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SHORT-LATENCY INHIBITION OF SOLEUS MOTONEURONES BY IMPULSES IN Ia AFFERENTS FROM THE GASTROCNEMIUS MUSCLE IN HUMANS

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SUMMARY

1. The possibility that the Ia afferent fibres from the gastrocnemius medialis muscle could be responsible for a decrease in excitability of the soleus motor pool was investigated.

2. The soleus H reflex, evoked by tibial nerve stimulation in the popliteal fossa, was conditioned by a single stimulus to the gastrocnemius medialis nerve at various stimulus intensities and conditioning–test intervals. Care was taken to avoid spread of current from the conditioning stimulus to the tibial nerve, and the results obtained by surface stimulation were compared with those obtained by stimulation through a needle whose tip was positioned closer to the nerve.

3. Stimulation of the gastrocnemius medialis nerve induced two short-lasting periods of inhibition in the soleus H reflex, peaking at about 0 and 5 ms of conditioning–test delay. The early inhibition could begin at a stimulus strength as low as 0·5 × MTh (the Motor Threshold). The later inhibition appeared on greater stimulus strength than the earlier.

4. Prolonged vibration of the Achilles tendon abolished the capability of the conditioning stimulus to induce the short-latency inhibition of the soleus H reflex.

5. By stimulating the gastrocnemius medialis nerve at two points separated by a known distance, the conduction velocity of the fibres responsible for the early inhibition was estimated, and found to be around 100 m s^{-1}.

6. Isometric leg flexion, accomplished by tonic activation of gastrocnemius medialis and lateralis but not soleus, was able to induce an inhibition of the soleus H reflex even at very low levels of gastrocnemius electromyographic activity.

7. These findings strongly suggest the existence of an inhibitory effect of primary spindle afferent fibres from the gastrocnemius medialis muscle onto the soleus motor pool. This is not unexpected, since the gastrocnemius medialis muscle can be either agonist or antagonist to the soleus muscle in the performance of different movements.

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INTRODUCTION

Passive dorsiflexion of the ankle or triceps stretch are known to have an inhibitory effect on the motoneurone pool of the soleus muscle (Mark, Coquery & Paillard, 1968; Delwaide, 1971; Gerilovsky, Gydikov & Radicheva, 1977; Gottlieb & Agarwal, 1978; Robinson, McComas & Belanger, 1982; Burke, Gandevia & McKeon, 1983; Romanò & Schieppati, 1987; see Schieppati, 1987).

The mechanisms subserving this phenomenon have received various explanations, which when viewed retrospectively appear reciprocally contradictory, or in conflict with conclusions from other lines of research. For example, Robinson *et al.* (1982) proposed a role for an autogenetic inhibition mediated by the soleus group II spindle afferent fibres, whereas Matthews (1984) has given evidence for an autogenetic excitatory effect of the same fibres.

As to the functional role of this inhibition, it has been hypothesized that it could play a role in the proper performance of a lengthening muscle contraction by contributing to motor unit derecruitment (Romanò & Schieppati, 1987). In addition, it has recently been shown that during a voluntary triceps surae contraction involving lengthening of the muscle, as occurs when opposing a dorsiflexing load while yielding to it gradually at controlled velocity, the soleus often decreases its activity, whereas the gastrocnemii become active (Nardone & Schieppati, 1988). Incidentally, the shift in activity which occurs between these synergic muscles during the lengthening contraction appears to take place also between different types of motor units, since high-threshold units within each muscle appear to be recruited during that task, at the same time that low-threshold units become silent (Nardone, Romanò & Schieppati, 1989).

The above mentioned facts prompted this investigation, aimed at testing the hypothesis that group I spindle afferent fibres originating from the gastrocnemii are involved in the inhibition of the soleus motor pool. This would explain both the soleus H reflex inhibition induced by the triceps stretch (which obviously induces also stretch of the gastrocnemii) and the decrease in the electromyographic activity of the soleus, which takes place during build-up of activity in the gastrocnemii, when the triceps surae undergoes active lengthening. In fact, in the latter case, it would appear likely that the lengthening of the active gastrocnemii would induce a large Ia afferent fibre discharge.

Fetz, Jankowska, Johannisson & Lipski (1979) demonstrated that adequate stimulation of group Ia muscle spindle afferents in the cat's triceps surae is able to evoke inhibitory postsynaptic potentials in a large proportion of the motoneurones directed to the homonymous muscles; these effects could be evoked also by stretch of the synergistic muscles alone. A recent report by Hayward, Breitbach & Rymer (1988), showing that selective stretch of the gastrocnemius medialis muscle in the cat induces inhibition of soleus tonic contraction, can also be consistent with the above reasoning.

That hypothesis, and the implied neural circuitry, envisages a functional antagonism between gastrocnemii and soleus, which contrasts with the view that both muscles contribute to foot plantar flexion. However, this is not a real contradiction, since functional synergism and functional antagonism may be expressed by the same pair of muscles in different tasks. This view is supported by the different insertions of soleus and gastrocnemii, the one being monoarticular, the other biarticular. For example, while a plantar flexion can be performed by synergic action of both muscles, especially a ballistic one (Nardone & Schieppati, 1988), a withdrawal reflex induced by a painful stimulation of the foot sole is performed through soleus inhibition and activation of both tibialis and gastrocnemii (together with the hamstrings) for foot dorsiflexion and leg flexion, respectively (see Gravel, Arsenault & Lambert, 1987). Some of the preliminary results have been briefly reported (Schieppati & Gritti, 1988).

METHODS

Nine subjects between 21 and 40 years of age participated in this study, which was approved by the local Ethical Committee. All gave informed consent to the experimental procedure. They were seated on an examination chair, the knee and ankle joint angles at 110 and 90 deg, respectively. Surface electrodes, set 2 cm apart, recorded the electromyographic activity (EMG) of the soleus muscle (posteriorly on the lower third of the leg), of the gastrocnemius medialis and lateralis (on the upper third of the leg, in a posteromedial and posterolateral position) and of the pre-tibial muscles (anterolaterally).

