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REFLEX EXCITABILITY OF HUMAN SOLEUS MOTONEURONES DURING VOLUNTARY SHORTENING OR LENGTHENING CONTRACTIONS

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SUMMARY

1. We investigated the possibility that increase or decrease in the monosynaptic reflex excitability of the soleus muscle in man might play a role in matching the muscle mechanical output to the voluntary command aimed at performing isotonic contractions or relaxations, at various velocities.

2. Rectified and integrated electromyographic activity (e.m.g.) and the H reflex of soleus were measured during plantar flexions against a constant load (shortening contractions) or dorsal flexions resisting the load (lengthening contraction), performed without activation of pretibial muscles.

3. At the same ankle joint angle, integrated e.m.g. was larger during shortening contractions than during lengthening contractions. During shortening contractions, integrated e.m.g. increased as a function of the velocity of plantar flexion. During lengthening contractions, integrated e.m.g. decreased as a function of dorsal flexion and angular velocity and nearly disappeared in the last part of the most rapid lengthening contractions.

4. During shortening contractions, the H reflex increased beyond the extent expected for the level of e.m.g. activity; during lengthening contractions, reduction of the H reflex below control values at rest occurred in spite of background e.m.g. activity.

5. When the level of e.m.g. activity was kept constant, the above changes in H reflex were larger in both directions as a function of the velocity of the movement.

6. Passive rotation in the dorsal direction contributed to the inhibition observed during lengthening contractions.

7. It is suggested that these changes in the excitability of the H reflex, probably presynaptic in origin, serve the purpose of appropriately modulating the rate and extent of motoneurone recruitment during shortening and lengthening contractions. This allows the foot to follow a constant-velocity path in spite of the perturbing effects of the spindle afferent inputs and of the muscle characteristics described by the force–length and force–velocity diagrams.

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INTRODUCTION

Changes in the H-reflex magnitude are normally induced by variations in the baseline electromyographic activity (e.m.g.), in all the muscles in which the reflex is elicitable (Paillard, 1955; Gottlieb, Agarwal & Stark, 1970; Iles, 1977). In the case of the soleus muscle, the H reflex is increased as a function of the degree of voluntary innervation, to a different extent according to various reports, and depending on the amplitude of the reflex that is taken as control in resting conditions (see Verrier, 1985). However, it has been demonstrated that, during time-varying isometric contractions of the soleus muscle, the amplitude of the H reflex is not necessarily correlated with the amplitude of the e.m.g. The amplitude of the reflex can in fact be even smaller than that of the controls at rest, when the muscle contraction is being voluntarily reduced (Gottlieb & Agarwal, 1973; Schieppati & Crenna, 1984). Since this happens in spite of ongoing e.m.g. activity, an inhibition of the reflex arc rather than of the motoneurones was envisaged. Several lines of evidence have been reported in favour of a presynaptic inhibitory mechanism, probably acting on the Ia afferent inputs from the spindles of the relaxing muscle (Schieppati & Crenna, 1985). In fast relaxations, performed in reaction-time conditions, the H-reflex inhibition precedes e.m.g. termination and accompanies its decay, and outlasts e.m.g. termination at least until complete return of force to base line (Nardone & Schieppati, 1985; Schieppati, Nardone & Musazzi, 1986). These findings led to the conclusion that presynaptic inhibition is actively modulated in parallel with the descending command to the motoneurones (see Schieppati, 1987).

The present research was undertaken to test the hypothesis that this presumed presynaptic inhibition would be appropriately modulated in order to contribute to the control of the voluntary recruitment–de-recruitment of the motoneurones during shortening or lengthening muscle contractions, in the assumption that spindle Ia afferent discharge plays an important role in maintaining motor activity (Angel, Eppler & Jannone, 1965; Hagbarth, Hongell & Wallin, 1970; Marsden, Merton & Morton, 1976; Hugon, Massion & Wiesendanger, 1982). It is known in fact that a contracting muscle, owing to its in-series elastic properties, develops considerably more force during a lengthening contraction than during a contraction in which it is allowed to shorten, under the same level of activation. This behaviour is described by the force–velocity diagram, the additional force being proportional to the velocity of stretch (Katz, 1939; Abbot, Aubert & Hill, 1951; Cavagna, Dusman & Margaria, 1968). Therefore, when a relaxing soleus muscle has to resist a constant load, yielding at a constant velocity, a conflicting situation would ensue, whereby both the muscle mechanical properties and the spindle reafference (Vallbo, 1970; Burke, Hagbarth & Löfstedt, 1978; Hulliger & Vallbo, 1979; Vallbo & Hulliger, 1981; Roll & Vedel, 1982) would lead to development of more force than required, the more so the faster the velocity of relaxation. In this view, a controlled decrease in force of the muscle can only occur if the activation of motoneurones is damped in proportion to the velocity of lengthening, in order to have a smaller number of motor units active, or motor units discharging at a lower frequency. The opposite occurs in the condition of shortening contraction: large loads can be lifted at increasing velocity provided that the muscle is able to deliver greater force, i.e. to increase the number of active motor units, or their discharge frequency, since each of them delivers necessarily less force at higher velocities of shortening.

