

Human H-reflexes are smaller in difficult beam walking than in normal treadmill walking

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Summary. Hoffmann (H) reflexes were elicited from the soleus (SOL) muscle while subjects walked on a treadmill and on a narrow beam (3.5 cm wide, raised 34 cm from the floor). The speed of walking on the treadmill was selected for each subject to match the background activation level of their SOL muscle during beam walking. The normal reciprocal activation pattern of the tibialis anterior and SOL muscles in treadmill walking was replaced by a pattern dominated by co-contraction on the beam. In addition, the step cycle duration was more variable and the time spent in the swing phase was reduced on the beam. The H-reflexes were highly modulated in both tasks, the amplitude being high in the stance phase and low in the swing phase. The H-reflex amplitude was on average 40% lower during beam walking than treadmill walking. The relationship between the H-reflex amplitude and the SOL EMG level was quantified by a regression line relating the two variables. The slope of this line was on average 41% lower in beam walking than treadmill walking. The lower H-reflex gain observed in this study and the high level of fusimotor drive observed in cats performing similar tasks suggest that the two mechanisms which control the excitability of this reflex pathway (i.e. fusimotor action and control of transmission at the muscle spindle to motoneuron synapse) may be controlled independently.

Key words: H-reflex – Muscle spindle – Locomotion – Human

Introduction

Strong evidence supports the notion that segmental reflexes are not fixed motor patterns, but rather are highly modifiable and can be made to suit the needs of the situation (e.g., reviewed in Stein and Capaday 1987; Prochazka 1989). The monosynaptic reflex arc involving

muscle spindle and motoneurons is somewhat unique in this regard because its gain can be controlled in two ways: by pre- and postsynaptic excitation and inhibition at the Ia to motoneuron synapse and by changes in the mechanical sensitivity of the muscle spindles via the fusimotor system. This dual control might allow special flexibility in how the muscle afferent information is controlled and channelled.

Three techniques have been used to study transmission in the reflex arc during natural movements, each addressing somewhat different aspects of the dual control mechanisms. 1) Direct recording from Ia afferents has been used to infer the degree of fusimotor drive (e.g., Prochazka et al. 1976). 2) Hoffmann (H) reflexes, which bypass the fusimotor system, reflect the state of the Ia to motoneuron pathway. 3) Tendon reflexes, which are evoked by a more physiological stimulus, provide a measure of the net effect of synaptic transmission and fusimotor drive (e.g., Hugon 1973; Llewellyn et al. 1987; Schieppati 1987).

Recordings from Ia afferents in cats suggested that fusimotor drive is low during routine tasks such as locomotion, but greatly enhanced during novel (e.g. exploratory) and difficult (e.g. beam walking) tasks (Prochazka et al. 1988). We posited that reflexes might also be larger during the performance of difficult or novel tasks. Accordingly, we examined transmission in the muscle spindle to motoneuron pathway during a difficult beam walking task in humans, by using the H-reflex technique. Surprisingly, the H-reflex gain during this difficult locomotor task was found to be lower than that during normal treadmill locomotion.

With hindsight, it is clear that our expectation was not well-founded. Enhanced fusimotor drive during the performance of a difficult task could lead to two control problems if synaptic transmission were also enhanced. First, the deeply modulated responses of the spindles could saturate the reflex pathway and this could disrupt the segmental control of movement on a moment-to-moment basis. Indeed, it has been suggested that the reflex gain is attenuated and modulated to prevent just this situation from occurring during normal stepping and running (Capaday and Stein 1987). Second, a large net

reflex gain could lead to instabilities in the reflex loop resulting, in the extreme case, in sustained tremor (Stein and Lee 1981). On the basis of our results, we suggest that in beam walking, the low reflex gain coupled with a high level of fusimotor drive may avoid motoneuron saturation and instability, while permitting greatly sensitized muscle afferent information to be used by higher centres. Preliminary results have been reported in abstract form (Llewellyn et al. 1989).

