

## DIFFERENCE IN THE AMPLITUDE OF THE HUMAN SOLEUS H REFLEX DURING WALKING AND RUNNING

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### SUMMARY

1. The Hoffman reflex, or H reflex, was strongly modulated in the human soleus muscle during both walking (4 km/h) and running (8 km/h). It was relatively low at the time of heel contact, increased progressively during the stance phase, and reached its maximum amplitude late in the stance phase. During ankle dorsiflexion the H reflex was absent.

2. During running the peak e.m.g. level of the soleus was on average 2.4 times higher than during walking but the maximum amplitude of the H reflex was never larger than during walking. In fact, the H reflex was on average significantly ( $P < 0.05$  for one-tailed  $t$  test) smaller during running than during walking. Furthermore, the slope of the least-squares line fitted to the relation between the H reflex amplitude and the background e.m.g. was always steeper for the walking data than for the running data.

3. The difference in the H reflex in the two tasks is evidence that the size of the H reflex is not simply a passive consequence of the  $\alpha$ -motoneurone excitation level, as indicated by the e.m.g., but is also influenced by other central neural mechanisms. We suggest that presynaptic inhibition is the most likely mechanism accounting for the change in the slope.

4. The modulation of the reflexes during walking and running can be interpreted in terms of the idea of automatic gain compensation. The decreased gain during running may be appropriate to reduce saturation of motor output and potential instability of the stretch reflex feed-back loop.

### INTRODUCTION

In a previous publication (Capaday & Stein, 1986) we reported that the H reflex of the human soleus muscle was strongly modulated in amplitude during the step cycle in a manner appropriate to the requirements of locomotion. The reflex output was largest late in the stance phase when it would assist in lifting the body off the ground. The same reflex was absent during the swing phase when it would oppose ankle dorsiflexion. The size of the H reflex was also much larger at an equivalent level of e.m.g. during standing than during walking. In particular, during quiet standing the background e.m.g. activity of the soleus is nominally zero as it is also

during ankle dorsiflexion in the swing phase of locomotion. However, during quiet standing the amplitude of the reflex is very large which would make it useful in counteracting forward body sway, but during the swing phase of walking the reflex is shut off when it would oppose ankle dorsiflexion. We therefore concluded that during walking the modulation of the amplitude of the H reflex was not simply a passive consequence of the  $\alpha$ -motoneurone excitation level (measured experimentally as the rectified surface e.m.g.) and that it depended on other central neural mechanisms.

Is the pattern and extent (minimum to maximum) of modulation of the H reflex similar in running and walking, and is the relation between the size of the H reflex and the background e.m.g. the same in the two locomotor tasks? *A priori* a difference in the pattern of modulation may be expected, since for example the impact force on the ankle at the time of heel contact during running is larger than during walking and therefore a larger reflex response may be desirable to further increase the stiffness of the ankle. If the relation between the H reflex amplitude and the e.m.g. were different in the two tasks, it would be further evidence that the size of the H reflex depends on central neural mechanisms other than the excitation level of the  $\alpha$ -motoneurons. Furthermore, any such change in the relationship between these two variables may provide some clues on how the stretch reflex is adapted to the motor task. The validity of inferring changes in the short-latency stretch reflex from changes in the H reflex is discussed in detail in Capaday & Stein (1986). Briefly, while the extent of potentiation or depression of the H reflex may not be identical to that of the stretch reflex (Van Boxtel, 1986) the two never undergo changes in the opposite direction (Akazawa, Aldridge, Steeves & Stein, 1982; Aldridge & Stein, 1982). Furthermore, during locomotion, the effects of the fusimotor system on the muscle spindles tend to reinforce the effects of the modulation of the H reflex (Taylor, Stein & Murphy, 1985; Loeb & Hoffer, 1985).

The contribution of the stretch reflex to sprinting, which is a digitigrade locomotor pattern, was investigated by Dietz and colleagues (Dietz, Shmidbleicher & Noth, 1979). They showed that, during sprinting, the stretch reflex produces a large increase of (e.m.g.) activity in the triceps surae group following contact of the foot with the ground. The reflex also contributes significantly to the muscular tension exerted by this group during the short (150–200 ms) stance phase.

In this study, we have investigated the modulation of the H reflex in various phases of running, in which the locomotor pattern is plantigrade (heel to toe), and compared it to that during walking in the same subject.

