor muscles helps control the duration of the stance phase in walking. For example, enhanced group I input from extensor muscles increases the amplitude and duration of the extensor electromyographic (EMG) burst associated with the stance phase, and delays the onset of the subsequent swing phase. This is true of group I input from electrical stimulation of the muscle nerve (Conway et al. 1987; Pearson and Collins 1993; Guertin et al. 1995), direct stretch to the muscle (Duysens and Pearson 1980; Guertin et al. 1995), or vibration of the muscle tendon (Guertin et al. 1995). These same afferents can entrain the locomotor rhythm (Conway et al. 1987; Pearson et al. 1992), providing further evidence for their access to the rhythm generator itself. The presumed functional significance of these results is that afferent activity from extensor muscles in the supporting limb: (a) increases support in response to increased load, and (b) prolongs the stance phase until unloading of the limb has occurred.

Do group I afferents from extensor muscles have a similar function in the intact human? Intuitively, signals

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that indicate the readiness of a limb to progress to the swing phase from the stance phase should be especially important for a biped, whose postural stability is easily disrupted. In an earlier report, the behaviour of a putative group Ib reflex in extensor muscles at the ankle was studied during sitting and walking. During walking, the inhibition produced by afferents from the medial gastrocnemius nerve in the soleus muscle was decreased (Stephens and Yang 1996a), but the change from sitting to walking was small. Moreover, no excitation was found at longer latencies, in direct contrast to results in the cat (Pearson and Collins 1993; Gossard et al. 1994; Guertin et al. 1995). One possible explanation for this small effect is that we were using an artificial, electrical stimulus to one muscle nerve. Johansson and Westling (1987) have shown that reflex response to artificial stimuli in the intact human can be reduced if the subject is aware of its presence and benign nature. Moreover, afferent input from some muscles may be weaker than others (Whelan et al. 1995; Fouad and Pearson 1997). Perhaps the afferents from the medial gastrocnemius muscle do not have a strong influence on the soleus motoneurons.

The amplitude and duration of the extensor EMG burst varies with load during walking in the adult human, for loads less than body weight (Finch et al. 1991; Harkema et al. 1997). Unloading in these studies was achieved by raising the subject with a harness (Finch et al. 1991). This form of unloading decreases the maximum distance over which the foot can make contact with the treadmill. Thus, the changes in timing may have resulted largely from this mechanical effect. Others have added loads to the body. These loads were added to the hands, front or back of the trunk (Eke-Okoro and Larsen 1984; Ghorri and Luckwill 1985; Simonsen et al. 1995). The muscle responses to such loads are confounded by postural adjustments that are necessary to stay balanced.

In our recent study of supported walking in the human infant, we added load directly by changing the amount of weight supported by the infant (Yang et al. 1998). Adding a load of approximately 22% of the infant's body weight increased both the duration of the stance phase (30%) and step cycle (28%). The amplitude of the EMG from extensor muscles (quadriceps and gastrocnemius) did not change. These results confirmed the importance of load in controlling the stepping rhythm, at least for the immature human.

The current study was designed to avoid problems of artificial stimuli and differential potency of afferents from different muscles. We added or removed loads directly to the walking subjects, similar to the study on infants. Load was applied near the centre of mass to avoid the problem of postural adjustments. We tested whether loading during the stance phase prolongs the stance phase and delays the onset of swing. We used both sudden, unexpected changes in load, and sustained changes in load over the entire trial. Adding loads in this way, of course, activates many types of afferents originating from muscle, skin, joint and bone. We do not attempt to separate the

contribution of these different afferent types in this report. These results have been presented in preliminary form (Stephens and Yang 1996b).

## Methods

Twenty subjects (23–41 years of age) were studied under different conditions of loading and unloading. Approval was obtained from the human ethics committee at the University of Alberta. Informed written consent was obtained from all subjects. Thirteen subjects were studied with either a transient addition or removal of load (equivalent to 30% of body weight), or with a sustained addition of the same weight. Eleven subjects were studied with a sustained removal of 30% body weight using a body harness. Four subjects were studied under both conditions.