Methods

H-reflexes were elicited from the soleus (SOL) muscle of five healthy volunteers by stimulation of the tibial nerve. Ethical approval for these experiments was granted by the University of Alberta Hospitals ethics committee. The cathode, a Beckman type disk electrode (8 mm in diameter), was placed in the popliteal fossa over the tibial nerve, and the anode was placed on the anterior aspect of the thigh over the patella. Single monophasic pulses (1 ms in duration) were applied at an intensity which produced a small M-wave and a submaximal H-reflex. Recording electrodes (Beckman type similar to the stimulating cathode electrode) were placed over the SOL muscle just distal to the insertion of the gastrocnemius muscles into the Achilles tendon, in a bipolar configuration, 2 cm apart. The electromyogram (EMG) signal was band-pass filtered (10 Hz to 10 KHz).

The beam was 3.5 cm wide, 4 m long and raised 34 cm from the floor. The walking surface of the beam was covered with conductive material so that a circuit was completed when the subject's shoe (also covered with conductive material) made contact with the beam. The step cycle time could then be monitored and used to trigger averaging. Subjects were given some time to become familiarized with beam walking. The SOL and tibialis anterior (TA) EMG associated with beam walking was full-wave rectified, low-pass filtered (30 Hz) and averaged on-line using initial foot contact as the trigger event. Generally, five steps could be made on one traverse, during which measurements were taken from the middle two or three steps only. The undisturbed walking pattern was averaged at the beginning and the end of the beam walking trials to ensure that the EMG profile had not changed significantly with time. A total of 50 steps were included in each average.

Stimuli were applied during beam walking at random intervals from 0.5 to 2 s apart. The step cycle was divided into 16 equal segments and responses which arrived within any given segment were averaged together (approximately 10 responses per segment). The effective stimulus intensity, as reflected by the amplitude of the M-wave, varied through the step cycle because of large movements at the knee. At any one stimulus intensity, for example, the M-wave amplitude could vary from clearly visible in some segments of the walking cycle to completely invisible in others. Therefore, the experiment was repeated at a number of different stimulus intensities. The data were then examined post-hoc and different segments of the step cycle could be compared in which approximately the same number of efferents (as reflected by the M-wave amplitude) and presumably the same number of afferents were stimulated throughout the step cycle (Capaday and Stein 1986).

The same experimental paradigm was then repeated for treadmill walking. A walking speed was selected which required roughly the same range of SOL activity as that required for beam walking. Foot-contact patterns were monitored with footswitches attached to the shoe. In some experiments, a goniometer was used to record the ankle angle during both treadmill and beam walking.

These experiments generally required about six hours to complete, so control trials were interspersed to ensure that both the recording and stimulating conditions remained stable. The M and H waves were elicited under quiet standing conditions at various stimulus intensities to verify that the M versus H relationship remained constant.

Results

The beam walking task was different from treadmill walking in a number of ways. In general, the difficulty of beam walking led to more co-contraction at the ankle and greater step-to-step variability in both timing and EMG activation patterns.

Variability in the step cycle duration was reflected in the transitions in the foot contact signals in Fig. 1 (top traces). When the cycle duration is relatively constant from step to step (left top), the averaged foot contact signal shows a sharp fall at the end of the stance phase and a sharp rise at the beginning of the following step. In beam walking, on the other hand, the rise and fall was less abrupt, indicating that cycle duration was more variable. In addition, the swing phase was shorter on the beam, allowing a longer double support period.

The two tasks were quite well matched for ankle angle excursions (Fig. 2) during most of the stance phase when the reflexes were active. Differences observed in the H-reflex amplitude between the two tasks were therefore not attributable to differences in muscle length (Mark et al. 1968; Weiss et al. 1986). Two minor differences were noted. The normal plantigrade pattern of making ground contact with the heel first was absent on the beam. Most subjects preferred to make contact with their forefoot or the whole foot, probably because this is more stable. A diminished dorsiflexion excursion during the swing phase was also noted. Normally, dorsiflexion during swing prevents the toes from dragging on the ground. This was not necessary on the beam, since it was narrow and raised well above ground level, allowing lateral clearance.