#### METHODS

The details of the experimental procedures and the data analysis methods were described in detail in a previous publication (Capaday & Stein, 1986). Here, we briefly describe these as well as some of the modifications that were made in the present experiments.

H reflexes of the soleus muscle were obtained from eight human subjects during level walking (4 km/h) and running (8 km/h) on a treadmill. The average walking cycle time was 1100 ms and that for running was 640 ms. The e.m.g.s of the soleus and the tibialis anterior muscles were recorded with surface silver disc electrodes. A similar silver disc electrode was used to stimulate the tibial nerve in the popliteal fossa. The stimulus return electrode was placed either above the patella or above the popliteal fossa.

The major problem with electrical stimulation of the tibial nerve during locomotion using surface electrodes is that the distance between the stimulating electrode and the nerve changes because of the large displacements at the knee joint. Therefore, the effective stimulus strength (the current density) is not constant throughout the locomotor cycle. However, by repeating the experiment at several stimulus intensities and using the M-wave (which is the electrical response of the muscle to electrical stimulation of its nerve) as a measure of the effective stimulus strength, H reflexes occurring at various phases of the step cycle could be compared at essentially the same stimulus intensity (details in Capaday & Stein, 1986). The M-waves were also closely matched in comparing the walking and running data of each subject. We tried to select values of the M-wave which fell on the relatively flat region of the curve relating H reflex amplitude and stimulus intensity (Capaday & Stein, 1986). The position of this flat region of the curve did not seem to change between walking and running (i.e. it occurred at about the same range of values of the M-wave as in standing). In some subjects, however, the M-waves could only be matched at high amplitudes (i.e. in the portion of the curve where the H reflex decreases). In all cases the results were qualitatively similar.

It is important to have a good measure of the average e.m.g. activity in each of the two locomotor tasks so that the reflex responses can be compared at corresponding levels of activity. The average e.m.g. activity of the soleus and the tibialis anterior muscles during the locomotor cycle was measured by triggering the averaging computer from the suitably conditioned output of a switch placed under the heel inside the subject's shoe. The switch closed and hence triggered the computer at about the time when the foot was flat on the ground. Typically, the e.m.g. activity of each muscle during the locomotor cycles (high-pass RC filtered at 10 Hz, full-wave rectified, and low-pass RC filtered at 100 Hz) was averaged in real time ( $n = 100$ ) and the standard error of the mean was also computed.

This procedure was repeated several times during the course of an experiment to ensure that the pattern of activity remained essentially the same throughout the duration of the experiment. The extent of any possible cross-talk between the ankle extensors (medial gastrocnemius, lateral gastrocnemius and soleus) was determined by direct transcutaneous maximal stimulation of the lateral or the medial gastrocnemius while recording simultaneously the e.m.g. response of the stimulated muscle and its spread over the soleus. This was done to insure that the e.m.g. activity recorded over the soleus muscle was in fact produced for the most part by soleus and not by some combination of soleus activity and that of the other foot extensors. The extent of the cross-talk measured in this way was less than or equal to 10% (0.1 mV of activity picked up at the soleus electrodes for every 1 mV of gastrocnemius activity).

The method of obtaining the reflex responses of the soleus muscle in the various phases of the step cycle is described in detail in the paper by Capaday & Stein (1986) and by Akazawa *et al.* (1982). Briefly, the computer received a step mark, generated by the heel switch, and a stimulus mark. On the occurrence of the stimulus mark the soleus e.m.g. (unrectified, and RC filtered between 10 and 300 Hz) was sampled for approximately 60 ms. The latency between the step mark and the stimulus mark was used to decide in which of sixteen phases of the step cycle the stimulus occurred. Having determined this, the sampled signal from soleus was averaged with other signals which occurred in the same phase. By this method the average H reflex response (usually,  $n = 10-20$ ) of the soleus in each of sixteen different phases of the locomotor cycle was obtained.

The reason for dividing the locomotor cycle into sixteen phases is that this gives a good temporal resolution of events in the step cycle. The procedure of 'phase-dependent' averaging was done in real time and allowed the experimenter to determine, after averaging a suitable number of responses, the size of the M-wave (effective stimulus strength) in each of the sixteen phases of the step cycle. The experimenter could then adjust the output voltage of the stimulator for the next series of averages in order to obtain M-waves in the desired range. By repeating this procedure several times during the course of an experiment M-waves of approximately the same size could be obtained in all sixteen phases of the step cycle.