One set of stimulating electrodes was placed in the popliteal fossa (cathode) and on the knee (anode) to elicit the H reflex in the soleus muscle through stimulation of the posterior tibial nerve. Care was taken to avoid spread of current to the gastrocnemius medialis, lateralis, or peroneal nerves, (a) by using low stimulus strengths (soleus H reflex was usually kept at 10–20% of its maximum value) and durations (0·2–0·8 ms), (b) by inspecting any direct mechanical or electromyographic response in the gastrocnemius medialis, lateralis or in the pre-tibial muscles and (c) by checking the absence of an H reflex in the pre-tibial muscles at rest and during tonic or phasic voluntary dorsiflexion of the foot (a small H reflex in the gastrocnemius medialis muscle was present in some experiments).

The nerve to the gastrocnemius medialis muscle was stimulated by a bipolar electrode (distance between leads 2 cm) placed on the course of the nerve, identified as the line joining the points from which a direct motor response in the muscle was obtained by minimum current strength. In most cases the electrode was spaced 8–10 cm distally from that in the popliteal fossa. The same electrode could be displaced a known distance further distally with the aim of identifying the conduction velocity of the fibres responsible for the effects (see below). The stimulus strength (duration 0·2–0·6 ms) ranged between 0·4 and 1·1 times the motor threshold (× MTh) for the gastrocnemius medialis muscle. As a test that nerve stimulation affected Ia fibres, the appearance of an H reflex in the gastrocnemius medialis on voluntary tonic or phasic contraction of the gastrocnemii was carefully inspected, and the stimulating electrodes were moved some short distance about the chosen point in order to get the largest reflex response. During gastrocnemius medialis nerve stimulation, care was taken to avoid spread of current to the posterior tibial nerve, (a) by inspecting any direct response in the soleus muscles, (b) by checking the absence of a soleus H reflex on tonic or phasic plantarflexion of the foot and (c) by progressively increasing the stimulus strength in order to discover the value at which a direct or reflex response in the soleus muscle could be evoked. If this value was judged to be too close to that used for the conditioning stimuli (i.e. less than 2 times the gastrocnemius medialis motor threshold), another stimulating point was chosen and the procedure repeated.

These procedures did not appear to be completely free of artifacts. In the first experiments of this series, in fact, it turned out that, in the same subject and in different experimental sessions, the effect of conditioning could occasionally be markedly different. Figure 1*A* shows that the inhibition of the soleus H reflex was very large when the conditioning and test stimuli were overlapping in time (left bars), while it levelled off to about 20% of the control values when the stimulus duration was less, so that they did not encroach upon each other, even when given at the same interval as before (right bars). It is worth noting that, when the H reflex was markedly depressed, the M response was also affected by the conditioning stimulation, as if the stimulus

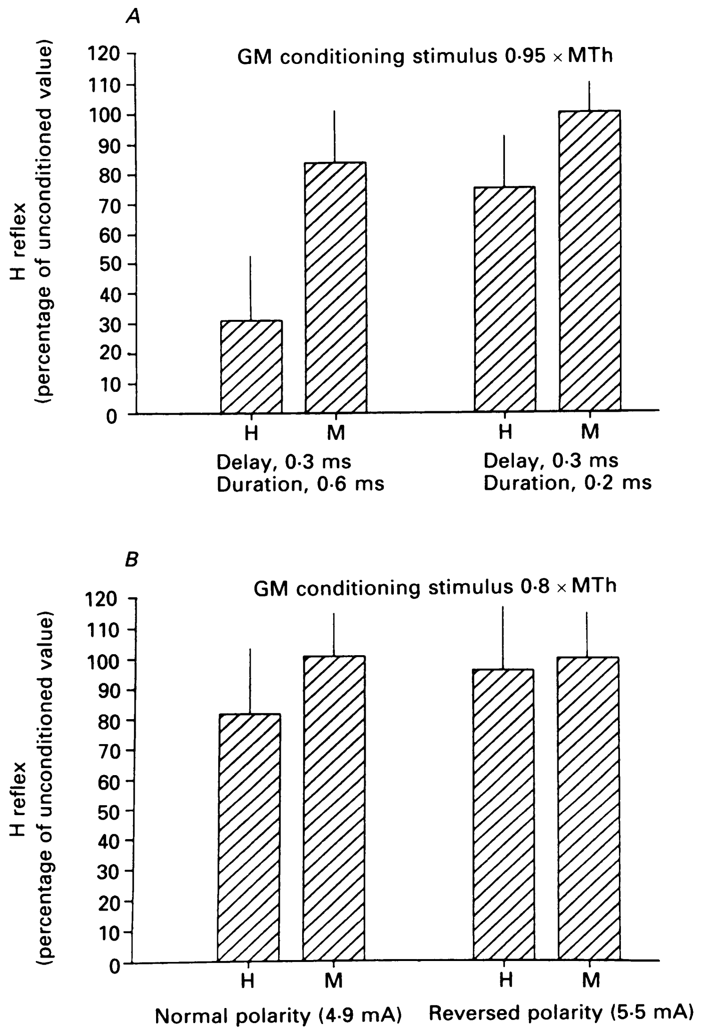

Fig. 1. *A*, left: the amplitude of the soleus H reflex, conditioned by stimulation of the nerve to the gastrocnemius medialis (GM) at 0·3 ms of delay, is decreased to 30% of its control value, and the corresponding 'conditioned' M response is also decreased, as if the stimulus strength had been diminished (the effect of the conditioning stimulus was tested on an M response of an amplitude equal to that of the H reflex). Under this condition, the GM conditioning (0·95 × MTh) and the soleus test stimuli were overlapping in part, since their duration was longer than the interstimulus interval. The distance between the site of conditioning stimulus along the GM nerve and the test stimulus along the tibial nerve in the popliteal fossa was 8·5 cm. Right: a case is shown in which the stimuli, although very close to each other (same interstimulus interval as above), were not overlapping. The M response was not altered, while the soleus H reflex inhibition was reduced to 75% of the control value. *B*, changes in the inhibitory effect, induced by the GM conditioning stimulation, on changing the polarity of the conditioning bipolar stimulus (distance between the two leads, 2 cm). Same subject and stimulation points as in *A*. In this case, the delay between the stimuli was −0·5 ms (i.e. soleus first) and the duration of both stimuli was 0·4 ms. Under 'normal' conditions, corresponding to the largest inhibition of soleus H reflex, the stimulus strength to reach GM motor threshold was lower than under 'reverse' conditions, and therefore the conditioning current spread was presumably less. All bars are averages of thirty responses ± S.D.