METHODS

Seven volunteers aged between 22 and 38 years participated in this study. They sat in an examination chair, with the knee and ankle joint angles at 110 and 80 deg of rotation, respectively (resting conditions). The right foot was strapped to a mould mounted on a metal plate, allowing a plantar–dorsal rotation of 30 deg about an axis through the medial malleolus. The foot position was recorded by a linear potentiometer centred on the axis of rotation. One end of a flexible steel wire was attached to the plate at a point corresponding to the position of the metatarso-phalangeal joints. The other end of the wire carried a load which exerted a force of 100 N upon the foot plate, so that the load opposed plantar flexion of the foot. The wire ran over two ball-bearing pulleys, in such a way that the direction of power was approximately parallel to the long axis of soleus muscle, and this parallelism was preserved throughout the angle of rotation of the tibio-tarsal joint angle. A strain gauge was inserted in series with the wire, between the metal mould and the first pulley. In these conditions, it was calculated that the over-all force exerted by the triceps surae muscle to sustain the weight was approximately 350 N, irrespective of the tibio-tarsal joint angle. This figure takes into account the distances between the axis of rotation and (a) the point of application of the load-bearing wire, and (b) the insertion of the Achilles tendon into the calcaneum. This force is shared by the elastic elements and the contractile mechanism, to a different extent, depending on the angle of rotation. The contribution of the elastic elements was roughly estimated by measuring at various joint angles, in passive static conditions, the force necessary to maintain the foot in position: at 0 deg (80 deg of tibio-tarsal joint angle) the elastic elements exerted between 240 and 280 N, in the various subjects; at 30 deg of plantar flexion (110 deg of tibio-tarsal joint angle) their contribution was reduced to 50–90 N (see also Sale, Quinlan, Marsh, McComas & Belanger, 1982; Gerard, Tardieu, Bussel & Tardieu, 1985).

An oscilloscope was mounted on the frame in front of the subject; the screen displayed the angular rotation of the foot as a vertical deflection of a spot, while the time-base could be set in free-run mode, at different velocities. The subjects were instructed to keep the spot within a narrow double track patterned on the screen, featuring a linear change in foot position at rotation velocities of either 12, 25 or 50 deg/s, by appropriately contracting or relaxing the triceps surae muscle. In the first case an active plantar flexion (a.p.f.) was achieved through a shortening contraction and in the latter a lengthening contraction resisted the load while the foot was dorsiflexed; these 'active' dorsal flexions (a.d.f.) were never performed by contraction of pretibial muscles, whose e.m.g. was continuously monitored by electrodes positioned on the antero-lateral surface of the leg, but only by controlled decrease in activation of the soleus muscle. These tasks were easily achieved, regardless of beam velocity or direction of angular rotation. The strain gauge monitored the changes in force occurring during the task and those resulting from the acceleration of the load. Foot rotations of similar extent and velocity were reproduced passively, by inviting the subject to relax completely, and having one of the experimenters pull (passive dorsal flexion, p.d.f.) or let go (passive plantar flexion, p.p.f.) the wire, under visual control of the foot position on the oscilloscope. The rotations obtained in this way matched perfectly those actually produced by the subjects, as controlled by superimposition of the stored traces of active and passive flexions.

In order to elicit H reflexes in the soleus muscle, the posterior tibial nerve was stimulated electrically with single pulses of 1 ms duration. The cathode was housed in a plastic foam support, held in place against the nerve by means of a rubber band strapped around the leg. The anode was a large silver plate placed on the knee. Recording surface electrodes, spaced 3 cm apart, were taped to the skin of the lower third of the leg, posteriorly. If not otherwise stated, the reflex amplitude was set at about half the maximal attainable amplitude. Stimuli were delivered either at rest or during (active and passive) plantar and dorsal foot flexions, at various foot positions, in pseudo-random conditions. Foot rotations were not carried out in sequence, such as in rhythmical movements, but at least 20 s elapsed between each performance. A.p.f.s started from resting conditions; a.d.f.s were performed by releasing an isometric triceps contraction of a few seconds duration. In some experiments, the reflex-evoking stimulus was triggered by the output of a threshold discriminator, whose input was either the rectified and integrated (time constant 100 ms) e.m.g. of the soleus muscle, or the position signal, so that the stimulus could be triggered at the required foot position or background soleus e.m.g. activity, by changing the threshold level.

At the stimulus intensities used, the direct M response was usually a small fraction of the H reflex, which lay on the ascending part of the recruitment curve, obtained by plotting H-reflex and M-response amplitudes *versus* stimulus intensity (see Fig. 3). In this region of the curve, changes in the effective strength of the stimulus, possibly connected to alterations in the spatial relationship between cathode and nerve, might induce considerable changes in H-reflex amplitude without significantly affecting the magnitude of the M response. Therefore, recruitment curves were drawn at different foot positions (in static or dynamic conditions) to discriminate between effects on the H reflex connected with the intended tasks and those caused by movement artifacts.

RESULTS

Soleus e.m.g. during shortening or lengthening contractions

The rectified and integrated e.m.g.s recorded during repeated a.p.f.s or a.d.f.s, performed at various angular velocities, were averaged and compared. Fig. 1 shows the time course of foot rotation and of the integrated e.m.g. envelopes obtained during a.p.f. (*A*) and a.d.f. (*B*), lifting a 100 N weight, or yielding to it, respectively, at three different velocities; the centres of the bottom traces (force) correspond to a force of 100 N: the oscillations around that value refer to changes in force connected with the initiation and termination of foot rotation. During the tasks, the integrated e.m.g. increased as a function of the degree of plantar flexion, and diminished at the end of foot rotation, to level at a plateau in a few seconds. During dorsal flexions, integrated e.m.g. decreased from the level corresponding to that necessary to hold the weight in position, and disappeared as the foot came back to the initial position. These events took place regardless of constancy in torque, as expected from the force–length diagram. Besides, for the same muscle length, the integrated e.m.g. was far larger during a.p.f. than a.d.f., as predicted by the force–velocity diagram.