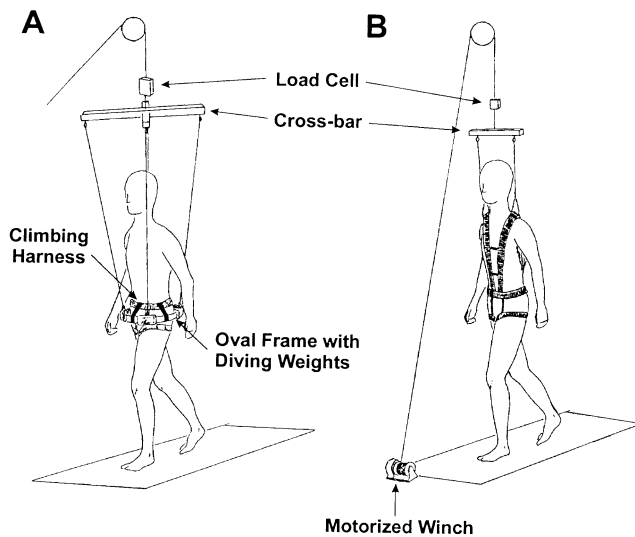
### Recording procedures

Electromyographic data were collected either bilaterally from the soleus (SOL) and tibialis anterior (TA) muscles or unilaterally from the SOL, TA, vastus lateralis (VL) and biceps femoris (BF). Beckman Ag/AgCl surface electrodes, 1 cm in diameter, were placed 1 cm apart rim-to-rim over the muscles. The signals were amplified and band-pass filtered (10–30 kHz). Footswitches were mounted under the ball and heel of both feet to monitor foot contact. In two subjects, force sensitive resistors (FSRs) (Interlink Electronics, Camarillo, CA), 2.5 cm in diameter, were placed under the heel, and under the heads of the first and fifth metatarsals of the left foot, while footswitches were placed beneath the right foot. The FSRs were sandwiched between two metal plates, to improve their accuracy (Zehr et al. 1995). Electrogoniometers (Penny and Giles Inc., Santa Monica, CA) were placed at the ankle and knee joints. Electrogoniometer signals were amplified and band-pass filtered (0–300 Hz). Data were recorded on magnetic tape (VHS) using the Vetter Digital PCM Recording Adaptor (Model 4000 A).

### Experimental procedures

Loads were applied through a belt (used for mountain climbing, commonly referred to as a climbing harness) worn on the pelvis, with leg straps (Fig. 1A). An oval metal frame that encircled the subject was attached to the belt with straps. Diving weights were secured to this frame. The combined weight of frame and weights was 30% of the subject's body weight. Thirty percent is a substantial but safe load. The frame was suspended from a cross-bar connected to a pulley system, above the subject's head. The frame could be raised or lowered manually, allowing the subject to support either no extra weight or the full weight of the frame. A load cell, in series with the pulley system, monitored the load. The subject walked on a treadmill at a comfortable walking speed (0.9–1.0 m/s), with: (1) no added weight, (2) added weight for 70 strides, and (3) added weight applied suddenly during the stance phase. In the third condition, the weight remained on the subject for three to ten steps. The load was applied and removed repeatedly at random times throughout a trial. To reduce potential auditory cues associated with loading or unloading, the subjects listened to music through a set of headphones.

To remove 30% body weight, subjects wore a body harness (Production en readaptation et activite physique, Montreal, Quebec) that was suspended on a tripod (Fig. 1B). A motorized winch controlled the amount of weight supported by the harness. The amount of weight supported by the system was recorded by a load cell. Subjects walked with: (1) harness on but no body weight removed, and (2) 30% body weight removed through the harness/winich system. In the trial with unweighting, the winch was adjusted so that the force equalled 30% of the subject's body weight in standing. The changes in height of the hip were estimated from video in three subjects, using a marker on the greater trochanter.



**Fig. 1A, B** Schematic diagram of how load was added and removed during walking. **A** Illustration of how loads were added. The subject wore a climbing harness, which was attached to the oval frame containing the weights. The oval frame could be raised (supported by the cross-bar) to give no additional load, or lowered (supported by the subject through the climbing belt) to give loading. **B** Illustration of subject in a body harness for experiments in which 30% of body weight was removed. The motorized winch was used to control the amount of unloading. In both **A** and **B**, a load cell monitored the loading condition

In addition, the maximum reach of the lower limbs under the two conditions was estimated. Subjects stood with weight on one foot, and reached maximally forward and backward in turn. To standardize the measurement, both feet were required to make full contact with the ground.

#### Data analysis

The EMG was full-wave rectified and low-pass filtered at 30 Hz, then A/D converted with the footswitch/FSR, force transducer and electrogoniometer data at 350 Hz (Axotape, Axon Instr. Inc., Foster City, CA).

