

GATING OF THE AFFERENT VOLLEY OF THE MONOSYNAPTIC STRETCH REFLEX DURING MOVEMENT IN MAN

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SUMMARY

1. The time course of the changes in presynaptic inhibition of Ia fibres to soleus motoneurons has been investigated during a voluntary ramp-and-hold plantar flexion.

2. Monosynaptic Ia facilitation of the soleus H reflex was evoked by stimulation of the inferior soleus (homonymous) and femoral (heteronymous) nerves. Changes in presynaptic inhibition of the Ia fibres mediating the conditioning volleys were inferred from changes in the amount of reflex facilitation evoked by such constant conditioning stimulations.

3. At the beginning of the voluntary contraction, both homonymous and heteronymous Ia facilitations were markedly increased with respect to their rest values. Then, they dropped abruptly in the middle of the ramp, whatever the ramp duration.

4. The stronger the contraction at the end of the ramp, the larger the initial increase in reflex facilitation.

5. These results indicate that presynaptic inhibition of Ia terminals on motoneurons of the contracting muscle is decreased during the first half of the ramp and then returns to its rest level. It is argued that these changes in presynaptic inhibition are centrally programmed, and it is suggested that, under certain conditions, presynaptic inhibition can be modulated according to both the strength and timing of the contraction.

6. The functional role of the resulting changes in the gain of the stretch reflex is discussed.

INTRODUCTION

The monosynaptic stretch reflex has often been regarded as a system for the servo-control of limb position, but its low gain during steady contraction (Matthews, 1972) has led to questioning of its functional importance (Gottlieb & Agarwal, 1980). However, this gain may change during the course of a movement (Rack, 1981), as various mechanisms modulate it. One of them is presynaptic inhibition of Ia

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terminals which can substantially modulate the efficiency of the afferent volley of the stretch reflex in facilitating motoneurons (Eccles, 1964).

Using a recently developed method to study presynaptic inhibition of Ia fibres in man (Hultborn, Meunier, Morin & Pierrot-Deseilligny, 1987*a*), it has been shown that at the onset of voluntary contraction presynaptic inhibition is markedly decreased on Ia afferents projecting to voluntarily activated motoneurons (Hultborn, Meunier, Pierrot-Deseilligny & Shindo, 1987*b*). This would probably lead to an increase in the gain of the monosynaptic stretch reflex which might be of functional importance. However, a stretch reflex with a high gain for a prolonged period (as any negative feedback system) would be likely to break into oscillations (Matthews, 1972; Rack, 1981). The present study was therefore undertaken to investigate the time course of the changes in presynaptic inhibition of Ia terminals during ramp-and-hold isometric voluntary contractions. Some of the results presented here have been published in abstract form (Meunier & Pierrot-Deseilligny, 1988).

METHODS

General experimental arrangement

The experiments were carried out on seven healthy subjects aged 27–53 years, all of whom gave informed consent to the procedure. They were tested several times in order to ensure the reproducibility of the results. Experiments with ischaemia of the leg (see Results section) were only performed on the two authors.

The subjects were seated in a comfortable armchair with the hip semi-flexed (120 deg), the knee slightly flexed (160 deg) and the ankle 100 deg on the examined side. Presynaptic inhibition of Ia terminals was assessed at rest and during a ramp-and-hold voluntary isometric plantar flexion of the foot. The foot was attached to a torque meter and the torque was displayed on an oscilloscope placed in front of the subject. The torque was expressed as a percentage of that obtained during the maximum tonic plantar flexion that was possible to maintain for about 20 s.

The subject initiated the contraction after an acoustic start signal presented every 4 s. The first (rectified) electromyogram (EMG) signal triggered the oscilloscope, and the subjects were asked to perform contractions which caused the torque to follow a line drawn on the oscilloscope screen. The conditioning and test stimuli were pre-set in relation to the EMG onset. If the developed torque deviated significantly from the prescribed ramp or if stimuli were not triggered by the first EMG potential, it was possible to discard that particular trial.