In Fig. 2, the amplitude of the averaged integrated e.m.g., obtained in the above conditions, is plotted *versus* the angle of foot rotation. The graph shows that, at the various degrees of rotation, the integrated e.m.g. was larger at higher velocities during a.p.f., whereas the reverse was true during a.d.f., so that the differences in height of the integrated e.m.g. in the two tasks, at a given position and therefore muscle length, were negligible at slow velocity and became very large at high velocity of rotation.

Soleus H reflex during shortening or lengthening contractions

Preliminary experiments were designed to investigate possible changes in the amplitude of the H reflex connected with variations in foot position under static, passive conditions. To this aim, in all the subjects the H reflex was evoked in static, relaxed conditions by fixing the foot mould at various angles of rotation. Fig. 3 *A* shows that a slight facilitation of the H reflex was indeed present when the foot was situated in a plantar-flexed position. This increase in H-reflex amplitude was not connected with changes in the spatial relationship between stimulating electrode and nerve, as demonstrated by the H-reflex–M-response recruitment curves drawn for three different angles of rotation, and reported in Fig. 3 *B*.

Fig. 4 shows the amplitude of the H reflexes evoked during plantar (*A*) and dorsal (*B*) foot flexions, at two different velocities (left, 12 deg/s; right, 25 deg/s). In each