#### Sustained loading or unloading

The walking pattern (i.e., EMG, footswitch or FSR) for sustained loading was obtained by averaging across all the steps ( $n > 70$  for each condition). This average was compared with the average of trials in which no extra load was carried. Foot contact provided the trigger for averaging, and averages were obtained for the full step cycle. The magnitude of extensor EMGs during the stance phase was quantified by the average amplitude of the signal during the stance phase (i.e., area under the rectified EMG profile divided by the duration of the stance phase). The muscle was defined as being active when the EMG magnitude exceeded two standard deviations of the noise level (this noise level was calculated from periods of inactivity). The burst duration of the SOL during the stance phase was estimated based on the definition of activity above. The SOL was active at the beginning of the stance phase in all subjects, so the duration represented the time from heel-contact to the time the SOL EMG burst terminated.

#### Transient loading or unloading

The response to transient loading was averaged based on the time at which the load was applied. Each trial was assigned to one of

three groups, depending on whether it occurred in the first, second or last third of the stance phase. Each group was averaged separately. A minimum of 20 trials were averaged for each group. The amplitude and the duration of the burst were calculated separately. For the calculation of the burst amplitude, the disturbed steps were aligned using the onset of the disturbance. This guarded against the inclusion of responses with different latencies. The trigger for averaging was obtained from the force transducer. The trigger level was set arbitrarily to half the total load (see arrow in bottom trace of Fig. 3). The average EMG of normal walking was subtracted from the average EMG during loading (or unloading), to obtain the EMG response to sudden changes in load. The amplitude of the response was defined as the average EMG amplitude during the first 200 ms. The 200-ms time window was chosen because of the relatively slow time course of such disturbances and the additional time needed for the load to be experienced by the muscles of the lower limb.

The duration of the extensor EMG burst was estimated by aligning the disturbed steps using the time of heel-contact. This preserved the timing of the signal. If the disturbances were aligned to the time of onset of the disturbance (as in the calculation of the burst amplitude), there would be a distortion of the timing, because the disturbances could occur at any time within the 1/3 duration of the stance phase (typically over 200 ms in duration).

#### Calibration of FSRs

The FSRs were calibrated with weights up to 1334 N in increments of 108 N. The calibration values were best fit with a hyperbolic function, reflecting the highly non-linear characteristics of the transducer. The signals from walking were scaled accordingly (see Zehr et al. 1995).

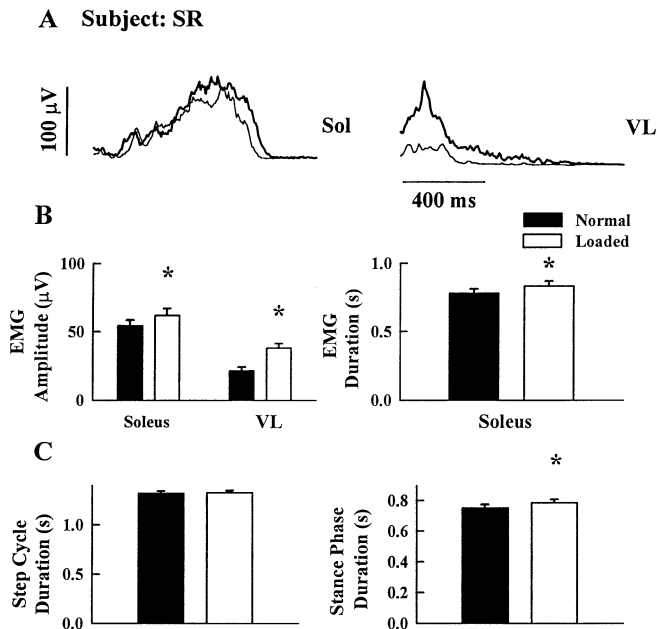
#### Statistical analysis

Data for normal walking and data for sustained changes in load were compared using paired Student's *t*-tests. Data for transiently applied disturbances during the early, middle or late part of the stance phase were compared using a repeated-measures ANOVA. The variables considered included the duration of the stance phase and step cycle, the duration and the amplitude of the extensor EMG burst during the stance phase. Bonferroni *t*-tests were used for post hoc analysis. The significance level was set at 0.05 for all tests.