Finally, the normal reciprocal pattern of the SOL and TA was considerably altered on the beam. While the SOL EMG pattern was very similar in the two tasks (Fig. 1), the TA pattern was quite different. The TA normally exhibits a two-burst pattern in treadmill walking, the first burst occurring at heel-contact to control the lowering of the foot to the ground, and the second burst during the swing phase clearing the toes of the ground. The first burst was missing in beam walking, because the forefoot makes contact first. The EMG burst during the swing phase was present, but somewhat reduced in amplitude because the ankle does not need to dorsiflex as much, since toe clearance is not a problem on the beam (as described above). The most notable difference was the strong TA activity during the stance phase on the beam, co-activated with the SOL muscle. The TA is normally inactive during the stance phase in treadmill walking. Co-activation of antagonist muscles probably increases the stiffness at the ankle and perhaps improves stability.

The H-reflex was modulated through the step cycle in the typical pattern previously reported for treadmill walking (Garrett et al. 1981; Capaday and Stein 1986; Crenna and Frigo 1987). The reflex amplitude is low at heel-contact, and rises either in parallel with or slightly in advance of the SOL EMG during the stance phase (Fig. 2). The reflex is deeply inhibited during the swing phase. This dramatic modulation of the reflex occurs in spite of a constant stimulus intensity over the step cycle, as reflected by the relatively constant M-wave amplitude. The reflex