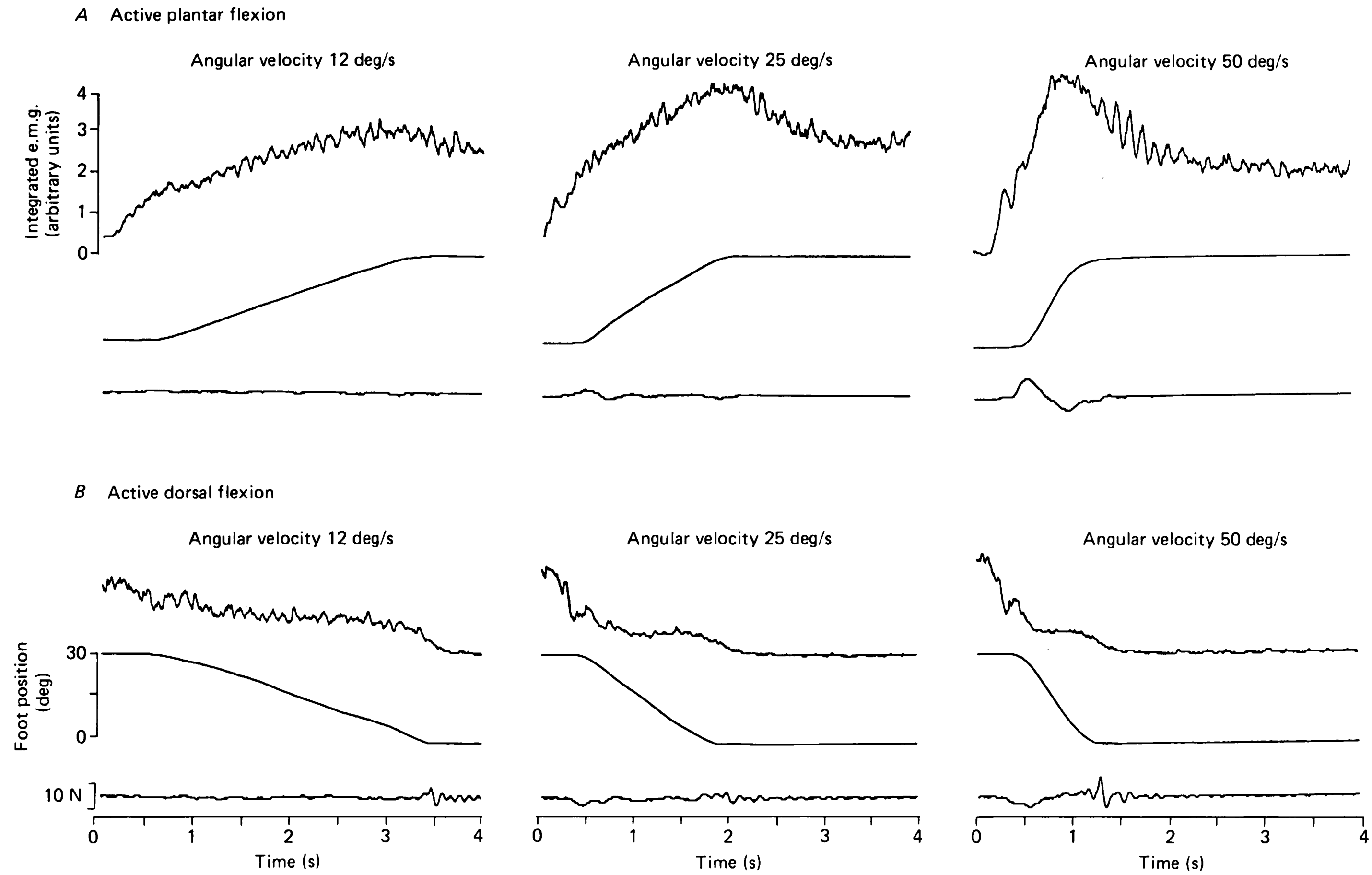

Fig. 1. Records of soleus integrated e.m.g. (arbitrary units, time constant 7·5 ms), foot position (deg) and force changes (N) during voluntarily performed plantar or dorsal foot flexions, at three different velocities (left, 12 deg/s; centre, 25 deg/s; right, 50 deg/s). Fifteen individual responses from one subject were averaged in every case. In this and in the following Figures 0 deg corresponds to 80, and 30 to 110 deg of tibio-tarsal joint angle, respectively. Note that the force trace is centred at the 100 N level. These tasks were invariably performed without activation of pretibial muscles in all subjects.

graph, the reflexes obtained during the active tasks (a. p. f. and a. d. f.) are compared with those evoked during passive rotation (p. p. f. and p. d. f.), in order to discriminate between effects connected with the voluntary command and those connected with foot rotation. In all cases the H-reflex amplitude is expressed as a percentage of the H reflex obtained under static, passive conditions, at corresponding positions, as described above. It appears that p. p. f. induced a slight decrease in amplitude of the reflex, which was influenced by the degree of rotation rather than by the angular velocity. In the case of a. p. f., the reflex was increased to very high values, and to a greater degree the higher the velocity. The reflexes elicited during a. p. f. have been compared with those recorded under active isometric conditions at the corresponding tibio-tarsal joint angles. These reflexes were obtained by (a) changing the stimulus strength so as to yield a reflex at rest equal to that obtained during p. p. f., at corresponding positions, and (b) asking the subject to contract his soleus muscle under static conditions to such a degree as to produce an integrated e. m. g. equal to that recorded during a. p. f. The intermediate curves in the Fig. 4*A* were obtained in this way, and represent the 'references' with which to compare the effects of the command to dynamically plantar flex the foot.

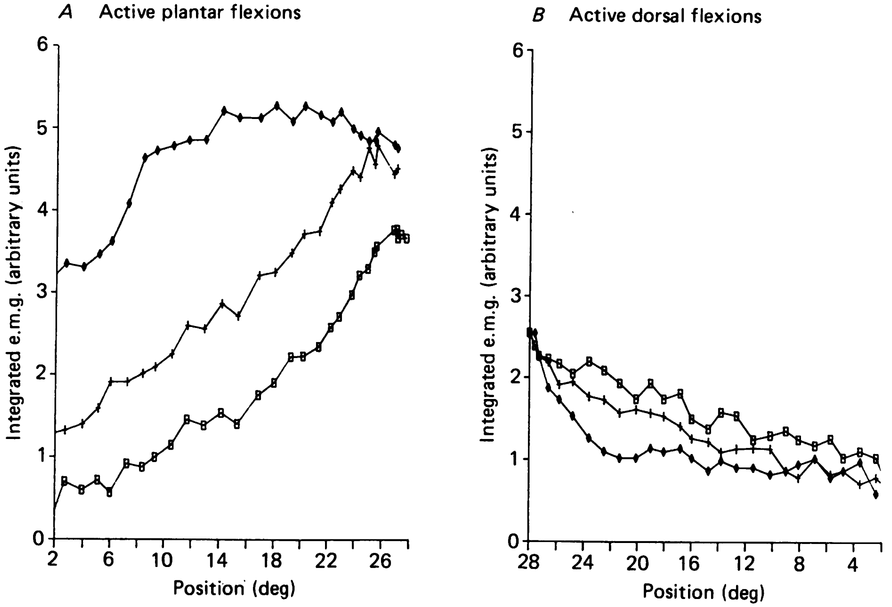

Fig. 2. Plots of the averaged integrated e. m. g. profiles *versus* the angle of the foot rotation, obtained in another subject during the same tasks as in Fig. 1. It is shown that at equal positions, the integrated e. m. g. is larger during active plantar flexion (*A*), and lower during active dorsal flexion (*B*); the respective differences increase as a function of the velocity of rotation (□, 12 deg/s; +, 25 deg/s; ◊, 50 deg/s).

The graphs depicting the H-reflex changes during the dorsal flexions (Fig. 4*B*) have been drawn according to a similar procedure. P. d. f. *per se* had a striking inhibitory effect that was evident just beyond a few degrees of dorsal flexion, and nearly abolished the reflex, particularly when the latter was evoked upon attainment of the resting position. Reflexes evoked during a.d.f. were also markedly depressed over most of the rotation range. Since during a.d.f. the soleus motor pool is subject to facilitatory influences, as a consequence of the ongoing e.m.g., an estimate of the net inhibitory effect of the command to gradually relax the muscle is made possible