Method of assessing presynaptic inhibition of Ia fibres

Principle of the method. The recently developed method of estimating presynaptic inhibition of heteronymous Ia fibres from quadriceps to soleus motoneurons (Hultborn *et al.* 1987*a*) was used (Fig. 1*A*). It is based upon the measurement of the soleus H reflex facilitation produced by femoral nerve stimulation. During its first half-millisecond this monosynaptic Ia facilitation is not yet contaminated by any non-monosynaptic effect. Thus we first established the earliest conditioning-test interval at which it was possible to elicit this facilitation, using steps of 0.1 ms; the interval then chosen was 0.2–0.4 ms longer (Fig. 1*B*). Under these conditions the reflex facilitation depends only on the size of the conditioning excitatory postsynaptic potential (EPSP). A constant conditioning stimulation should elicit an EPSP of constant size in motoneurons, and thus a constant reflex facilitation, unless the amount of presynaptic inhibition of Ia fibres is changing: the smaller the presynaptic inhibition, the larger the reflex facilitation.

A similar method was used to estimate changes in presynaptic inhibition of homonymous Ia fibres. The conditioning stimulation was applied to the inferior soleus nerve and the resulting facilitation was assessed during its first half-millisecond (Fig. 1*C*), when the monosynaptic Ia excitation has been shown to be uncontaminated by Ib effects (Pierrot-Deseilligny, Morin, Bergego & Tankov, 1981).

Stimulation and recording. Surface electrodes were used both for stimulation and recording. The

stimuli were 0.5 ms rectangular pulses delivered from constant-current stimulators. The stimulus intensity, which was measured by a current probe (Tektronix 6021), is expressed in multiples of the threshold intensity for the M wave (\times motor threshold: \times MT). The surface EMG was recorded from pairs of non-polarizable disc (0.9 cm diameter) electrodes placed 1 cm apart over the distal third of the soleus (approximately 10 cm above the calcaneus) and over the vasto-crureus (6–8 cm above the patella).