In a few experiments the WATSMART system (Northern Digital, Waterloo, Canada) for reconstruction of the three-dimensional kinematics of points in space was used to determine the ankle displacement as a function of time in each of the two locomotor tasks. Thus, the changes in length of the soleus muscle, which acts only at the ankle joint, were estimated.

## RESULTS

The H reflex of the soleus during the running cycle increased progressively during the stance phase reaching its peak value usually at about the time of the peak e.m.g. activity. The H reflex rapidly decreased at the end of the stance phase and was absent during the swing phase (ankle dorsiflexion). An example from one subject of the H reflex modulation during the running cycle is shown in Fig. 1.

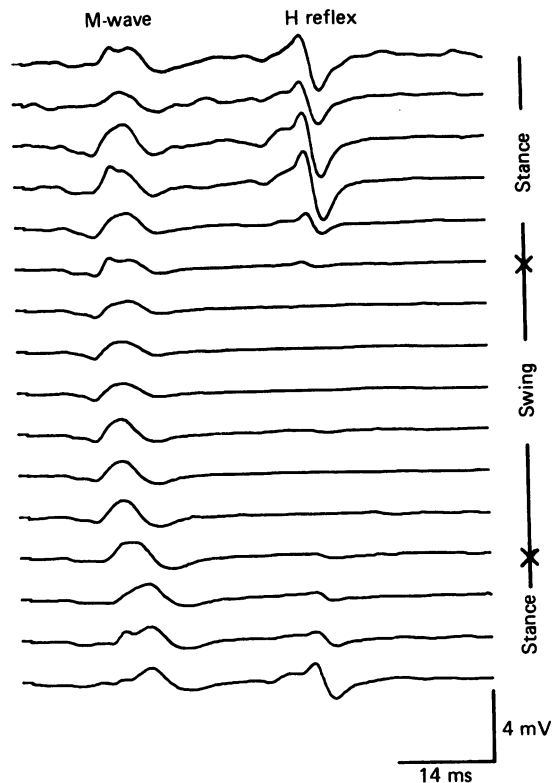


Fig. 1. Amplitude modulation of the H reflex during the sixteen phases of the running cycle. Each record is the average of about fifteen responses of the soleus muscle to stimulation of the tibial nerve. The first record from the top is the response that occurred at about one-third of the way through the stance phase. Note how the reflex increases progressively during the stance phase and that it is absent during the swing phase.

In Fig. 2 the peak to peak amplitude of the H reflex in each of the sixteen phases of the running cycle is plotted as well as the average soleus e.m.g., the average tibialis anterior e.m.g. and the peak to peak amplitude of the M-wave in each phase of the cycle. This subject had the largest phase difference between the H reflex and the e.m.g. (a lag of 2/16 of a cycle). In many subjects little or no phase difference was observed while in others a small phase lead occurred. Overall, no significant phase difference was observed between the peak soleus e.m.g. and the peak H reflex.

In this subject, heel contact occurred at about the 14th phase of the cycle, but the H reflex was relatively low at this time as it was in other subjects. The e.m.g. level

at the time of heel contact of both the soleus and the tibialis anterior increased on average 1.8 times during running compared to walking. The increase of activity in these two muscles at the time of heel contact serves to stiffen the ankle joint and thus prevent the foot from extending too quickly towards the ground after the heel