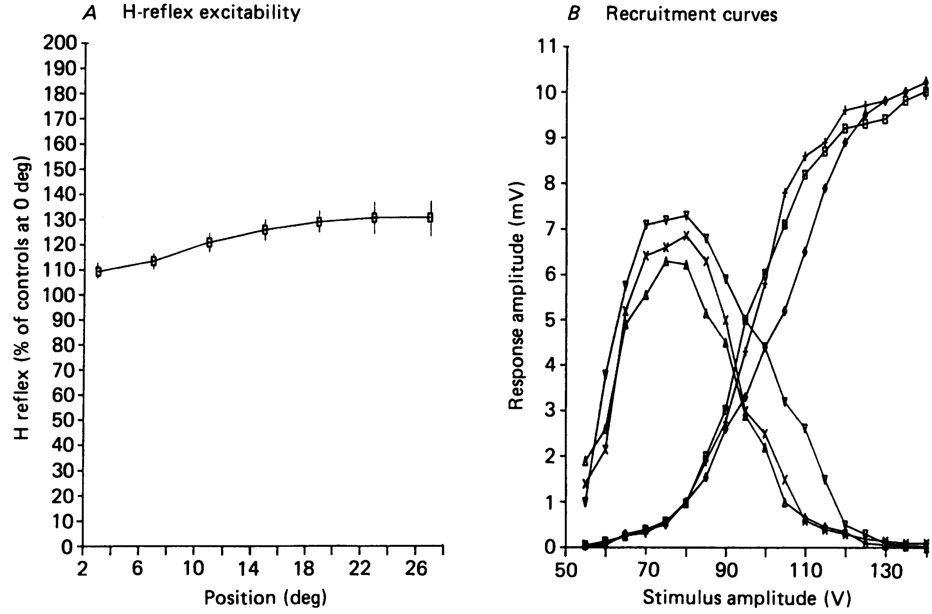

Fig. 3. Changes in H-reflex amplitude as a function of foot position. In *A*, each point represents the grand mean (± standard error, S.E.) of the peak-to-peak amplitude of the H reflexes evoked in six subjects, in stationary, relaxed conditions. *B* shows H-reflex–M-response recruitment curves obtained in one subject, at three different foot positions (□ and △ , H reflexes and M responses, respectively, at 8 deg; † and X, H reflexes and M responses at 16 deg; ◊ and ▽, H reflexes and M responses at 24 deg; each point is the mean of six measurements.

by comparison of the a.d.f. reflexes with those evoked, in the corresponding static conditions, when the subjects voluntarily 'facilitated' a small H reflex (equal to that evoked during p.d.f. at a corresponding position, see above), innervating their soleus muscle to the same extent (same integrated e.m.g.) as during a.d.f. These 'references' have an amplitude which exceeds that of the reflexes evoked during a.d.f. in the first half of the muscle relaxation.

Recruitment curves during plantar or dorsal flexions

Recruitment curves for the H reflex and M response have been established during p.p.f. or p.d.f. at three angular velocities, but at the same angle (15 deg) by having the stimulus triggered by the position signal, to exclude the possibility that movement artifacts led to the observed effects. The results are reported in the graphs of Fig. 5, in which it is clearly shown that, at equally effective stimulus intensities (M responses), the H reflexes were consistently inhibited during p.d.f., the inhibition being proportional to the angular velocity. In the case of p.p.f. the H reflexes also