strength would be diminished. This effect cannot be explained by any known biological phenomenon, as it is probably connected to some devious path travelled by the stimulating current under conditions in which the two currents coincide in time. Therefore, the duration of the stimuli was always kept very short, and, when any risk of current spread was present (i.e. at very short conditioning–test intervals) the following procedure was adopted. The posterior tibial nerve was first stimulated at an intensity high enough to yield a small M response in the soleus muscle (of the same magnitude as the H reflex employed as control). The stimulus to the gastrocnemius medialis nerve was then given and the amplitude of the 'conditioned' soleus M response was monitored. The experiment was continued only if no changes in the soleus M response were induced by the gastrocnemius medialis stimulation.

Figure 1*B* shows that even the polarity of the conditioning stimulation was not irrelevant to the induced effect. The two bars on the left correspond to the effects obtained under 'normal' conditions, i.e. with cathode proximal, on both H reflex and M response. On the right are shown the effects observed by reversing the polarity and adjusting the stimulus strength to maintain its intensity constant in relation to that necessary to yield the gastrocnemius medialis motor response. In this case, the induced inhibition of the soleus H reflex is negligible, and can sometimes be turned into facilitation. We feel that this can be due to a spread of the conditioning current to the tibial nerve and therefore to the activation of some soleus Ia fibres, since, whenever this behaviour was observed, the absolute intensity of the current necessary to reach motor threshold was higher. Therefore, we always also checked that the polarity of the conditioning stimulus was such as to evoked a direct motor response in the gastrocnemius medialis muscle at the minimum possible current strength.

In the two authors, the conditioning stimulation to the gastrocnemius medialis nerve was also delivered by means of a co-axial needle electrode, inserted into the muscle for 2–3 cm, close to a point which, on surface stimulation, gave an M response in the gastrocnemius medialis itself. It was also checked that, on slight voluntary innervation of the muscle, the needle stimulation was able to induce a gastrocnemius medialis H reflex on appropriate stimulus strength.

The effect of gastrocnemii voluntary activation on the soleus H reflex was tested in two subjects, by asking them to perform a tonic isometric flexion of the leg against a strain gauge positioned behind the heel. Under this condition, no electromyographic activity was recorded from the soleus muscle. The subjects were provided with both the signal of the force and of the rectified and integrated gastrocnemius medialis EMG (time constant, 100 ms) on an oscilloscope screen, in order to obtain tonic contractions of constant amplitudes. The stimulus strength to the tibial nerve in the popliteal fossa had to be continuously controlled owing to the possible displacement of the electrode connected to the contraction of the leg flexor muscles. To this aim, the stimulating electrode was positioned in such a way as to yield both an H reflex and an M response in the soleus at rest. Then, during contractions of different extent, the stimulus strength was adjusted when necessary to give a constant M wave.

In order to test the hypothesis that the soleus H reflex inhibition in response to the gastrocnemius medialis nerve stimulation was due to activation of Ia fibres, we repeated the conditioning–test procedure (at a conditioning–test interval of 0 ms) in two subjects prior to and after 25 min of vibration applied to the Achilles tendon. The rationale was that prolonged vibration would have produced a depression of excitability of the Ia fibres on electrical stimulation (Coppin, Jack & MacLennan, 1970; Jankowska & McCrea, 1983; Heckman, Condon, Hutton & Enoka, 1984; Hayward, Nielsen, Heckman & Hutton, 1986; Cavallari, 1988), therefore depressing or abolishing any Ia-mediated inhibition. The vibrator used was a Brüel and Kiaer 4809, evoking a displacement (unloaded) of 2 mm, at a frequency of 80 Hz. During vibration, the soleus H reflex was markedly depressed, or unexcitable, even if a full-blown tonic vibration reflex was not consistently evoked, and the subjects perceived dorsiflexion of the foot (Goodwin, McCloskey & Matthews, 1972).

In each experimental run, soleus H reflexes were evoked at a fixed frequency (ranging in different sessions from 0·1 to 0·15 Hz) throughout the session, since this procedure proved capable of minimizing the variations in the control reflexes. The conditioning stimulation was presented in a pseudorandom manner, with twenty to thirty unconditioned and conditioned H reflexes collected for statistical analysis under each condition. The difference between the amplitudes of conditioned and control reflexes were evaluated by means of Student's t test ($P < 0{\cdot}05$). The conditioning–test interval ranged from -2 to 10 ms (negative values mean that the conditioning stimulus was delivered after the test stimulus).

RESULTS

Time course of the effects of gastrocnemius medialis nerve stimulation on the soleus H reflex

In all the subjects a clear-cut inhibitory effect was induced on the soleus H reflex by the percutaneous stimulation of the nerve to the gastrocnemius medialis, at a stimulus strength below the motor threshold. This inhibitory effect was significant in most subjects at a conditioning–test interval of −0·5 ms (soleus stimulus first), peaked at about 0 ms and had a total duration of less than 2 ms. In most subjects, a second period of inhibition was evident, albeit of a lesser magnitude (the inhibition was statistically significant only in three subjects), and prominent at about 4–7 ms of conditioning–test interval. Before, after and between these two periods, the conditioned soleus H reflex recovered to control values. This is illustrated in Fig. 2*B*, obtained by pooling and averaging the data from all the subjects, which shows the time course of the soleus H reflex inhibition on stimulation of the nerve to the gastrocnemius medialis at 0·8 × MTh. The grand mean of the conditioned reflexes is significantly smaller than the control reflexes at the intervals from −0·5 to +0·5 ms and from 5 to 6 ms. In Fig. 2*A*, the recording of conditioned and test soleus H reflexes and the gastrocnemius medialis EMG are reported, as obtained in one representative subject.