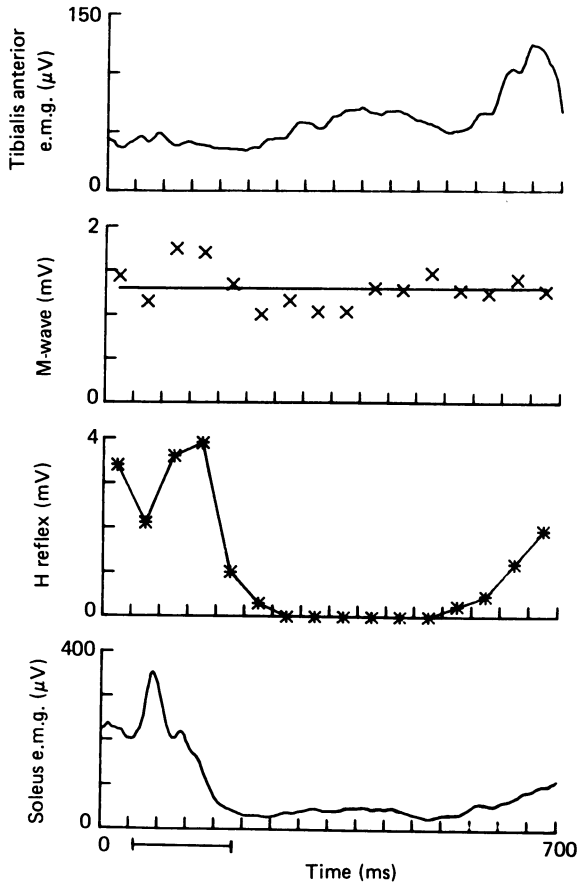


Fig. 2. Plot of the peak to peak value of the soleus H reflex in each of the sixteen phases of the running cycle (same data as in Fig. 1), as well as the corresponding average soleus and tibialis anterior e.m.g. activity ( $n = 100$  steps). The marker below the soleus e.m.g. represents the period in the running cycle when this muscle is undergoing a lengthening contraction. The size of the peak to peak value of the M-wave in each of the sixteen phases of the cycle is shown above the plot of the H reflex *vs.* phase. The horizontal line through the M-wave values represents the mean value (1.3 mV, s.d. = 0.26 mV).

contact. Therefore, the adaptation to the higher impact forces on the ankle at the time of heel contact is at the level of the command signals to the muscles rather than at the reflex level.

In Fig. 2 the period in the stance during which the soleus muscle is lengthening is indicated. In running the soleus undergoes a lengthening contraction during most of the stance phase. The same is true during walking (Fig. 3), and hence the spindle afferents will be firing at relatively high rates (Prochazka, Westerman & Ziccone,

1976; Loeb, Hoffer & Pratt, 1985). Since the presence of an H reflex indicates that there is transmission from the Ia afferents to the  $\alpha$ -motoneurons during this phase of locomotion, part of the muscular activity in this phase must be due to the stretch reflex.

The peak value of the H reflex during running was on average significantly smaller

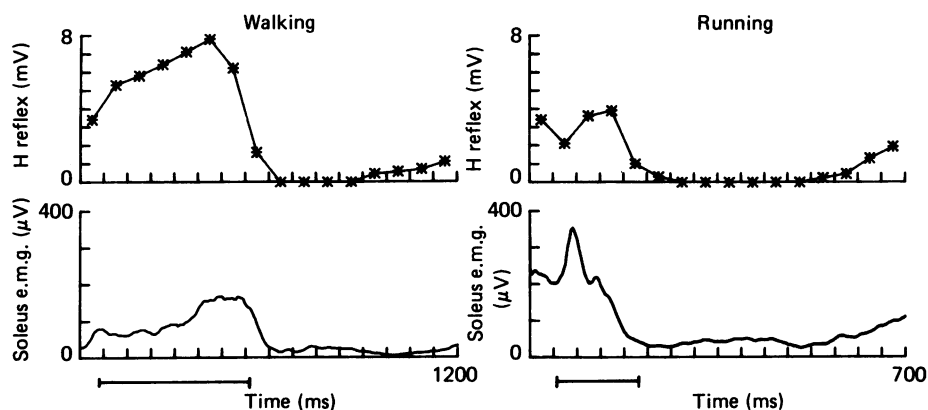


Fig. 3. Comparison, in the same subject, of the extent (minimum to maximum) of the amplitude modulation of the soleus H reflex during the walking and running cycles. Note that the extent of the modulation is much less during running than during walking despite the fact that the peak value of the e.m.g. is 3.2 times bigger during running than during walking. The marker below each of the average soleus e.m.g. records indicates the period in the locomotor cycle during which this muscle is lengthening.

( $P < 0.05$  for a one-tailed  $t$  test) than during walking. This finding is especially noteworthy as the peak e.m.g. levels of the soleus attained during running were on average 2.4 times greater than during walking. An example of the pattern of the H reflex modulation during walking, as compared to that during running in the same subject, is shown in Fig. 3. The peak value of the H reflex during running in this subject was 3.8 mV and that during walking was 7.8 mV. The peak e.m.g. level of the soleus was 3.2 times larger during running than during walking.

The relation between the H reflex peak to peak amplitude and the mean level of the e.m.g. at the time the reflex was elicited is shown for two subjects in Fig. 4. In all eight subjects the slope of the least-squares fitted line was always steeper for walking data than for running. There was no significant or systematic difference in the  $y$ -intercepts. Therefore, the threshold of e.m.g. activity at which the H reflex appears is essentially the same during walking and running. This is in marked contrast to the large change in the value of the  $y$ -intercept which occurs between standing and walking (i.e. the H reflex is very large during quiet standing; Capaday & Stein, 1986).