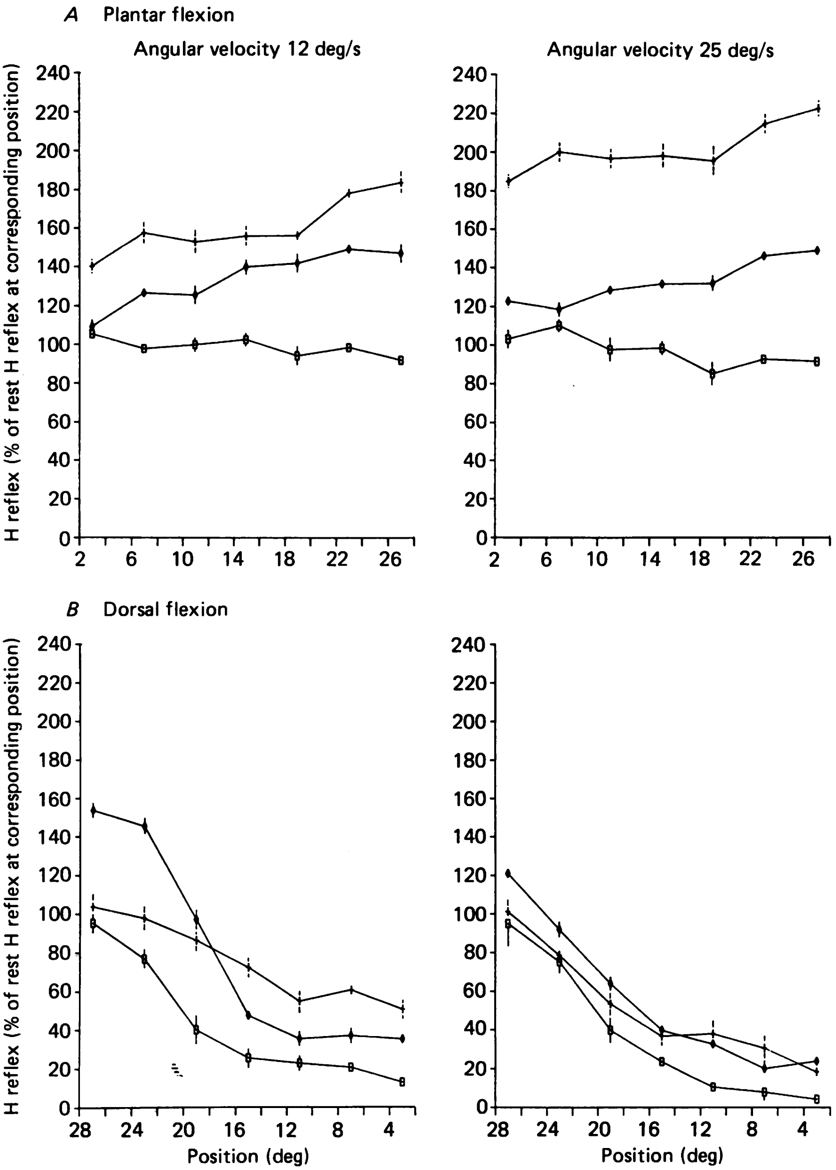

Fig. 4. Changes in H-reflex amplitude during active (+) or passive (□) plantar (*A*) or dorsal (*B*) foot flexions, at two different velocities (left, 12 deg/s; right, 25 deg/s), plotted as a function of foot position. In all panels, the data points marked with ◊ refer to the amplitude of the 'reference' H reflexes. These were obtained under stationary, relaxed conditions; the stimulus strengths capable of eliciting H reflexes equal to those obtained during passive flexions at every indicated angle were determined; the subjects were then invited to isometrically contract their soleus muscle in such a way as to produce integrated e.m.g.s equal to those recorded during the active tasks; the reflex-eliciting stimuli were then delivered under these conditions. Each point is the grand mean (±S.E.) of at least six measurements (normalized to the H reflexes evoked at rest at the corresponding positions) for each condition and subject (six).

showed a decrease in amplitude (compare with Fig. 4, right), but this inhibition was small and not influenced by the velocity of rotation.

Effects of velocity of contraction on the H reflex

These results have been obtained by triggering the stimulus evoking the H reflex with a certain level of integrated e.m.g., so that, regardless of position or velocity, the reflex was superimposed onto a fixed degree of activation of the soleus motoneurone pool. The graph in Fig. 6*A* (upper part) depicts increases in amplitude as a function of the velocity of shortening contraction (a.p.f.). This effect is independent of the level of integrated e.m.g. chosen, but is connected to the extent of angular velocity, as shown by the approximate parallelism among the lines fitting H reflexes obtained during rotations of increasing speed at different levels of integrated e.m.g. In the lower half of the graph in Fig. 6*A* are reported the reflexes elicited during lengthening contractions (a.d.f.) performed at the same three velocities as above. The over-all trend of the reflexes is a decrease in amplitude as a function of a decrease in integrated e.m.g., as expected; but, in addition, their amplitude decreases as a function of the velocity of lengthening.

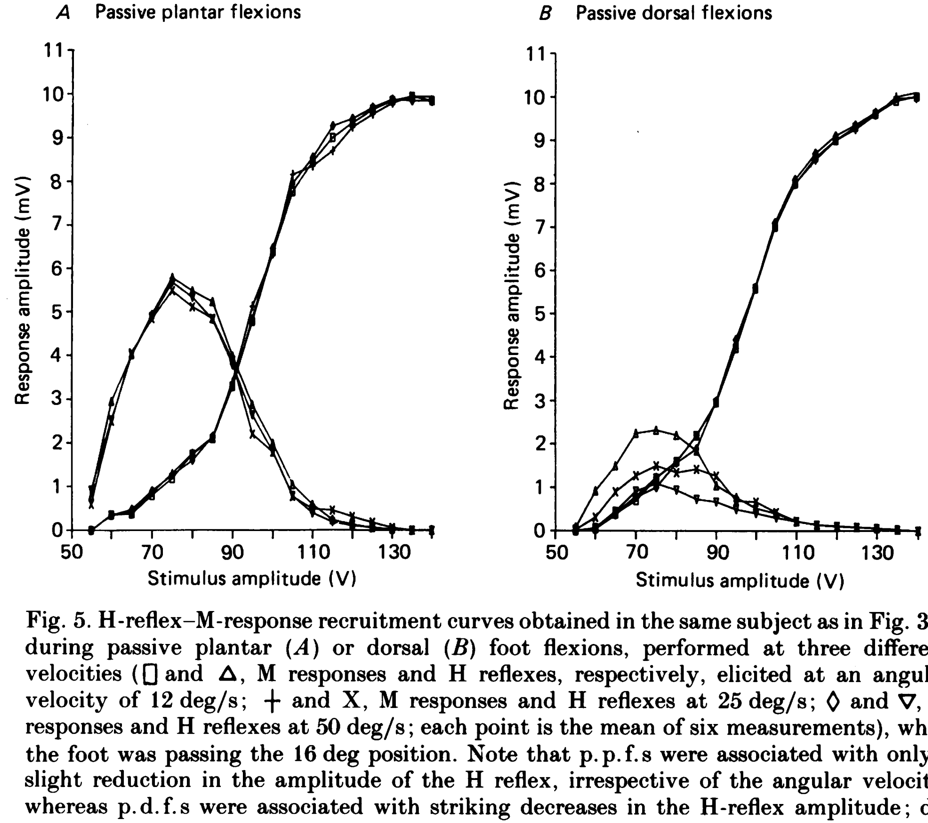

Fig. 5. H-reflex–M-response recruitment curves obtained in the same subject as in Fig. 3*A* during passive plantar (*A*) or dorsal (*B*) foot flexions, performed at three different velocities (☐ and △, M responses and H reflexes, respectively, elicited at an angular velocity of 12 deg/s; + and X, M responses and H reflexes at 25 deg/s; ◇ and ▽, M responses and H reflexes at 50 deg/s; each point is the mean of six measurements), while the foot was passing the 16 deg position. Note that p.p.f.s were associated with only a slight reduction in the amplitude of the H reflex, irrespective of the angular velocity, whereas p.d.f.s were associated with striking decreases in the H-reflex amplitude; decreases were greater at higher velocities.