Both inhibitory effects are not due to stimulation of cutaneous fibres, since shift of the stimulating electrodes to nearby positions abolished the effects on the soleus H reflex, in spite of comparable cutaneous sensation. Also, effects on the H reflex have never been demonstrated on stimulation of cutaneous fibres, originating in the leg or foot, at conditioning–test intervals as short as those used here (see Schieppati, 1987).

Effect of changing stimulus strength

The intensity of the conditioning stimulus to the gastrocnemius medialis nerve was systematically changed in four subjects in order to identify the minimum strength necessary to induce the inhibitory effects in the soleus H reflex, at both conditioning–test intervals of 0 and 5 ms. Significant decreases in the amplitude of the soleus H reflex, at the conditioning–test interval of 0 ms, were obtained at 0·5, 0·6 and 0·7 × MTh in the various subjects. The pooled results are illustrated in Fig. 3. When the conditioning–test interval was 5 ms, however, stimulus strengths from 0·8 to 1·0 × MTh were necessary in order to induce a significant inhibition in the various subjects. There is also a suggestion that the inhibition peaking at 5 ms levels off at high intensity, while the 0 ms inhibition steadily increases on increasing stimulus strength.

Needle stimulation

The results obtained by using needle stimulation are quite consistent with those described above. Figure 4 shows the data obtained in two subjects by using a conditioning stimulus strength to the gastrocnemius medialis nerve of 0·8 × MTh (corresponding to a much lower absolute value of current than that delivered by surface stimulation). Both the duration and the maximum value of the inhibitory

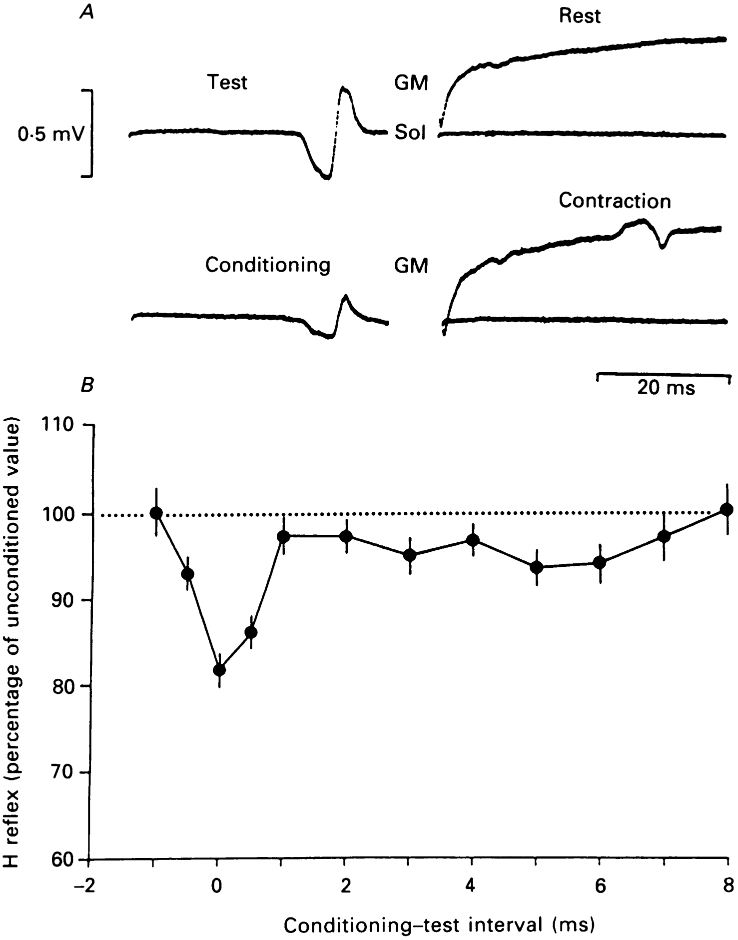

Fig. 2. *A*, left: example of decrease of amplitude of the soleus (Sol) H reflex upon conditioning stimulation of the gastrocnemius medialis (GM) nerve (0 ms delay, 1·05 × MTh). Right: recordings from soleus and GM muscles on stimulation of the GM nerve alone; the appearance of a small H reflex in the GM muscle, and only in this muscle, during slight voluntary contraction of the triceps surae is a guarantee that the GM Ia fibre was selectively activated by the conditioning stimulus. *B*, time course of the effects induced by the GM conditioning stimulus (intensity 0·8 × MTh, duration 0·25–0·6 ms in the various subjects, distance from popliteal fossa 8·5–9·5 cm) on the soleus H reflex (15 % of maximum H reflex). Data are grand means ± S.E.M. of the pooled data from all subjects. Two periods of inhibition are evident, around 0 and 5 ms of conditioning–test delay. The conditioned reflexes at −0·5, 0, 0·5, 5 and 6 ms were significantly different from their respective controls (pooled data, $P < 0\cdot05$).

effect are comparable to those induced by surface stimulation. The amplitude of the M response in the soleus was never affected by that type of stimulation. Again, inhibitory effects were already present in those two subjects at 0·5 × MTh (not shown). The different onset latency of the inhibitory effects in the two subjects might be related to the different distance between the points of application of the conditioning and test stimulus and/or to a difference in the conduction velocity of the fibres.