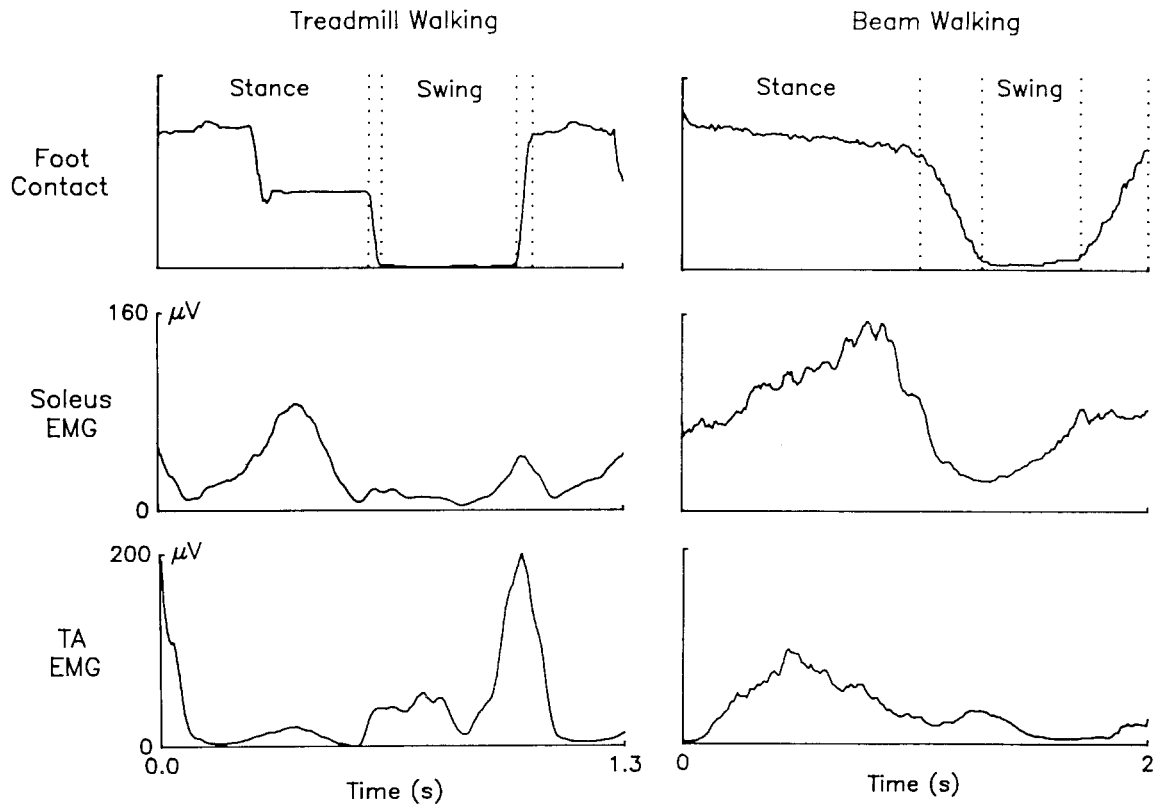


Fig. 1. The muscle activation and foot contact patterns for one subject during undisturbed treadmill (left) and beam walking (right). Each trace represents the average of 50 steps. The foot contact signal is high during the stance phase and low during the swing phase. The step duration is relatively regular on the treadmill, as indicated by the limited time range (dotted lines) over which the stance phase ends and the following step begins. The step cycle in beam walking was

considerably more variable in duration. The activation pattern of the SOL was similar for the two tasks, although the amplitudes differed in this case. Note that the amplitude scales (vertical axes) are the same for the two tasks. In contrast, the TA pattern was very different in the two tasks; the normal reciprocal pattern of the TA and SOL was replaced by more co-contraction on the beam

was similarly modulated during beam walking, although the peak amplitude achieved was lower (Fig. 2). Averaged across five subjects, the mean H-reflex amplitude during the stance phase was 40% lower during beam walking as compared to treadmill walking.

The relationship between the H-reflex amplitude and the excitability of the SOL motoneuron pool can be represented by plotting the reflex amplitude versus the average background EMG of the SOL muscle at the time the reflex was elicited (Fig. 3). The relationship between H-reflex and background EMG can be estimated only when the background EMG is non-zero. H-reflex values obtained during the swing phase were therefore not included in this figure because there is no appreciable EMG from the SOL during swing. It is clear from Fig. 3 that the H-reflex amplitude was lower during beam walking, at comparable activation levels of the SOL muscle. Moreover, the slope of the regression line (Fig. 3) was lower in all subjects. This slope was on average 41% lower on the beam than on the treadmill.

The data from all subjects are combined in Fig. 4. Since the surface EMG amplitude recorded from different subjects differ considerably, normalization was necessary before the data could be combined. Both the background level of SOL EMG and the SOL H-reflex amplitudes were

divided by the peak SOL EMG and the peak H-reflex, respectively. While the scatter in the data obtained from different subjects is considerably larger than the data from individual subjects, the H-reflexes were significantly lower during beam walking than treadmill walking at all levels of background EMG (t-test, $p < 0.05$).

Discussion

At comparable background EMG levels, the SOL H-reflex was lower in the difficult task of beam walking than in treadmill walking. This is in contrast to the enhanced firing rates of the Ia afferents during a similar beam walking task in cats (Prochazka et al. 1988). These results suggest that the two mechanisms that control the gain of the monosynaptic reflex mediated by primary muscle spindle afferents may be modulated independently.

Technical considerations

One factor that might artificially lower the H-reflex during certain phases of beam walking is the greater variability in cycle duration. Since the H-reflex amplitude rises in a