## Results

### Increase in load

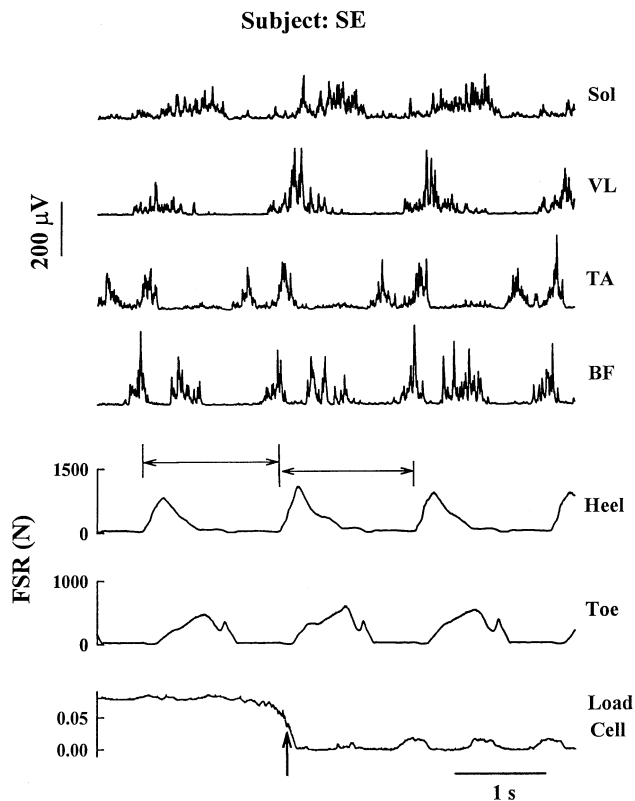
Walking with sustained increases in load produced significant increases in the magnitude of the extensor EMG during the stance phase. Figure 2A shows the extensor EMG from one subject during walking, averaged over many steps. The pooled data from 13 subjects (Fig. 2B) show a significant change in the average amplitude of the extensor EMG (14% and 78% for the SOL and VL, respectively). There was also a significant but smaller change in the EMG duration (7% for the SOL). The burst duration of VL was not compared, because some subjects showed no VL activity during normal walking. The stance phase duration was significantly prolonged, but only by a small amount (5%) (Fig. 2C). The step cycle duration was unchanged (Fig. 2C), however, since the swing phase duration was significantly shortened. There



**Fig. 2A–C** Response to loading sustained over the whole trial. **A** Average extensor EMG ( $n > 70$  steps) from one subject walking with no extra load (*thin lines*) and with additional load equivalent to 30% of body weight (*thick lines*). **B** Pooled across 13 subjects, the EMG amplitude is significantly increased in both extensors. The duration of the SOL burst is also increased, but less so. **C** The stance phase duration is significantly increased, whereas the step cycle duration is unchanged

were no consistent changes in EMG amplitude of the flexors (not shown).

Similar changes were seen with transient loading. Results from a single subject are shown in Fig. 3, where load was applied transiently during early stance (see decrease in force in bottom trace). The amplitude of both the heel and toe FSRs increased when the load was applied. The extensor EMGs (SOL and VL) increased substantially in amplitude, whereas the burst durations hardly changed (see also Fig. 4A). The duration of the step cycle was largely unchanged. Pooled across subjects, the amplitude of the extensor EMGs increased when load was applied (Fig. 4B). Significant increases in amplitude were seen in the SOL EMG, whenever load was applied during the stance phase (40%, 21%, and 59% for early, middle and late, respectively). Amplitude increases were only seen in the quadriceps muscle if loads were applied early in the stance phase (average increase was 134%) (Fig. 4B). Thus, in general, the amplitude of the EMG from extensor muscles increased substantially with load. This effect was strongest when the muscle was most active (i.e. VL in early stance only, while SOL throughout the stance phase). Some differences were found between individuals, however. Four showed little response ( $< 5 \mu\text{V}$ ) in the SOL muscle, while two showed little response in the quadriceps. Most subjects responded with both muscles. The burst duration of the SOL muscle increased slightly (5%, 3% and 3% for early, middle and late, respectively). The stance phase was slightly lengthened