This procedure (triggering by means of the level of integrated e.m.g.) suffers from the disadvantage that positions attained at a given e.m.g. vary as a function of the velocity (i.e. the higher the velocity, the less plantar- or dorsal-flexed is the foot, during a.d.f. or a.p.f., respectively). Yet this fact would be of minor importance in the case of plantar flexion, because passive movements in plantar direction hardly affect H-reflex excitability (see Fig. 4). On the other hand, in the case of active dorsal flexions performed at different velocities, changes in the position attained at a given level of integrated e.m.g. lead to a conspicuous underestimation of the decrease in H-reflex excitability as a function of increase in the velocity of lengthening contraction. In fact, a given level of e.m.g. activity is reached earlier during fast than during slow muscle relaxation, i.e. when the inhibitory effect of passive rotation *per se* is comparatively small.

DISCUSSION

The results reported show that, during voluntary movements of the tibio-tarsal joint, the excitability of the soleus muscle H reflex is subject to various, powerful influences. In particular, it has been shown that, at equal levels of integrated electromyographic activity, the excitability of the reflex arc of the soleus muscle is increased during a voluntary plantar flexion, and is diminished when the contraction is gradually released to allow a dorsal foot flexion at a given velocity against the dorsiflexing load. These effects are the sum of influences exerted by the command to contract or relax the triceps surae muscle and of the influences connected with changes in the peripheral input from the moving muscles or joint. In fact, passive dorsal flexion of the foot leads to H-reflex inhibition (see also Mark, Coquery & Paillard, 1968; Gottlieb & Agarwal, 1978; Robinson, McComas & Belanger, 1982; Davies & Lader, 1983; Etnyre & Abraham, 1986), while afferent inputs from passive rotation in the plantar direction do not appear to have major effects on the excitability of the H reflex, at least within the rotation range studied in these experiments.

As far as the influences exerted by the reafference from the periphery are concerned, a few considerations are needed: (1) The excitatory influences of the Ia inputs from the soleus spindles onto soleus motoneurones would induce an effect opposite to the one observed: in shortening contractions they should become less relevant, the higher the velocity of shortening, whereas in lengthening contractions they should greatly increase in power (Burke *et al.* 1978). (2) The inhibitory influences from the Ib afferents should increase as a function of the level of e.m.g., but instead the greatest inhibition of the reflex appeared when the e.m.g. level was very low at the termination of dorsal flexions, and vice versa. (3) Cutaneous inputs, e.g. those from the sole of the foot, should remain relatively constant during all the tasks, because the pressure exerted by the foot plate on the foot remained constant, at least when the velocity of rotation was constant. (4) The inputs coming from spindle type II or articular receptors might actually be those responsible for that part of H-reflex inhibition connected with passive rotations: it has been proposed that group II afferents from the spindles are able to cause a decrease in the H-reflex amplitude observed during passive foot dorsal flexion or soleus passive stretch (Robinson *et al.* 1982); on the other hand, experiments in the cat have shown that inputs from the ankle joint can inhibit the soleus monosynaptic reflex during foot rotation in both directions (Schieppati & Crenna, 1984).