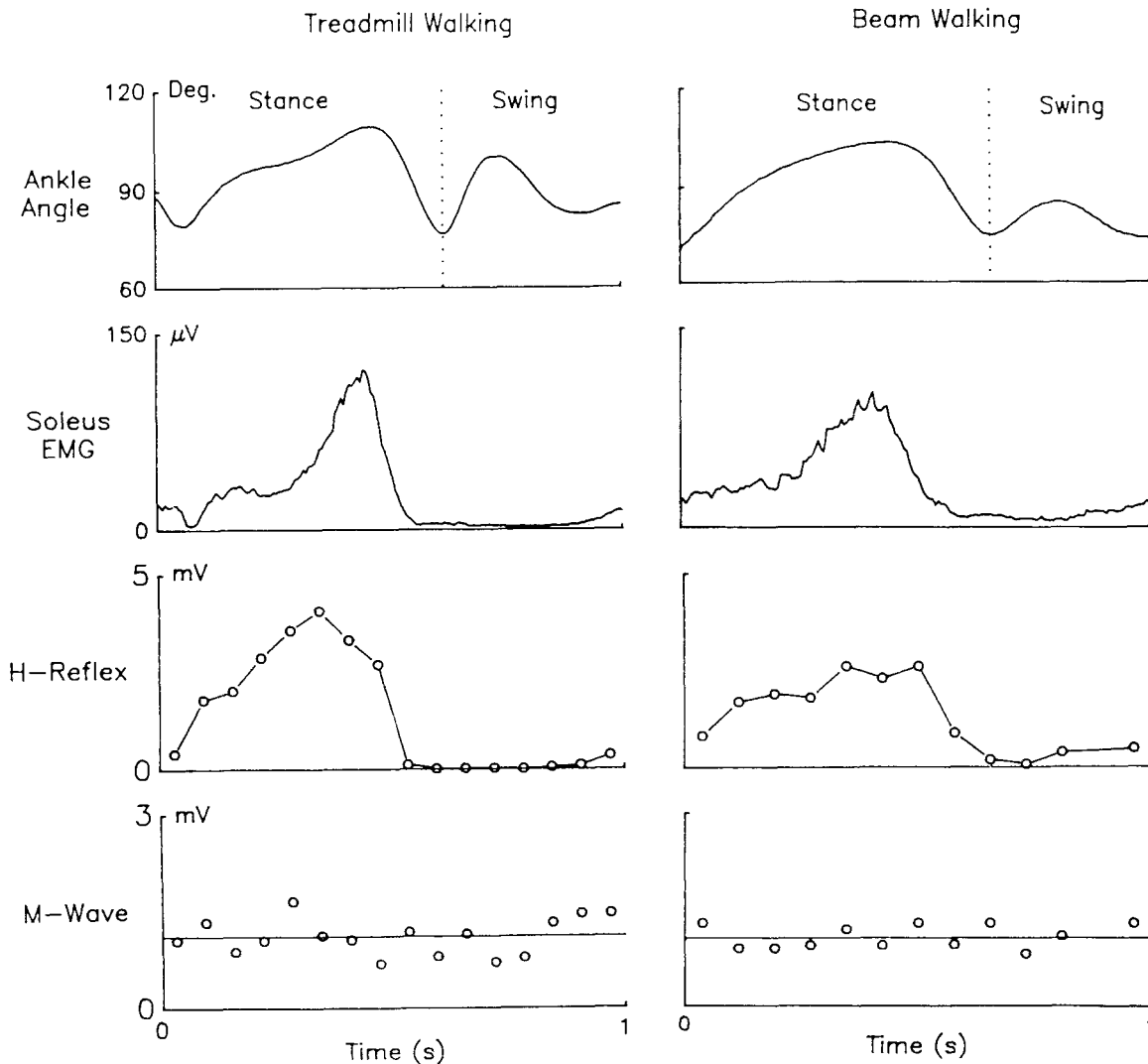


Fig. 2. The ankle angle and SOL EMG pattern associated with treadmill and beam walking represent the average of 100 and 85 steps, respectively, from one subject. The trajectory of the ankle angle was quite similar for the two tasks, particularly during the stance phase. All amplitude scales (vertical axes) are the same for the two tasks. The neutral position is 90 degrees, larger values represent dorsiflexion. The SOL activation pattern is also similar for the two tasks, with minor differences in the peak EMG at push-off. In contrast, the H-reflexes were considerably lower during beam walk-

ing, particularly during the push-off phase. The differences in the H-reflex could not be accounted for by differences in the effective stimulus strength, since the M-wave amplitudes were well matched for the duration of both tasks. It is not clear from this figure whether the differences in H-reflex amplitude between the two tasks can be explained by the small differences in the activation level of the SOL. The contribution of the SOL background activation level is more clearly shown in Fig. 3