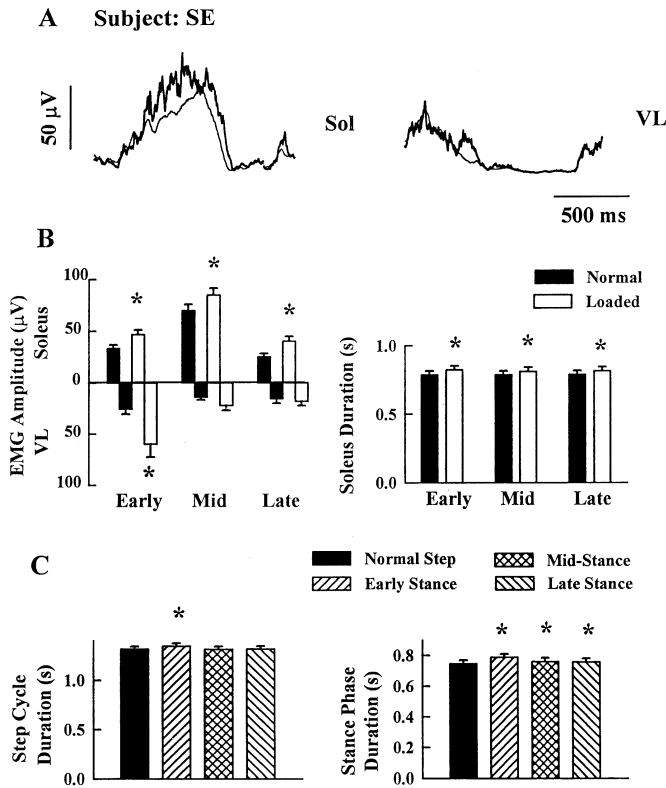


**Fig. 3** Example of EMG and FSR recordings from a single subject during steps preceding, during and following the sudden application of load. The load cell indicates the onset of load application, which was arbitrarily defined as when 50% of the load was applied (*arrow*). In this case, the load was applied early in the stance phase. The addition of load resulted in an increase in the extensor EMG amplitudes (SOL and VL), with little change in the duration of the step cycle (*horizontal bars above the heel FSR signal*). There was also no change in the time of onset of TA activity after the disturbance

(6%, 2% and 2% for early, middle and late, respectively). Cycle duration only changed if the load was applied early in the stance phase (2%,  $-0.5\%$ , 0% for early, middle and late, respectively).

The response to the first occurrence of the load was compared with the average response to transient loads. No differences were observed in the average amplitude of the extensor EMGs between the first and subsequent applications of load. The stance phase duration was significantly longer for the first loaded step ( $769 \pm 45$  ms) compared to the others ( $746 \pm 43$  ms), but the difference was small (23 ms). There were no significant differences in the duration of the step cycle.

Onset of the EMG response in the SOL and VL was compared with the onset of changes in ankle and knee angle, respectively. In the majority of cases, the EMG changes preceded changes in joint angle. Thus, it is unlikely that the responses were stretch induced.



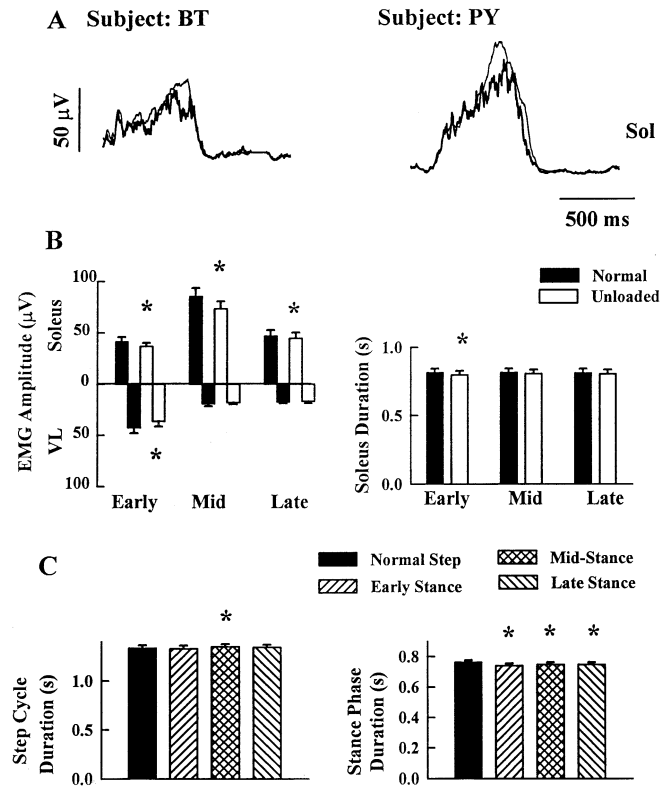
**Fig. 4A–C** Response to a sudden increase in load during the stance phase. **A** The average EMG pattern is shown from two extensor muscles during normal walking (*thin lines*,  $n=523$ ) and when loads were added suddenly during the middle of the stance phase (*thick lines*,  $n=22$ ), in one subject. **B** Pooled across 13 subjects, the SOL EMG amplitude (*upward bars on the left*) increased significantly (\*) with loading, regardless of when the load was applied during stance. The VL EMG (*downward bars on the left*) increased significantly only when loads were applied early in stance. The duration of the SOL EMG burst (*bar graph on the right*) increased slightly, but significantly. **C** The stance phase duration was similarly prolonged, but the changes were small. The duration of the step cycle was significantly prolonged only when disturbances were applied early in the stance phase. \* in **C** indicates a significant difference from the normal step