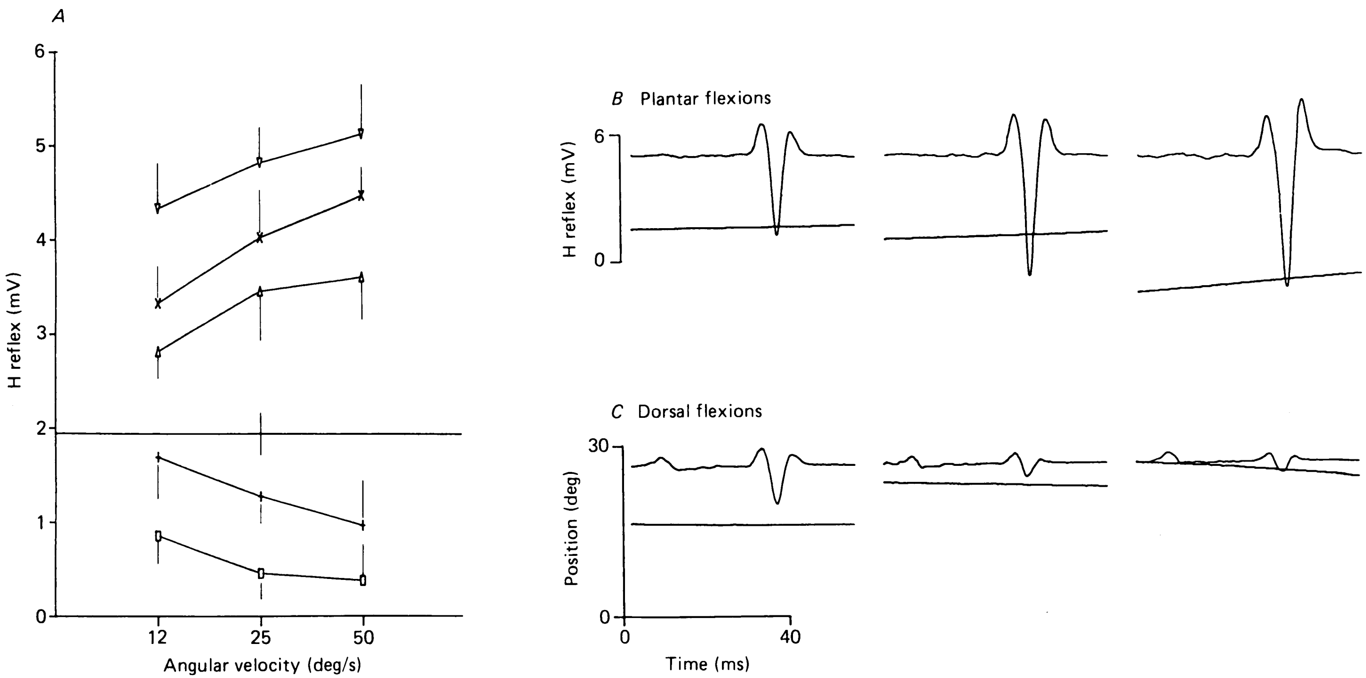

Fig. 6. Effect of the velocity of muscle contraction on the amplitude of the H reflex. In *A* are reported mean values (± standard deviation, S.D.) of reflexes evoked during active plantar (upper curves) or dorsal (lower curves) flexions, at the indicated velocities (each point is the mean of ten measurements, in one subject). The reflex-evoking stimulus was automatically delivered when the integrated e.m.g. reached a predetermined value (□, 1 arbitrary unit (a.u.); + and △, 2 a.u.; X, 3 a.u.; ▽, 4 a.u.). The horizontal line indicates mean (±S.D.) of control H reflexes, evoked at rest at 0 deg of plantar flexion. Depicted in *B* and *C* are computer averages ($n = 5$) of H reflexes and positions obtained during active plantar (*B*) or dorsal (*C*) foot flexions, performed by another subject under the same conditions. (In the case of a.d.f.s, the stimulus strength was increased to yield an H reflex of about two-thirds of its maximal value in order to get measurable responses, as shown by the larger M response.)

The influences connected with the command to perform the required motor tasks, i.e. to gradually contract the muscle to plantarflex, or yield to the dorsiflexing load so as to allow a gradual dorsal flexion at various velocities, are superimposed on the 'passive' effects and contribute to the final attainment of the appropriate changes in the excitability of the reflex arc. These changes in the reflex excitability of the soleus motoneurones accompany the variations in the e.m.g. envelope, which can be used as a measure of the combined number and discharge frequency of muscle fibres that are being employed during the shortening or lengthening soleus contractions (Bigland-Ritchie & Lippold, 1954; Bigland-Ritchie & Woods, 1976). In fact, the higher the e.m.g. level during plantar rotation, the higher the amplitude of the H reflex; likewise, the lesser the e.m.g. during dorsal flexion, the smaller are the reflexes. But, during active plantar flexions, for a *given* e.m.g., the amplitude of the H reflex increases as a function of the velocity of muscle shortening; and, during active dorsal flexions, the amplitude of the H reflex decreases as a function of the velocity of muscle lengthening, notwithstanding the constancy in the level of the background e.m.g. at which the stimulus is delivered. Therefore, these changes in reflex excitability cannot be attributed to the level of descending excitatory drive directed to the motoneurones. A modulation in amplitude of the H reflex has also been observed by Capaday & Stein (1986) during human locomotion, and ascribed to intervention of a central mechanism other than that which modifies motoneurone excitation.

We favour the hypothesis that these changes in reflex excitability, probably of presynaptic origin owing to the striking discrepancy between e.m.g. and H-reflex amplitude, appear appropriate in matching the nervous command to mechanical properties of the muscle. During shortening contractions they increase the central effect of the Ia inputs, allowing soleus muscle to increase its force by recruiting more motor units, just when the force would decrease owing to the decrease in length. In addition, the increase in excitability is very much dependent on the velocity of contraction, other things being equal (e.m.g. and position). This result is congruent with the view that the additional motor units necessary to overcome the mechanical disadvantages connected with the force–velocity relation can be recruited due to an increased efficacy of the excitatory connections between Ia inputs to motoneurones. The results obtained in the case of lengthening contractions can be interpreted according to the same reasoning: when the muscle under contraction would develop greater force owing to its increase in length and to the increase in the lengthening velocity, its reflex excitability becomes progressively less (and much less than the control value at rest), or even negligible, as happens when the muscle's elastic elements are going to take over nearly all the load, or when few active motor units are sufficient to resist the load owing to the high velocity of lengthening. Indirect support to this interpretation comes from previous experiments performed in spastic patients, which supposedly suffer from alteration in presynaptic inhibition (Delwaide, 1985), showing severely hindered muscle relaxation accompanied by absence of H-reflex inhibition (Schieppati, Poloni & Nardone, 1985; Crenna & Frigo, 1985).

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