ramp-like fashion through the stance phase to a peak at push-off, it is conceivable that variability in the duration of the stance phase could cause the reflex peak to be less pronounced (e.g., Fig. 2). However, this type of distortion should not affect the average reflex amplitude over the whole step cycle. The average reflex amplitude was lower in all subjects during beam walking, suggesting that variability in timing could not alone account for the difference in reflex amplitude. Moreover, this variability in cycle duration would affect the average SOL EMG amplitude in the same way, such that the relationship between the two variables should not be affected. The relationship between H-reflex amplitude and SOL EMG amplitude was clearly different in the two tasks (Fig. 3).

If the Ia afferents do indeed fire at a much higher rate during beam walking in humans as in cats, it is possible that a larger proportion of these fibres are refractory during beam walking and unable to respond to the electrical stimuli. The effect this refractoriness might have on the H-reflex is likely to be quite small, however. The firing rate of Ia afferents is generally much lower in humans than in cats (Vallbo 1974). Even if we assume that the SOL Ia afferents fired at 100 ips during beam walking, twice the highest rates recorded in humans, and are refractory for 1 ms, only 10% of them would be refractory to the H-reflex stimulus, compared with say 3% during treadmill locomotion. The 40% mean difference in H-reflex amplitude observed here between treadmill and

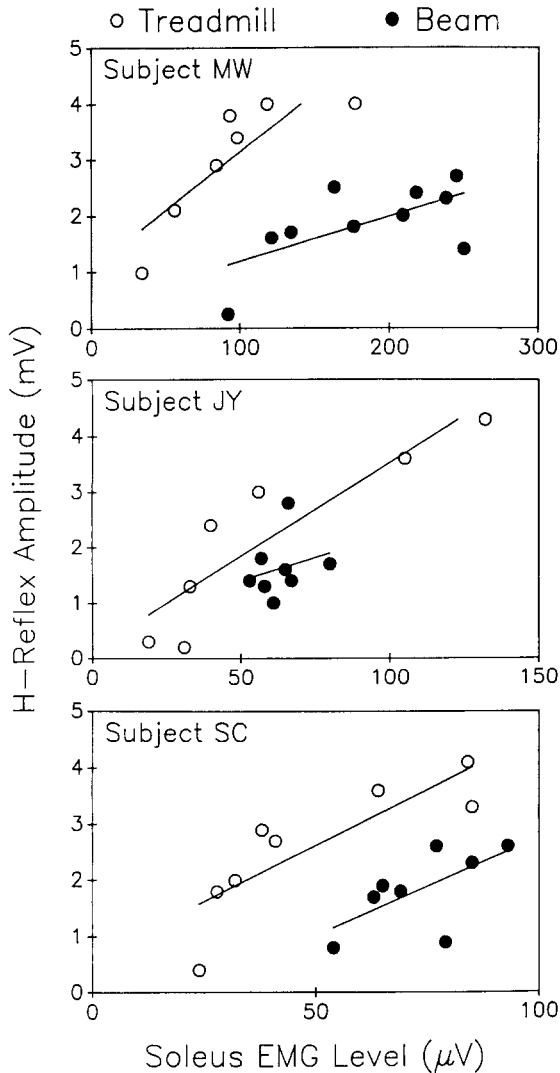


Fig. 3. The H-reflex amplitude during different parts of the stance phase are plotted against the background activation level of the SOL muscle at corresponding times in the step cycle. Examples from three subjects show the typical responses obtained. In all three cases, the H-reflex amplitude was lower during beam walking than treadmill walking at comparable levels of SOL background EMG

beam walking could not be explained by this 7% discrepancy alone.

The M and H waves are associated with muscle contractions that generate small mechanical perturbations. Does the presence of these small disturbances significantly alter the walking pattern on the beam? A comparison of ankle angle and EMG patterns during beam walking in sequences with and without electrical stimuli indicated that the walking patterns were extremely similar under the two conditions.