#### Removal of load

When the added load was transiently removed, opposite effects were seen (Fig. 5). The SOL EMG amplitudes decreased (14%, 6% and 5% for early, middle and late disturbances, respectively). Vastus lateralis EMG amplitudes decreased during early stance only (14%). The soleus burst duration changed significantly only when the load was removed early in the stance phase. The stance phase duration shortened slightly (3%, 2% and 2% for early, middle and late, respectively) (Fig. 5C). Again, the duration of the step cycle was hardly affected (1% or less) (Fig. 4C).

#### Sustained unloading

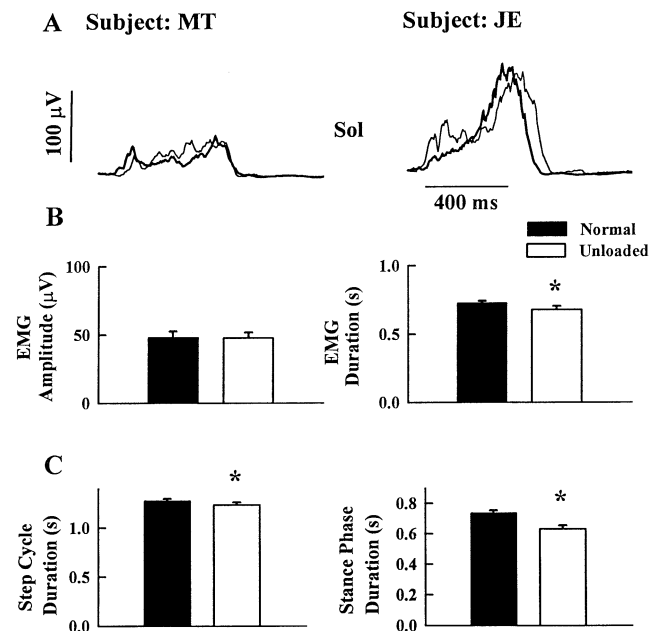
Sustained removal of 30% body weight by supporting part of the body weight with a body harness caused



**Fig. 5A–C** Response to the removal of the added weight. **A** Average SOL EMG during steps with the added weight (*thin lines*,  $n>300$ ) and the step when the added weight was removed (*thick lines*,  $n=10$ ). **B** Pooled across subjects, the magnitude of the SOL EMG decreased whenever the load was removed, whereas the VL EMG decreased significantly only when the load was removed early in the stance phase. The burst duration of the SOL was significantly decreased only when loads were removed early in the stance phase. **C** The duration of the stance phase was significantly decreased. The step cycle duration was relatively unchanged except when the load was removed in the middle of the stance phase

greater changes in step cycle duration. The stance phase shortened by 14%, and the swing phase lengthened, so the total cycle duration was only shortened by 3% (Fig. 6C). Interestingly, the SOL EMG amplitudes did not change significantly, while the burst duration decreased. Quadriceps EMG was not collected in these subjects.

Supporting body weight with a harness, however, requires lifting the individual. Lifting decreases the distance over which the foot can make contact with the ground (i.e., in the extreme case, no contact can be made). Thus, we estimated the change in vertical position of the hip with 30% body-weight support during walking in three subjects. The measures were taken at the highest position achieved by the hip joint during walking (i.e., the mid-stance phase). The average change in the vertical position of the hip was 2 cm. The maximum reach, defined as the distance between the farthest forward and backward position a foot could be placed, decreased by 38% on average.