Effects of vibration

Vibration of the Achilles tendon was employed with the aim of ascertaining the role of the Ia fibres in the short-latency inhibition produced in the soleus motor pool excitability on stimulation of the nerve to the gastrocnemius medialis. It was in fact demonstrated previously that the electrical threshold of soleus muscle spindle Ia afferent fibres is raised by prolonged tendon vibration (see Methods). We therefore reasoned that tendon vibration would have raised the threshold of both the soleus and gastrocnemius nerve Ia fibres, since both muscles attach to the same tendon. Figure 5 shows that indeed the soleus H reflex inhibition disappeared after a vibration period of 25 min, to gradually return to control value, with a time course compatible with that described for the electrical excitability of the soleus Ia fibres (Heckman *et al.* 1984). It must be mentioned here that the H reflexes subjected to conditioning by gastrocnemius nerve stimulation were of the same absolute amplitude as the pre-vibration ones, since the tibial nerve stimulus strength (but *not* that of the gastrocnemius nerve) was appropriately increased (to about 1·2–1·3 times its original intensity) to overcome the post-vibration effects.

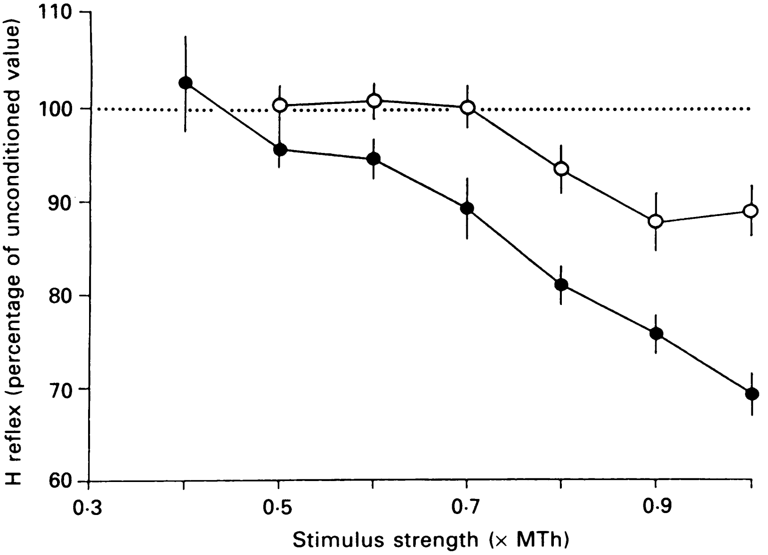

Fig. 3. Effects of increasing gastrocnemius medialis conditioning stimulus strength (duration 0·4 ms, mean distance from the popliteal fossa 10·5 cm) on the soleus H reflex (14% of maximum H reflex) at two delays (0 and 5 ms). Data are grand means ± S.E.M. of the pooled data from four subjects. The stimulus strength necessary to yield the same inhibition of the soleus H reflex at 5 ms delay, ○, was higher than that at 0 ms, ●. The conditioned reflexes were significantly different from their controls (pooled data, $P < 0{\cdot}05$) at and beyond 0·6 and 0·8 x MTh, at 0 and 5 ms interstimulus delay respectively.

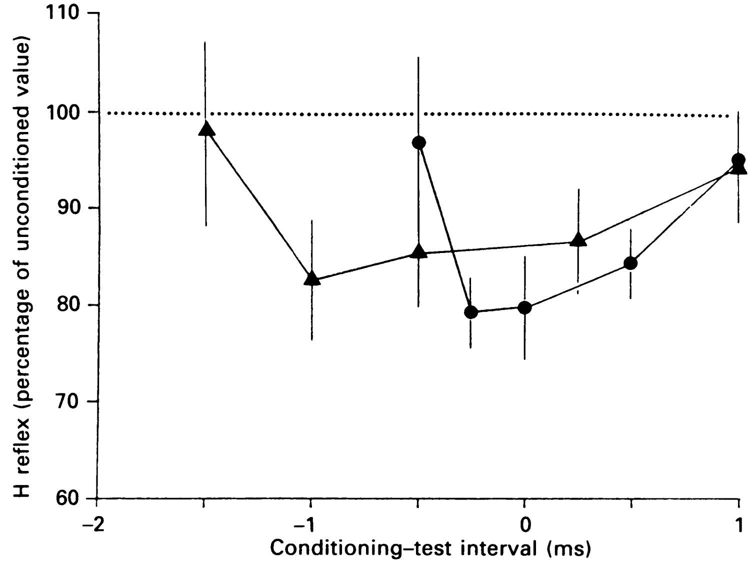

Fig. 4. Time course of the effects induced on the soleus H reflex in two subjects by needle stimulation of the gastrocnemius medialis (GM) nerve (intensity 0·8 × MTh, duration 0·35 ms; distance from popliteal fossa 11·5 cm, ●, and 9·5 cm, ▲. All the conditioned reflexes were significantly different from their respective controls ($P < 0.05$), except those evoked at −1·5, 0·5 (circle only) and 1 ms interstimulus delay. The data points are means ± S.D. of eighteen to forty-two reflexes.

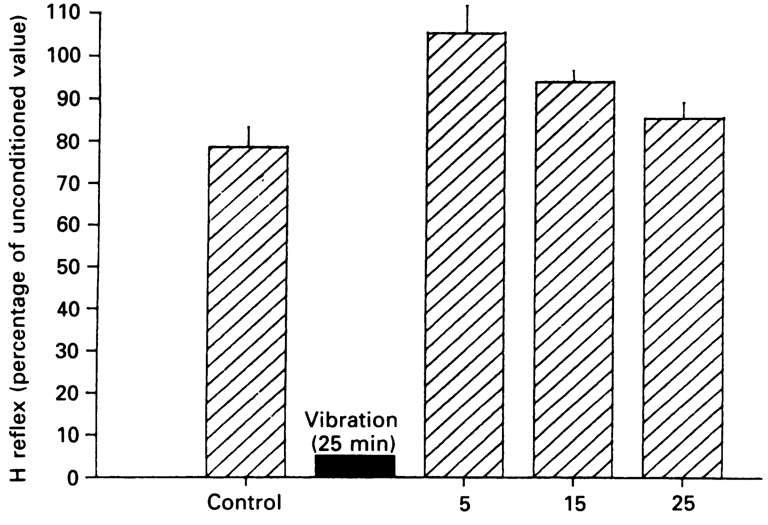

Fig. 5. Effects of prolonged vibration (25 min) of the Achilles tendon on the soleus H reflex inhibition induced by stimulation of GM nerve (0·8 × MTh, duration 0·3 ms, interstimulus delay 0 ms). The data are grand means ± S.E.M. of the pooled data from two subjects. While the strength of the stimulus to the tibial nerve was increased to overcome the decrease in the excitability of the Ia fibres, that of the conditioning stimulus to the GM nerve was not. The conditioned reflexes are significantly decreased by GM stimulation ($P < 0.05$) only prior to (control) and 25 min following vibration.