It may be argued that the decreased size of the H reflex during running is due to a saturation of the motoneurone pool, since the soleus e.m.g. was greater during running than during walking. The more motoneurons are recruited, the fewer are left to recruit, and this may explain why the H reflex decreases at high levels of the e.m.g. However, the H reflex is reduced in size at all levels of e.m.g. (Fig. 4). Thus,

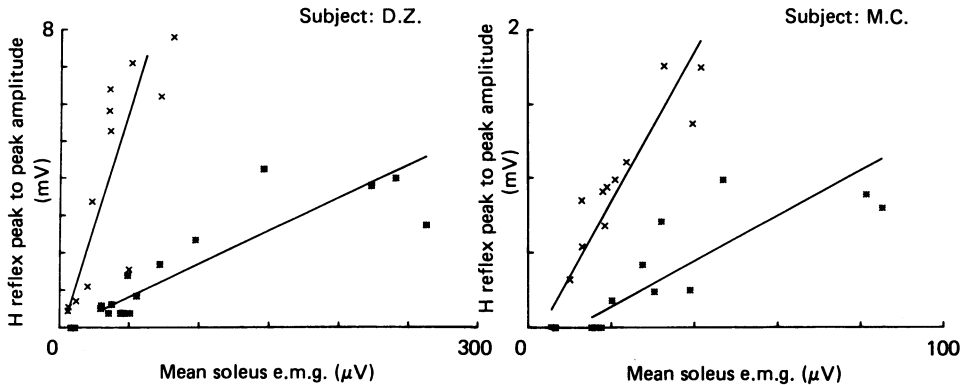


Fig. 4. Relation between the peak to peak value of the H reflex and the mean level of soleus e.m.g. activity at the time the reflex was elicited during walking ( $\times$ ) and running ( $\blacksquare$ ). The data from two different subjects are shown; subject D.Z. is the one whose data are presented in Figs 1, 2 and 3. The mean value of the e.m.g. at the appropriate time in the step cycle was determined from the computed average locomotor pattern.

a mechanism other than a simple saturation of the motoneurone pool is the cause of the reduction of the H reflex during running.

#### DISCUSSION

The first new finding reported in this paper is that the H reflex is modulated in amplitude during running. The reflex sensitivity is relatively high during the stance phase of the running cycle, when the soleus muscle is undergoing a lengthening contraction during most of that phase. Since the spindle afferents are also firing at high rates during stance in cats (Prochazka *et al.* 1976; Loeb *et al.* 1985) and presumably in man, the stretch reflex would contribute to the muscle tension required to decelerate the downward and forward motions of the body and to lift the body off the ground. The reflex is absent during the swing phase, since a high reflex sensitivity at this time would activate the soleus muscle and thus oppose the active dorsiflexion of the ankle. Thus, the pattern of modulation of this reflex is appropriate to the requirements of running.

The second new finding is that during running the soleus H reflex was on average less than that during walking, despite the fact that the peak e.m.g. activity was on average 2.4 times greater during running than during walking. Moreover, there was a decrease in the slope of the least-squares line fitted to the relation between the H reflex amplitude and the mean level of background e.m.g.

#### Neuronal mechanisms

What mechanism(s) can account for these observations? Evidence was presented in the Results section to support the idea that the reduction of the H reflex size and the reflex slope (H reflex *vs.* e.m.g.) were not due simply to a saturation of the motoneurone pool. Alternatively, saturation may occur on the afferent side. During unrestrained locomotion in cats, the Ia spindle afferents never discharge anywhere

near their maximum possible rate (500 impulses/s or more). Typically, the peak firing levels attained are about 200 impulses/s (Prochazka *et al.* 1976; Loeb *et al.* 1985). Thus, most of these afferents should discharge an additional impulse in response to an electrical stimulus. In addition, several minutes of tonic stimulation of the Ia fibres (e.g. 20 min at 200 impulses/s) are required to appreciably increase their electrical threshold (Jack, 1978). Therefore, during the brief stance phase of running (600–700 ms) the electrical threshold of these fibres should not significantly increase.