Possible neural mechanisms

The neural mechanisms involved in lowering the H-reflex gain during beam walking cannot be tested easily in humans. A number of possibilities might be suggested, which will require verification with animal experiments.

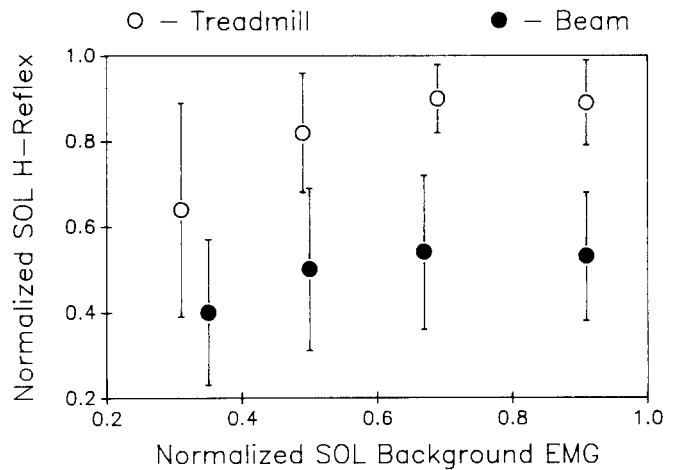


Fig. 4. The H-reflex amplitude, averaged across 5 subjects, is plotted against the background activation level of the SOL muscle at the corresponding times in the step cycle. The vertical bars about the mean represent \pm one standard deviation. Both the H-reflex amplitude and the SOL EMG levels were normalized to the maximum amplitudes observed for each subject prior to averaging. The H-reflexes were significantly lower during beam walking than during treadmill walking for all levels of background EMG (t-test, $p < 0.05$)

It is possible that cats and humans do not perform beam walking in the same way. Intuitively, one would expect beam walking to be far more difficult for the biped human than for the quadruped cat. Indeed, most subjects found beam walking challenging, whereas generally, cats are extremely agile at walking on narrow surfaces. The comparison made here, however, is between humans and cats when both found the beam walking task difficult. Enhanced Ia afferent firing is observed in cats only during periods of instability on the beam (Prochazka et al. 1988). Under comparable movement conditions, there are striking similarities in postural and locomotor control between the two species. The modulation pattern of H-reflexes in the lower extremity during locomotion in the cat (Akazawa et al. 1982) is very similar to that in humans (Capaday and Stein 1986). Even the method by which the quadruped cat responds to postural disturbances is similar to the methods used by the biped human under comparable mechanical conditions (Dunbar et al. 1986). The strategies used to cope with beam walking when both species found the task difficult are therefore likely to be similar.

Unlike the typical reciprocal activation of antagonists during treadmill walking, beam walking was characterized by much greater co-contraction of the SOL and TA muscles. Co-activation of an antagonist could generate reciprocal effects on the agonist. Activation of the TA during the stance phase (Fig. 1) could result in reciprocal inhibition of the SOL motoneuron pool via the Ia inhibitory interneuron (Eccles et al. 1956). If this were the mechanism for the reduced SOL H-reflex during beam walking, the SOL EMG should be equally reduced, since this pathway acts postsynaptically on the motoneuron pool. This was clearly not the case, since the reflex depression occurred in beam walking at levels of SOL EMG comparable to treadmill walking (Fig. 3).

Alternatively, it has been suggested that reciprocal inhibition may act presynaptically on the Ia terminals of antagonist motoneurons (Mizuno et al. 1971). Direct evidence for such a pathway remains unavailable, although recent experiments on humans using indirect methods suggest that reciprocal inhibition from the TA can act presynaptically on Ia fibres that synapse on SOL motoneurons (Crone and Nielsen 1989). Such a mechanism would be consistent with the present results, since the reflex depression appears to be independent of the SOL motoneuron excitability.