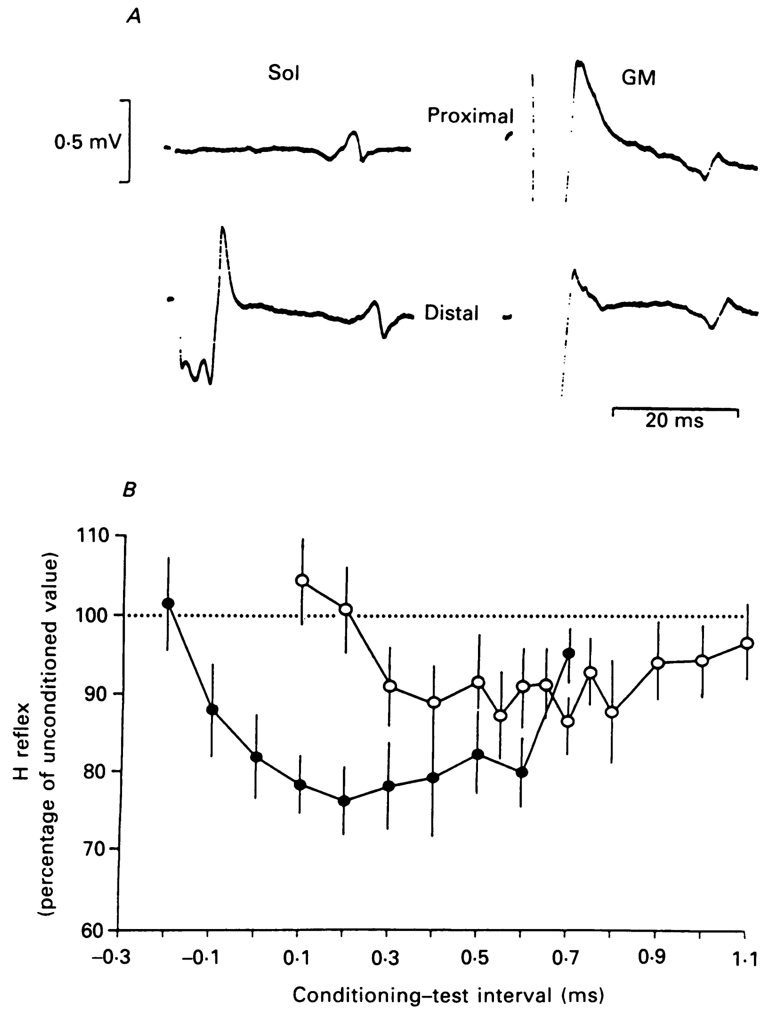

Fig. 6. *A*. left: soleus (Sol) H reflexes upon stimulation of the tibial nerve in the popliteal fossa (proximal) and of the inferior soleus nerve (distal). The distance between the two stimulating points was 23 cm. Right: gastrocnemius medialis (GM) H reflexes upon stimulation of the GM nerve at a distance of 5 cm (proximal) and 14·3 cm (distal) from the popliteal fossa. The GM H reflexes were obtained during slight voluntary contraction of the same muscle. *B*, time course of soleus H reflex inhibition upon conditioning GM stimulation (intensity 0·8 × MTh, duration 0·6 ms) delivered in two points along the GM nerve at 5·6 (●) and 11·6 cm (○) from the popliteal fossa. Each point is the mean ± S.D. of twenty to forty repetitions.

Conduction velocity of the fibres responsible for the inhibition

In one subject, the conduction velocity of the fibres responsible for the inhibitory effect was estimated by measuring the delay between the peaks of inhibition obtained when stimulating on two points along the gastrocnemius medialis nerve, spaced a known distance apart. Figure 6*B* shows the results obtained when the stimulus strength was 0·8 × MTh and the distance along the skin between the stimulating points was 6 cm. Within the (broad) limits represented by the shortest unit of conditioning–test interval (0·1 ms), the delay between the peak effects is 0·5 ms. This leads to a conduction velocity of 120 m s^{-1}. This value must be considered only indicative, since the true length of the nerve is unknown and probably shorter than the shortest distance between the two points on the skin. In addition, there is no guarantee that the current did not activate the nerve somewhat more proximally than the position of the distal electrode, since in this region of the leg the nerve can be rather deep-seated.