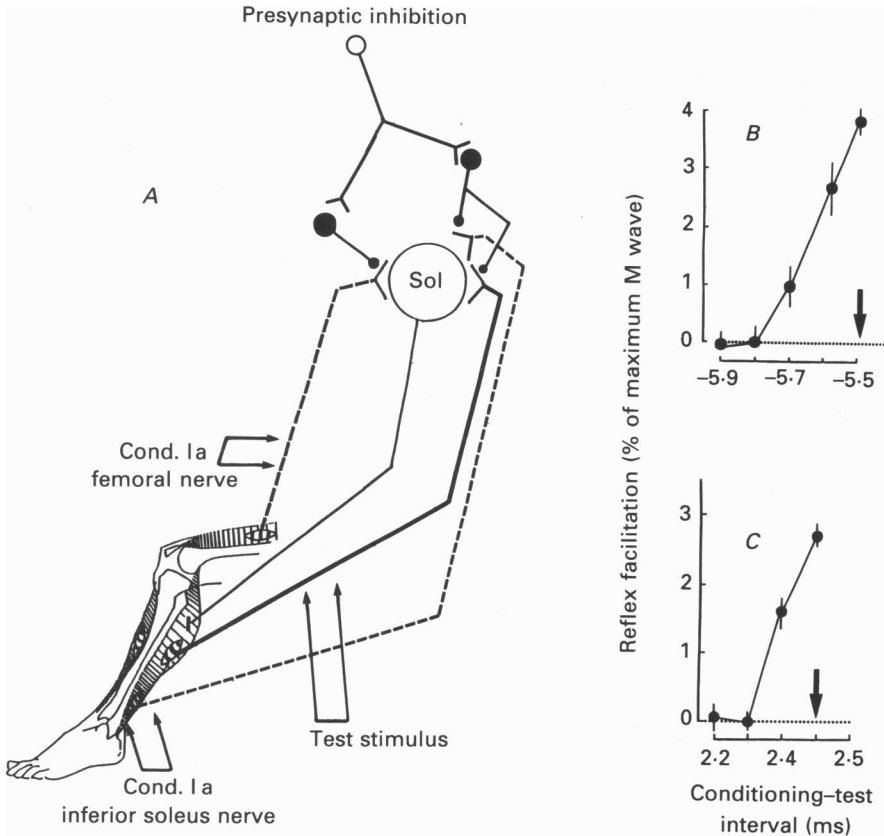


Fig. 1. *A*, schematic diagram of the experimental protocol. Continuous line, pathway of the soleus H reflex. The effectiveness of the Ia conditioning volleys from the homonymous inferior soleus and heteronymous femoral nerves (interrupted lines) in facilitating the soleus H reflex is modulated by presynaptic inhibition. *B* and *C*, the amount of reflex facilitation (expressed as a percentage of the maximum motor M wave) following femoral (*B*) and inferior soleus (*C*) nerve stimulation is plotted against the conditioning-test interval. Arrows indicate the intervals chosen in the experiment illustrated in Fig. 2. In experiments dealing with heteronymous facilitation (*B*) the test shock has to be delivered before the conditioning one owing to the more proximal position of the conditioning electrodes (in such cases the conditioning-test interval is said to be negative).

Test reflex. The soleus H reflex was evoked by stimulating the posterior tibial nerve through a unipolar electrode, the active electrode being placed in the popliteal fossa. The reflex amplitude was computer analysed and the results stored on disc for further analysis. The sensitivity of the H reflex to facilitation can vary with the size of the unconditioned reflex, since at low reflex amplitudes it increases with the increase in size of the unconditioned reflex (for references see Hultborn *et al.* 1987*a*). Thus in the experiments during contraction, the test stimulus intensity was adjusted so that the size of the reference H reflex attained the same size as at rest.

Conditioning stimuli. The femoral nerve was stimulated by a unipolar electrode, the active electrode being in the femoral triangle. The inferior soleus nerve was stimulated through a pair of

electrodes (1.5 cm² silver plates) placed 2 cm apart on the posterior aspect of the leg (16–20 cm above the calcaneus). The stability of the conditions of stimulation during contraction was inferred from the constancy of the M wave evoked by the conditioning stimulus (see below).

Stimulus protocol and analysis of results. Sequences at rest and during contraction were alternated. In each experimental run, control and conditioned reflexes were randomly presented. Twenty to forty responses of each alternative were collected and the statistical significance of the results was examined using variance analysis (*F* test).

RESULTS

Changes in heteronymous and homonymous Ia facilitation during contraction

In the experiment illustrated in Figs 2–4 the interval between femoral nerve and test stimuli was adjusted so that the heteronymous Ia facilitation was assessed 0.3 ms after its onset, whereas the homonymous Ia facilitation (Fig. 2) was assessed 0.2 ms after its onset. Under these conditions, changes in the reflex facilitation elicited by a constant conditioning stimulation faithfully reflect changes in the presynaptic inhibition of Ia fibres mediating the conditioning volley: the larger the facilitation, the smaller the presynaptic inhibition (see Methods).

It is of course essential that the conditioning stimulation elicits the same Ia volley in the different situations (rest and contractions). The size of the M wave evoked by the conditioning stimulus was used to measure the effective stimulus strength, and the stability of the conditioning Ia volley was inferred from the constancy of this M wave. In the experiment illustrated in Fig. 2 the intensity of the femoral nerve stimulation was kept above that required to elicit the maximum M wave in the quadriceps (supramaximal stimulation), thus ensuring that all quadriceps Ia fibres were activated, whereas the inferior soleus nerve stimulus evoked a small (6% of maximum M wave) M wave in the soleus. Both M waves remained constant throughout the contraction.

Subjects performed a ramp-and-hold plantar flexion; e.g. in the case shown in Fig. 2 the torque progressively increased during 500 ms (ramp phase) to reach 25% of the maximum force and then was held for another 500 ms. The degree of homonymous and heteronymous Ia facilitation, expressed as a percentage of the soleus maximum M wave, was assessed at rest and during contraction. The homonymous and heteronymous Ia facilitations were in the same order of magnitude at rest: 3 and 4.5% of the maximum M wave. The supplementary facilitation during contraction, i.e. the difference between the facilitation during contraction and that at rest (expressed as a percentage of maximum M wave), is plotted against the time elapsed after the onset of contraction. At the onset of contraction both homonymous (○) and heteronymous (●) Ia facilitations were largely increased since they exceeded rest value by 11 and 8% of maximum M wave respectively. During the first half of the ramp, both homonymous and heteronymous Ia facilitations, through somewhat decreasing, remained much larger than at rest, the supplementary facilitation being highly significant ($P < 0.001$). In the middle of the ramp (between 250 and 300 ms) both Ia facilitations dropped abruptly, even decreasing below their level at rest at the end of the ramp. Then they returned near to their rest level during the holding phase.