**Fig. 6A–C** Unloading with a body harness. **A** With 30% of the body weight supported by a harness, the SOL EMG changes were inconsistent between subjects. *Thin lines* show the average EMG while walking with normal load, and *thick lines* show it for unloaded walking ( $n > 70$ ). Subject MT showed a decrease in the EMG amplitude with no change in duration, while subject JE showed a small change in magnitude and a decrease in the burst duration. **B** Pooled across 11 subjects, there was no significant change in the SOL EMG amplitude, but a significant decrease in its burst duration. **C** The stance phase and step cycle durations were significantly shortened

## Discussion

This study shows that adding or removing weight from a walking subject during the stance phase changes the amplitude of the EMG from the extensor muscles (especially the quadriceps muscle). The duration of the extensor EMG burst, the stance phase and the step cycle were only slightly changed if at all. The independence of the duration and amplitude of extensor EMG activity in response to load suggests that the subject can control the two independently.

### Technical considerations

Walking on a treadmill forces the subject to keep a constant walking velocity. Were the reciprocal changes in the stance and swing phase durations a result of treadmill walking? This is unlikely, since subjects can step at different cadences at the same treadmill speed. At the speeds used here, a sixfold range is possible in both the stance phase and the cycle duration (Nilsson and Thorstensson 1987). Thus, subjects could have modified the duration of the step cycle, but chose not to do so. Furthermore, in separate experiments, load was added in two ways, one that produced a postural disturbance, and one that did not.

Under these conditions, cycle duration was prolonged only when posture was disturbed (Misiaszek et al., submitted). Thus, when necessary, subjects can change both the timing of the stance phase and step cycle. Load changes without a postural disturbance does not require a change in the stance phase or cycle duration. Whether overground walking would produce the same results remains unknown.

Removing body weight had the greatest effect on the duration of the stance phase and step cycle (Fig. 6). Unloading using a body harness requires raising the body. Our estimate of a 2-cm rise in the position of the hip is similar to that reported by others (1.5 cm in Finch et al. 1991). This rise decreased the maximum reach of the lower leg by an average of 38%. This effect presumably caused the shortening of the step length reported by Finch et al. (1991). This effect may also explain the greater change in stance phase and step cycle duration. Thus, the change in stance phase and step cycle duration with unloading is not a purely neural phenomenon.

Does the predictability of changes in load make a difference?

We studied both sustained and sudden changes in load, because the response to a known and continuous load might be different from the response to an unpredictable one. Moreover, the very first trial in which load was applied should constitute a truly novel task, and might be expected to elicit a different response from subsequent trials. The differences, however, were very small. There were no significant differences between the first and subsequent trials in the magnitude of the EMG response. Subjects modified the amplitude of the EMG burst with both continuous and sudden applications of load. The duration of the stance phase was significantly longer in the first trial than in subsequent trials, but the difference was very small (23 ms).

### Changes in amplitude and timing

Changes in load produced larger changes in the amplitude of the VL EMG than the SOL. This was true for both sustained and sudden changes in load. This difference between the muscles may be related to the role of these muscles in walking. The SOL in cats and humans is very active in standing and slow walking whereas the VL is not (Smith et al. 1977; Walmsley et al. 1978; Yang and Winter 1985; Duysens et al. 1991). This activity pattern matches the fibre type composition, as SOL is composed largely of slow twitch fibres whereas the VL is composed largely of fast twitch fibres (Johnson et al. 1973; Edgerton et al. 1975). With increasing task demand, such as with increasing walking speeds, walking on inclines, and running, the VL increases proportionately far more than the SOL in humans (Brandell 1977; Yang and Winter 1985; Duysens et al. 1991) and cats (Smith et al.

1977; Walmsley et al. 1978). Thus, the results may simply reflect the greater capacity of the VL to respond to changes in load. Our results agree with Harkema et al. (1997), who reported a curvilinear relationship between load and SOL EMG during walking. They reported that SOL EMG amplitudes changed little for loads of 50–100% body weight. This may also explain the lack of change in SOL EMG amplitude with sustained unloading in this study.