The amplitudes of excitatory post-synaptic potentials (EPSP's) generated by Ia afferents in motoneurons are rate dependent (Honig et al. 1983). An increase in the rate of Ia firing can be associated with a decrease in the EPSP amplitude, particularly in small motoneurons with large EPSP's (Collins et al. 1984). If the Ia afferents do indeed fire at higher rates during beam walking in humans as they do in cats, then this higher rate of firing may also lead to changes in the Ia EPSP amplitude. The H-reflex primarily reflects the response of small motor units to Ia activation (Buchthal and Schmalbruch 1970), motor units which are typically associated with large Ia EPSP's (Burke 1968). At high firing rates, these EPSP's tend to be attenuated, and this could lead to a reduction in the H-reflex amplitude (Collins et al. 1984). However, the attenuation reported was quite modest (generally less than 10%) at the Ia firing rate tested (167/s). Ia firing rates observed by neurography in humans have generally been lower than those in cats, though dynamic tasks such as beam walking are out of the range of current neurography techniques. Thus there is insufficient information to assess accurately the degree of rate-dependent EPSP attenuation during beam walking in humans. Both the reciprocal effects from the TA and the firing rate dependent behavior of Ia EPSP's could contribute to the H-reflex depression in this situation. In addition, task-related input from descending fibers may inhibit Ia fibers at a presynaptic level. Although primary afferent depolarization evoked from the cortex or red nucleus has not been found in Ia fibers, it is not clear whether competing inhibitory influences are masking its effect (reviewed in Baldissera et al. 1981).

Functional significance

On the basis of simulation experiments (Hulliger et al. 1987), the most likely mechanism for the higher firing rate of Ia afferents during beam walking in cats is stronger dynamic fusimotor drive (Prochazka et al. 1988). The increased stretch sensitivity of the spindles would result in a larger net input and a better signal-to-noise ratio for the information being conveyed to the central nervous system.

If the fusimotor drive is indeed enhanced while the H-reflex gain is lowered, this suggests that the two mechanisms controlling gain of the segmental reflex are operating in opposite directions. We propose the following hypothesis to explain this paradox: in difficult motor tasks, proprioceptive sensitivity is elevated, providing supraspinal areas with increased feedback gain and resolution, but in the segmental stretch reflex arc this increased gain could

cause instability and so is compensated for by attenuation of Ia-motoneuronal transmission. There are numerous documented examples of task-dependent modulation of somatosensory proprioceptive transmission to supraspinal areas (reviewed by Prochazka 1989). Generally speaking, transmission to higher centers is facilitated when the motor task involves elements of novelty, vigilance or exploration. In contrast, most evidence so far points to a reduction in transmission from Ia afferents to motoneurons as tasks become more vigorous and demanding (e.g. Capaday and Stein 1987).

Beam walking is more difficult than treadmill walking because the control of equilibrium is much more constrained. The foot placement is constrained by the beam and the base of support is reduced particularly in the medio-lateral direction. The projection of the total body centre of mass must remain close to the small base of support if the subject is to remain on the beam. The destabilizing potential of a high stretch reflex gain has been recognized for many years (Lippold et al. 1957; Cussons et al. 1980; Rack et al. 1984). Indeed the "safety margin" in reflexly-active individuals may be quite low, particularly under conditions of stress (Jacks et al. 1988). The resulting tremor and underdamped responsiveness to descending commands would obviously interfere with the performance of a task such as beam walking, and in critical situations this could be quite disadvantageous. Moreover, simple homonymous stretch reflexes may be out of place in complex tasks which require the adaptive and organized activation of a number of muscles orchestrated by the higher centers.

In conclusion, the current results showing task-related attenuation of H-reflexes in man, together with the evidence for augmentation of spindle sensitivity in cats, suggest that proprioceptive information might be differentially controlled at the segmental and supraspinal levels. More conclusive evidence would require simultaneous assessment of fusimotor "set" and segmental reflex gain in one and the same individual in a demanding motor task.

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