This results, i.e. an early, statistically significant increase in Ia facilitation which dropped abruptly in the middle of the ramp, was almost constantly observed: in

thirty-six out of the thirty-eight experiments dealing with the heteronymous Ia facilitation of the soleus H reflex; in all seven experiments performed in the three subjects in whom homonymous Ia facilitation from the inferior soleus nerve could be investigated (see Discussion).

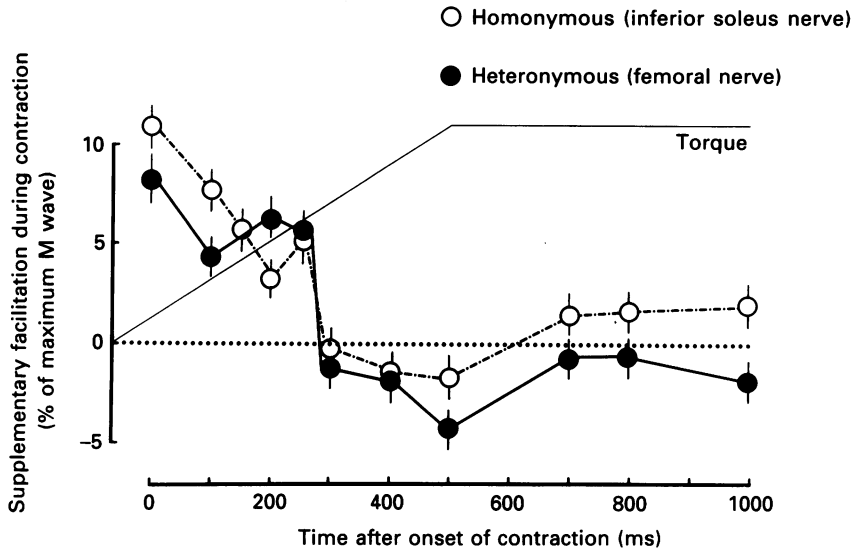


Fig. 2. Time course of the changes in homonymous (○) and heteronymous (●) Ia facilitation of the soleus H reflex during a ramp-and-hold voluntary plantar flexion. Continuous line represents the ramp to be followed by the subject. The force at the end of the 500 ms ramp was 25% of the maximum force that could be maintained for 20 s. The supplementary facilitation during contraction, i.e. the difference between the facilitation during contraction and that at rest (expressed as a percentage of maximum M wave) is plotted against the time elapsed after the onset of contraction. Each symbol represents the mean of forty measurements. Vertical bars one standard error of the mean.

A prolonged depression of the soleus H reflex exists after voluntary phasic plantar flexion (Sciepatti & Crenna, 1984), which could alter the changes in Ia facilitation observed during the following contraction. To discard this hypothetical bias, experiments were performed in which the control situation was the period between two consecutive contractions. Thus, in this control situation, reflexes were subject to the effects of the preceding contraction but not to those of the contraction performed 300–500 ms later. Under these conditions the same results as those illustrated in Fig. 2 were observed.

Effects of changes in the strength of the contraction

Results obtained with different contraction strengths (same subject, same day) are compared in Fig. 3. Conditioning stimulation applied to the femoral nerve ($1.2 \times MT$) evoked, at rest, a facilitation of the H reflex of 2% of maximum M wave. At the end of the 500 ms ramp, the force was either 50% (A) or 25% (B) or 12% (C) of the 'maximum' force. The time course of the changes in heteronymous Ia facilitation was largely similar in the three cases, with the supplementary facilitation disappearing between 200 and 300 ms, but the stronger the force, the larger the initial increase. Note that in the case of the weakest contraction, the initial increase in facilitation was very small and not statistically significant. Similar results were

obtained in all the experiments: six dealing with heteronymous Ia facilitation and four with homonymous Ia facilitation.