Adults and infants responded differently to load. In the adult, adding load caused an increase in the EMG amplitude of at least one extensor muscle of the lower limb, while unloading usually caused a decrease. Thus, the activation of extensor muscles covaried with the amount of load in the adult. The changes in EMG amplitude were not accompanied by large changes in the timing of either the EMG bursts or the step cycle. Thus, changes in load are accommodated by changes in EMG amplitudes rather than duration. This is in contrast to studies of similar disturbances in human infants, where a change in timing is seen. The addition of 22% of body weight in infants causes the step cycle to lengthen by 28% (Yang et al. 1998), thereby resetting the stepping rhythm. Surprisingly, in these same infants, there were no changes in EMG amplitude. The number of infants included in the calculation of the extensor EMG amplitude was small, however (four for Quad and six for SOL). Thus, the lack of change in EMG amplitude in infants can only be considered preliminary at this time. The method of force application was also necessarily different between infants and adults. The infants were supported by an experimenter to walk on the treadmill. Loads were added by pushing down on the pelvis manually. Thus, while the magnitude of load change, expressed as a percentage of body weight, was similar between the adults and infants, the duration of the load application was more variable with the infants. Future work will need to clarify whether these differences affected the response.

The studies on adults and infants provide evidence that the timing and amplitude of the extensor EMG burst in response to load are controlled independently. Moreover, the time course of maturation of the two responses to load is different. The control of sensory input shows rapid and dramatic changes within the first few days of life in the rat (Iizuka et al. 1997). Perhaps the response to load also changes with age in the human infant, but with a slower time course.

#### Differences between preparations

Different preparations of the cat respond differently to load. Activation of afferents from extensor muscles causes strong effects in the immobilized decerebrate cat (Gossard et al. 1994), weaker effects in the walking decerebrate cat (Whelan et al. 1995), and much weaker and more variable effects in the intact cat (Whelan and Pearson 1997). A similar reduction in the response to stimuli

delivered to cutaneous or mixed nerves of the foot is seen in premammillary compared with intact cats (cf. Duysens and Pearson 1976 with Duysens and Stein 1978). In the present experiment, intact, adult subjects knew the experimental protocol, and knew that the loads were not threatening to their walking. Under these conditions, it is possible that input from higher centres modifies the strength of appropriate reflexes, producing just enough response to compensate for the load. In contrast, infants may be unable to influence the response of lower centres to the disturbance, because of the immaturity of descending input from the brain.

The ability of any single sensory signal to affect the walking rhythm may depend on the presence and strength of other rhythmic input. Most of the studies on load-sensitive afferents in cats used a train of electrical pulses to a muscle or cutaneous nerve, a very synchronous input. Moreover, the nerve was cut before applying the stimulation, to avoid confounding problems with eliciting a direct motor response (Conway et al. 1987; Pearson and Collins 1993). In the extreme case, the animals were paralysed, totally removing rhythmic sensory input (Conway et al. 1987; Gossard et al. 1994; Guertin et al. 1995). Under these conditions, activation of any afferent is likely to produce a large effect, since it is acting against a background of relative sensory silence. With increasing presence of other rhythmic input, such as in the walking decerebrate cat with minimal denervation (Whelan and Pearson 1997), the effects are reduced. The study with decerebrate cats which most closely mimics the mechanical loading used here with humans is one in which the walking decerebrate cat was suddenly either lifted or lowered (Hiebert and Pearsory, in press), resulting in a doubling or halving of the patellar force. These results were similar to ours: changes in the EMG amplitude of the quadriceps muscle, but rather little change in the SOL and little change in the duration of the stance phase and step cycle. Orlovsky (1972) increased load on the limbs by raising the whole treadmill that decerebrate cats were walking on, while the cats were fixed to a frame. This increased the magnitude of the extensor EMGs, but did not change the burst duration. Load on the extensor muscles is also increased when walking up an incline. Intact cats walking up an incline did not modify the stance phase and cycle durations, but did increase the amplitude of the extensor EMGs (Carlson-Kuhta et al. 1998). Together, these data indicate that the more intact the cat, the smaller the changes in stance phase and cycle duration. Extensor EMG amplitudes, however, always seemed to change with load. Perhaps when competing rhythmic input from other afferents and descending pathways are present, the ability of any single input to entrain the rhythm is much reduced.

#### Conclusions

Transitions between stance and swing phases of walking are critical to the maintenance of balance in a biped. Per-

haps for this reason, the control of transitions between phases relies more heavily on supraspinal structures in the human. The responses seen in the infant might reflect how the brain stem/spinal cord responds to loading, whereas the response in adults might reflect higher levels of control. Whatever the mechanism, the control of the amplitude and duration of the response can be independently varied in the adult. Presumably, this provides greater flexibility for responding to changes in load under different conditions.

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