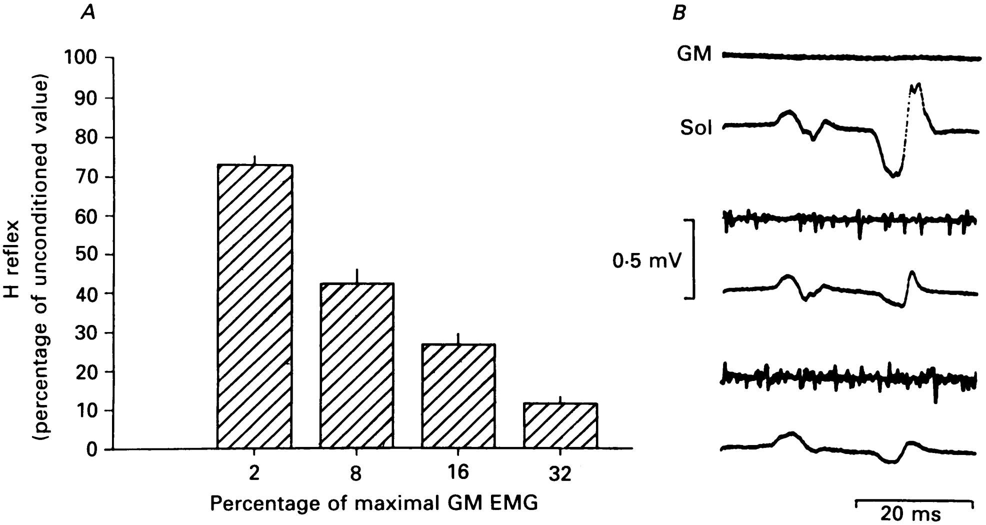

Fig. 7. Effects of contractions of different strengths of the gastrocnemius medialis (GM) muscle upon soleus (Sol) H reflex. Selective contraction of the GM muscle was obtained by voluntary isometric flexion effort of the leg. The soleus and pre-tibial muscle EMG remained silent during this manoeuvre. *A*, increase in soleus H reflex inhibition is proportional to the level of GM EMG. Bars are grand means ± S.E.M. of the pooled data from two subjects. *B*, examples of soleus H reflex conditioned by GM contractions of increasing amplitude (from top to bottom).

In another subject, a clear cut H reflex in the gastrocnemius medialis was obtainable on stimulation of its nerve, during slight tonic contraction of the same muscle (under oscilloscope control of the rectified and integrated EMG). Therefore, the presumed conduction velocity of the gastrocnemius medialis Ia fibres was measured from the shift in latency of the H reflexes (of equal amplitude) occurring on displacement of the stimulating electrodes to a known distance. Examples of the gastrocnemius medialis H reflexes, evoked by stimuli delivered to two points separated by 9·3 cm, are reported in Fig. 6*A*, right panel. The calculated conduction velocity of the fastest Ia fibres in the gastrocnemius medialis was on average 95 m s^{-1}. The same procedure was repeated in the same subject for the soleus H reflex (left panel), by stimulating in the popliteal fossa or at the level of the inferior soleus nerve (23 cm distally). The calculated conduction velocity of the soleus Ia fibres was then 76 m s^{-1}.

Effects of gastrocnemius medialis contraction on the soleus H reflex

Voluntary tonic contraction of the gastrocnemius medialis muscle, without concomitant activation of the soleus, was able to induce clear-cut inhibition of the soleus H reflex in the three subjects in which it was tested. This effect was already present at a very slight level of force, and steadily increased as a function of the gastrocnemius medialis voluntary innervation, as shown in Fig. 7.

DISCUSSION

Stimulation of the nerve to the gastrocnemius medialis muscle consistently induces in the soleus H reflex two periods of short-latency, short-lasting inhibition. The first peak occurs at about 0 ms, the second at about 5 ms of conditioning–test interval. Apart from the onset and peak latency, they differ in further aspects: (i) the first is evoked by stimulus strengths as low as 0·5 × MTh, the second by stimulus strengths larger than 0·8 × MTh and (ii) the first inhibition is stronger than the second, and increases on increasing stimulus strength up to 1 × MTh, while the second does not reduce the test reflex to more than 90% of the control value on average.

The first inhibition is induced by activation of nerve fibres having a high excitability on electrical stimulation, and a high velocity of conduction, whose estimated value was close to, or greater than, 100 m s^{-1}. Such characteristics can be confidently attributed to Ia fibres in the gastrocnemius medialis nerve. This conclusion is strengthened by the observation of a complete disappearance of the inhibitory effect after a prolonged period of tendon vibration, known to increase the threshold of electrical excitability of the Ia fibres; these inhibitory effects did not fully reappear within 25 min from the end of the vibration, in accord with the time course of recovery of the excitability of the Ia fibres (Hayward *et al.* 1986). The very high velocity of the fibres responsible for the effect can well explain the finding of an inhibition of the soleus H reflex even when the stimulus to the gastrocnemius medialis nerve is delivered 0·5–1 ms after that to the posterior tibial nerve, in spite of the former being positioned some 10 cm distally to the latter. In fact, the conduction velocity of the Ia fibres in the soleus nerve proved to be slower than 80 m s^{-1}. The difference in excitability and conduction velocity of Ia fibres between gastrocnemius medialis and soleus nerve are consistent with the data gathered in the cat by Hunt (1955), who found an average maximal velocity of 101·8 and 118·4 m s^{-1} for the soleus and gastrocnemius medialis Ia fibres, respectively. This relative slowness would then allow the impulses in the gastrocnemius medialis Ia fibres to reach the responsible inhibitory spinal interneurones, along a di- or trisynaptic pathway (Fetz *et al.* 1979; Harrison & Jankowska, 1985), in time to induce an inhibition in the soleus motor pool prior to arrival of the homonymous excitatory Ia volley.

The characteristics of the second period of inhibition of the soleus H reflex allow us to attribute it to the activation of the Ib fibres in the gastrocnemius medialis nerve, on the basis of the results obtained by Pierrot-Deseilligny, Morin, Bergego & Tankov (1981) and Fournier, Katz & Pierrot-Deseilligny (1984). Pierrot-Deseilligny *et al.* (1981) did not describe in detail the first component of inhibition. The earliest interval at which their conditioning effects were measured was 0·5 ms, at which delay a small inhibition indeed occurred (probably the tail of the effect described here). The above authors may have chosen not to investigate earlier intervals owing to the artifacts which are likely to occur when the conditioning and test stimuli overlap in time (see Methods).