Effects of changes in the duration of the ramp

Figure 4 shows results obtained with three different ramp durations (*A*, 1 s; *B*, 500 ms; *C*, 250 ms). In all cases the contraction strength was 50% of the maximum

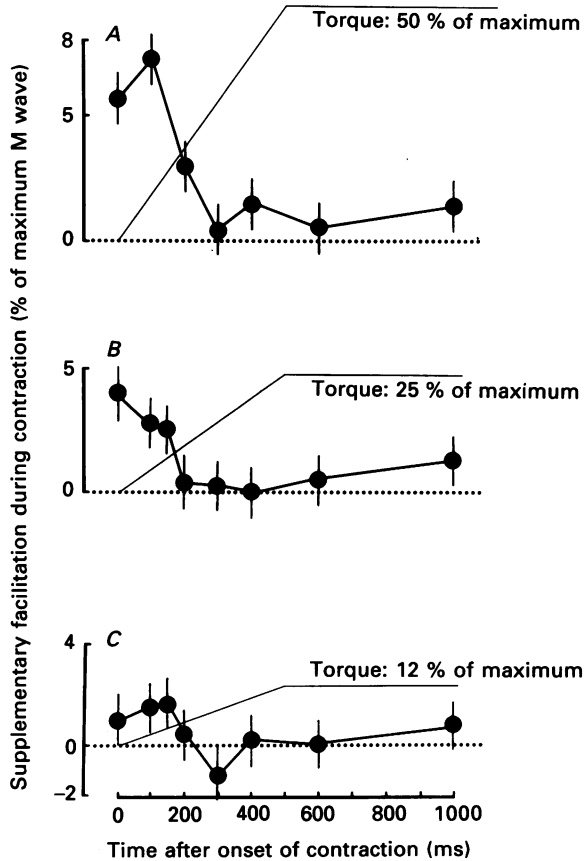


Fig. 3. Changes in heteronymous Ia facilitation are compared during contractions of different force: 50% (*A*), 25% (*B*) and 12% (*C*) of the maximum force (that was possible to maintain for about 20 s). Same legend as in Fig. 2.

force at the end of the ramp. Conditioning stimulation applied to the femoral nerve was strong (intensity above that required to elicit maximum M wave in the quadriceps) and evoked at rest a reflex facilitation equal to 4.5% of maximum M wave in the soleus, which was enhanced (about 5% higher) during the first part of the contraction. Whatever the ramp duration, the Ia facilitation dropped abruptly in the middle of the ramp, the duration of the increased facilitation depending therefore on the ramp duration and not on the time elapsed after EMG onset. Similar results were obtained in all the experiments.

Facilitation during tonic contraction

It is shown in Figs 2–4 that during the holding phase of a ramp-and-hold plantar flexion, both the homonymous and the heteronymous Ia facilitations returned close to the control (rest) level. However, during a long-lasting (1–2 min) tonic contraction the heteronymous Ia facilitation was slightly increased (not illustrated), but this increase only reached statistical significance in one out of the six experiments.

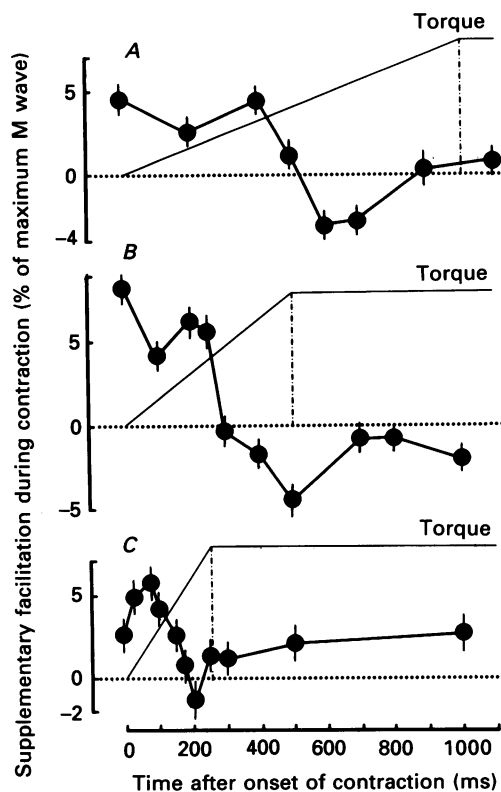


Fig. 4. Changes in heteronymous Ia facilitation are compared during ramps of different duration: 1 s (A), 500 ms (B), 250 ms (C). Same legend as in Fig. 2. The vertical interrupted line indicates the end of the ramp phase.