Another possible mechanism was proposed by Pierrot-Deseilligny (1985), based upon experiments on the depression of H reflexes in the triceps surae group of relaxed human subjects by paired (conditioning–test) stimuli to the soleus nerve. He proposed that during the stance phase of locomotion the Ib afferents of the triceps surae inhibit the stretch reflex output of this group. Such a reduction of the stretch reflex output, he argued, would allow for the ankle dorsiflexion in the stance phase to proceed unopposed by an excessive stretch reflex which would otherwise occur in this group when the triceps surae undergoes a lengthening contraction. However, relaxed subjects were used in his experiments, and it remains an open question whether the state of the Ib pathway to the motoneurons is the same at rest and during locomotion.

Computer modelling, on the other hand, allows for the systematic investigation of the factors that affect the input–output properties of the stretch reflex. We have recently analysed by computer simulation the influences of both presynaptic and postsynaptic mechanisms on the size of the reflex output of a motoneurone pool (Capaday & Stein, 1987). The model contains a representation of the subthreshold behaviour of the motoneurons (integration of synaptic inputs) and the statistical distribution of the motoneurons in the pool according to their resting conductance. This feature allows for the orderly recruitment of the motoneurons in the order of low resting conductance to high resting conductance. The range and distribution of the resting conductances fitted data obtained from cat motoneurons (Gustafsson & Pinter, 1985). Values for other motoneurone properties such as the membrane capacitance and the time constant of the after-hyperpolarization were obtained from the literature on cat motoneurons. There were some small quantitative differences depending on the assumptions we made about the distribution of excitation to the motoneurons but the results were in all cases qualitatively similar.

The main finding from this analysis was that regardless of the postsynaptic mechanisms by which the motoneurons were depolarized, the size of the reflex output remained tied to the level of excitation of the pool. This finding was surprising to us and contrary to our initial qualitative analysis (Capaday & Stein, 1986), but was also verified by mathematical analysis (Capaday & Stein, 1987). An increase in the amount of presynaptic inhibition decreased the size of the reflex output at all levels of excitation, as well as the slope and *y*-intercept of the curve relating these two variables.

In conclusion, more complex explanations are possible involving time-varying mixtures of conductances, perhaps through oligosynaptic pathways (Burke, Gandevia & McKeon, 1984; Pierrot-Deseilligny, 1985). However, the observed differences in the H reflex modulation during running and walking can be most simply accounted



for by a tonic increase in the amount of presynaptic inhibition of the Ia terminals to the  $\alpha$ -motoneurons during running.

### *Functional implications*

During the stance phase of the locomotor cycle the e.m.g. activity of the soleus during running was on average 2.4 times higher than during walking. The higher level of muscle activity and hence stiffness of the ankle muscles is required to decelerate the faster downward and forward motions of the body in a shorter period of time, as well as to push the body off the ground more rapidly. Concomitantly, there is a decrease of the slope of the H reflex *vs.* e.m.g. relation (Fig. 4). The increase of the stretch reflex, like the H reflex here, with the background activity level has been termed 'automatic gain compensation' (Marsden, Merton & Morton, 1972; Matthews, 1986). That is, the gain of the reflex increases as a function of the excitation level of the motoneurone pool. It follows from our data that the gain of the H reflex is reduced during running compared to walking. Why should the H reflex gain, which is a measure of one of the central components of the stretch reflex gain, be turned down during running?

At this stage no definite answer can be given, but some suggestions can be made. The stretch reflex output depends on both the extent and rate of muscle stretch (Matthews, 1970; Gottlieb & Agarwal, 1979) both of which are increased during running. Moreover, as we have suggested, the stretch reflex contributes part of the motor output of the soleus during locomotion. Therefore, a decrease in the central component of the reflex gain during running (as judged from the decrease of the slope of the H reflex *vs.* e.m.g. curve) may be an adaptation to ensure that the net motor output does not saturate. In addition, since the stretch reflex increases the stiffness of a contracting muscle (Hoffer & Andreassen, 1981; Nichols, 1985), the increased muscle stiffness coupled with a high reflex gain and the reflex delay may lead to instability (i.e. tremor) (Stein & Lee, 1981).

In conclusion, we suggest that the stretch reflex acting as a feed-back mechanism, contributes to the tension of the extensor musculature of the leg in both walking and running. However, there are advantages to reducing the central gain of the monosynaptic reflex during running, compared to walking, and a reduction does occur as indicated by the H reflex measurements we have made.

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