In humans, the effects of the stimulation of the gastrocnemius medialis nerve fibres on the soleus motor pool were also investigated some time ago by Bouaziz, Bouaziz & Hugon (1975). They found that stimulation of the gastrocnemius medialis nerve above motor threshold induced a silent period in the EMG of the soleus muscle under voluntary tonic activation, as early as 35 ms after the stimulus; this phenomenon had a counterpart in the inhibition of the soleus H reflex when it was conditioned by the same stimulation to the gastrocnemius medialis nerve at conditioning–test intervals as short as 0 ms (Bouaziz, Bouaziz & Hugon, 1971). They attributed this inhibition to the combined action of the Ib fibres from the tendon organs and of Renshaw recurrent inhibition (Bouaziz *et al.* 1975). During a study on the synaptic connections from large muscle afferents to the motoneurones of various leg muscles in man, Mao, Ashby, Wang & McCrea (1984) also found occasionally an inhibitory effect in the discharge of soleus motoneurones, voluntarily activated, during stimulation of low-threshold afferents in the medial gastrocnemius nerve. This effect was attributed to stimulation of Ib or group II fibres since it appeared at more than 0·9 × MTh; they saw no inhibition at lower stimulus strength, possibly since tonic voluntary activation of the soleus muscle decreased the excitability of the relevant inhibitory interneurones. Recently, Kudina & Pantseva (1988) found that the tonic discharge of single motor units in the soleus muscle was depressed by stimulation above motor threshold of the posterior tibial nerve in the popliteal fossa. On the assumption that their stimulus did not activate Ia fibres, since no H reflex was evoked in the soleus muscle, they proposed a role for recurrent inhibition.

As for the lack of excitatory Ia effects from gastrocnemius medialis to soleus in humans, it had also been reported by all the above-mentioned authors; this phenomenon has been connected with species differences (facilitation is present in the cat, as reported by Eccles, Eccles & Lundberg, 1957) and discussed by Mao *et al.* (1984) and Pierrot-Deseilligny (1985).

While our data are not contrary to the possibility that Ib or group II fibres in the gastrocnemius medialis nerve and Renshaw cells associated with the gastrocnemius medialis motor pool can inhibit soleus motoneurones, we want to emphasize that very low stimulus strengths, as low as 0·5 times the motor threshold in some subjects, were enough to induce clear-cut inhibition of the soleus motoneurones, and that the inhibition was certainly mediated by very fast fibres. This fact leads to some considerations connected with the use of the technique for evoking the H reflex in the soleus by stimulation of the posterior tibial nerve in the popliteal fossa. In fact, owing to the high excitability and conduction velocity of the Ia fibres from the gastrocnemius medialis muscle, the possibility cannot be excluded that the response of the soleus motor pool is the result of monosynaptic excitation *and* inhibition from the 'synergist' muscle. This would become more relevant (i) the larger the strength of the stimulus to the tibial nerve (as for instance that necessary in the procedure used for testing the recurrent inhibition induced by a previous H reflex stimulus, see Pierrot-Deseilligny, Katz & Hultborn, 1983) and (ii) the more distal the stimulation site in the popliteal fossa, since the higher conduction velocity of the gastrocnemius medialis Ia fibres would gain them a significant advantage over those of the soleus, the longer the path to be travelled up to the spinal cord. These considerations acquire importance in the light of the contribution of oligosynaptic excitatory pathways to the H reflex (Burke, Gandevia & McKeon, 1984), since the inhibition described here could actually cut off the last part of the H reflex, i.e. that sustained by those pathways.

The inhibition of the soleus H reflex observed during voluntary and selective tonic contraction (even a very slight one) of the gastrocnemius medialis muscle also suggests that its Ia fibres, activated in large numbers by the γ-motoneurones during the voluntary effort, are inhibitory to the soleus motor pool. Further, the large amplitude of this inhibition would suggest a summation at a pre-motoneuronal level of the effects of the Ia fibres with those of the Ib from the tendon organs (gastrocnemius Renshaw cells, able to inhibit soleus motoneurones, should be activated to a limited extent by such contractions). Clearly, this result does not allow one to deduce convergence of the two pathways onto common interneurones, whose existence has been demonstrated in the cat (Jankowska, Johannisson & Lipski, 1981). In fact, although the two phases of H reflex inhibition, obtained at rest on appropriate stimulus strength to the gastrocnemius nerve could be interpreted to result from the successive stimulation of the same interneurones at different times for different Ia and Ib conduction velocities, they may equally represent different involved interneurones, or one or more synapses for the second phase.

If voluntary contraction or stretch of the triceps surae muscle is adequate to activate Ia afferent fibres, which is reasonable enough, then what is the meaning of the opposite effect (autogenetic excitatory, and inhibitory from the synergists) of the Ia inflow to the soleus motor pool? It is probably a matter of the motor behaviour at hand. During stance and therefore when minor changes in length of the triceps surae take place, the high level of autogenetic excitability of the soleus motor pool may well overcome any inhibition coming from the gastrocnemius Ia fibres (Nardone, Giordano, Corrà & Schieppati, 1989). However, during active lengthening of the triceps surae, as when gradually yielding to a dorsiflexing load, the silencing of the soleus (Nardone & Schieppati, 1988) might be due to, among other things (Romanò & Schieppati, 1987), inhibition coming from the gastrocnemius, which is active during the task. Co-activation of the gastrocnemius may also explain why the soleus H reflex shows inconsistent increase in amplitude during voluntary isometric triceps surae contraction (see Gottlieb, Agarwal & Stark, 1970). Further, both muscles are active during a fast plantar flexion of the foot, and when the speed of the movement is increased under constant load (Duchateau, Le Bozec & Hainaut, 1986) the relative contribution of the soleus decreases, at a time when the gastrocnemius medialis plays a dominant role. Therefore, the most important reflex effect of the Ia fibres from the gastrocnemius in man could be inhibition of the soleus motor pool, rather than its excitation.

It is tempting on the basis of these and of recent results mentioned in the Introduction (Nardone *et al.* 1989) to extend the notion of soleus motor pool inhibition through gastrocnemius Ia activation to that of inhibition of the low-threshold, slow-twitch motor units, present in either muscle. If so, the mechanism described here would be one of those responsible for the selection of appropriate motor units during motor behaviour.

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