Effects of ischaemia of the leg on variations in heteronymous Ia facilitation during contraction

To investigate to what extent the afferent discharge evoked by the contraction contributes to the changes in Ia facilitation, experiments were performed during ischaemia of the leg. The ischaemia was produced by a sphyngomanometer cuff positioned around the upper part of the leg just below the electrode eliciting the soleus H reflex. The cuff was inflated to 200 mmHg and after 20–22 min the Achilles tendon jerk completely disappeared and, in one subject, there was total anaesthesia of the foot and the leg. Subjects performed a plantar flexion with a 500 ms ramp,

reaching 25% of the maximum force, and a 500 ms hold (as in Fig. 2). The amount of heteronymous Ia facilitation evoked by a supramaximal stimulation of the femoral nerve at rest, and 100, 400 and 600 ms after the onset on contraction, was measured 5–15 min and 30–40 min after the inflation of the cuff. In the two subjects so explored, identical results were obtained before and after the abolition of the Achilles tendon jerk: there was a significant increase in the facilitation at the beginning of the ramp (as compared to rest), and the facilitation had returned to its rest level during the second half of the ramp and during the holding phase.

DISCUSSION

Evidence for changes in presynaptic inhibition of Ia fibres during contraction

The most direct evidence of presynaptic inhibition of Ia fibres is the depression of the monosynaptic EPSP evoked in motoneurons by a constant stimulation of Ia fibres and occurring without any observable change in motoneuron membrane potential and conductance (Frank & Fuortes, 1957). However, it has been shown that changes in presynaptic inhibition of Ia fibres can be indirectly deduced from alterations in the amount of monosynaptic Ia facilitation elicited in motoneurons by a constant conditioning stimulation (Hultborn *et al.* 1987*a*). In the present experiments, both homonymous and heteronymous Ia facilitations of the soleus H reflex were significantly increased during the first part of a ramp contraction of the gastrocnemius–soleus, then dropped abruptly and returned to their control level. This should reflect changes in the size of the conditioning Ia EPSP, i.e. alterations in presynaptic inhibition of Ia terminals (Hultborn *et al.* 1987*a*).

An alternative hypothesis must, however, be considered. It is conceivable that the net result of the various peripheral and descending inputs activated during contraction has a differential effect on motoneurons with low and high recruitment levels. This could produce a narrowing of the 'usual' threshold range within the motoneuron pool and thus an increase in the slope of the input–output relation of the monosynaptic reflex (D. Kernell & H. Hultborn, personal communication). As a result, a constant conditioning Ia EPSP would fire more motoneurons than in the control situation and produce a larger facilitation of the reflex. However, such an increase in the slope of the input–output relation of the monosynaptic reflex should similarly enhance any H reflex depression, e.g. the depression evoked by a short train of vibrations (supposing that presynaptic inhibition of Ia fibres is unchanged). It is therefore of importance that the vibratory depression of the soleus H reflex has been shown to be dramatically decreased at the onset of a gastrocnemius–soleus contraction (Hultborn *et al.* 1987*b*).

Thus the increased Ia facilitation can be ascribed to a decrease in presynaptic inhibition of Ia terminals. The decrease in presynaptic inhibition seen here implies that there is a tonic presynaptic inhibition of Ia terminals at rest. A tonic level of presynaptic inhibition has been described in the cat with acute spinal transection and administration of dihydroxyphenylalanine (DOPA) (Andén, Jukes, Lundberg & Vyklický, 1966) where it is removed by activation of spinal systems normally controlled from supraspinal centres.

In the middle of the ramp, presynaptic inhibition of Ia terminals on soleus motoneurons returned abruptly to its rest level. This could be related to the finding that the variations of the torque did not exhibit a linear increase throughout the full ramp (following the line drawn on the oscilloscope screen), but rather a top convex

curve; thus the force increased more slowly (deceleration) during the second half of the ramp.

During tonic contraction significant changes in presynaptic inhibition of Ia fibres to soleus motoneurons were rarely found in the present study, which seems to contradict results by Iles & Roberts (1987) who have shown that vibratory inhibition of the soleus H reflex is decreased during tonic soleus voluntary contraction. However, with the prolonged vibration to the Achilles tendon, used in their study, several mechanisms other than presynaptic inhibition were able to contribute to H reflex depression (see Hultborn *et al.* 1987*a*).

It may seem surprising that, despite the refractoriness of Ia fibres activated by the conditioning stimulus to the inferior soleus nerve, homonymous Ia facilitation of the soleus H reflex could be seen at very early conditioning-test intervals. Most probably this indicated that only some of the Ia afferents recruited by the conditioning stimulation are activated by the test stimulus. This could be due to a particular anatomical situation, e.g. a deep location of the Ia afferents from the inferior soleus nerve within the posterior tibial nerve. However, this homonymous Ia facilitation was found in only three out of six subjects.

Changes in presynaptic inhibition on both homonymous and heteronymous Ia fibres to soleus motoneurons, which were assessed by the same method (Ia facilitation of the H reflex), were parallel throughout the contraction and quantitatively equivalent (Fig. 2). This suggests that presynaptic inhibition of homonymous and heteronymous Ia fibres to the same motoneurone pool could be mediated through the same interneurons.

Descending or peripheral origin of the changes in presynaptic inhibition during contraction

The Ia-Ib discharge from the contacting muscle has been shown to produce presynaptic inhibition of Ia fibres in the spinal cat (Devanandan, Eccles & Stenhouse, 1966). Such an afferent discharge from the contracting gastrocnemius-soleus could thus activate 'presynaptic interneurons', and increase presynaptic inhibition of Ia fibres. The opposite result found here during the first half of the ramp, i.e. a decrease in presynaptic inhibition, can therefore be ascribed to a descending inhibition of 'presynaptic interneurons', already established at the onset of the movement (Hultborn *et al.* 1987*b*). The question then arises whether the contraction-induced afferent discharge contributes to the brisk reinforcement of presynaptic inhibition of Ia fibres occurring in the middle of the ramp. Such a contribution is not major since 10 min after the disappearance of the Achilles tendon jerk, when ischaemia has been shown to block most of the Ia and Ib fibres from the gastrocnemius-soleus muscle (Pierrot-Deseilligny *et al.* 1981), the same time course of changes in presynaptic inhibition was observed. Also, if the group I afferent discharge played a major role in the reinforcement of presynaptic inhibition following the initial decrease, this reinforcement could be expected to occur at a fairly fixed time after the onset of the contraction. Since the time of the reinforcement systematically varied with the ramp duration, a peripheral origin appears to be unlikely. Thus the disappearance of the initial decrease in presynaptic inhibition of Ia fibres might also be centrally programmed.

It was found that, under the conditions explored (ramp not longer than 1 s,

contraction not stronger than 50% of the maximum force), the decrease in presynaptic inhibition of Ia terminals at the onset of the movement was adjusted to the force at the end of the ramp. This suggests that, under these conditions, presynaptic inhibition can be modulated according to both the strength (Fig. 3) and the timing (Fig. 4) of the contraction.

Functional implications

The decrease in presynaptic inhibition of Ia fibres should increase the gain of the monosynaptic stretch reflex during the first half of the ramp, which could be of functional importance. Thus, when running, a significant contribution of the monosynaptic stretch reflex to the gastrocnemius-soleus thrust has been shown (Dietz, Schmidtbleicher & Noth, 1979), and could compensate automatically for the unevenness of the ground (Dietz, 1981). More generally, at the beginning of a movement, when the load is not yet precisely known, a high gain may allow the monosynaptic reflex to compensate rapidly for the actual load.

Later, presynaptic inhibition is increased and the gain of the reflex is decreased. However, by that time several other mechanisms in the central nervous system are available to maintain the desired trajectory. In addition, the decrease in the gain after a certain time is probably required to prevent oscillations from building up (see Matthews, 1972; Rack, 1981).

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