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SELECTIVE RECRUITMENT OF HIGH-THRESHOLD HUMAN MOTOR UNITS DURING VOLUNTARY ISOTONIC LENGTHENING OF ACTIVE MUSCLES

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SUMMARY

1. We have investigated the possibility that voluntary muscle lengthening contractions can be performed by selective recruitment of fast-twitch motor units, accompanied by derecruitment of slow-twitch motor units.

2. The behaviour of motor units in soleus, gastrocnemius lateralis and gastrocnemius medialis muscles was studied during (a) controlled isotonic plantar flexion against a constant load (shortening contraction, S), maintained plantar flexion, or dorsal flexion resisting the load and gradually yielding to it (lengthening contraction, L), (b) isometric increasing or decreasing plantar torque accomplished by graded contraction or relaxation of the triceps surae muscles, (c) isometric or isotonic ballistic contractions, and (d) periodic, quasi-sinusoidal isotonic contractions at different velocities. The above tasks were performed under visual control of foot position, without activation of antagonist muscles. The motor units discharging during foot rotation were grouped on the basis of the phase(s) during which they were active as S, S + L and L. The units were also characterized according to both the level of isometric ramp plantar torque at which they were first recruited and the amplitude of their action potential.

3. S units were never active during dorsal flexion; some of them were active during the sustained contraction between plantar and dorsal flexion. Most S + L units were active also during the maintenance phase and were slowly derecruited during lengthening; their behaviour during foot rotations was similar to that during isometric contractions or relaxations. L units were never active during either plantar or maintained flexion, but discharged during lengthening contraction in a given range of rotation velocities; the velocity of lengthening consistently influenced the firing frequency of these units. Such dependence on velocity was not observed in S + L units.

4. A correlation was found between the amplitude of the action potential and the threshold torque of recruitment among all the units. In addition, the amplitudes of both the action potential and the threshold torque were higher in the case of L units than in the case of S and S + L units. Most L units could be voluntarily recruited only in the case of ballistic isometric or isotonic contraction.

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5. Occasionally, L units were directly activated by electrical stimulation of motor fibres and their conduction velocity was in the higher range for α-axons. In contrast, nerve stimulation could induce a reflex activation of S and S + L units.

6. The results suggest that a large proportion of high-threshold, fast-twitch motor units, most likely characterized by a short half-relaxation time, are active during lengthening contractions. The mechanical advantage of their selective recruitment and the possible neural mechanisms responsible for it are briefly considered.

INTRODUCTION

It is easy to predict that all the possible mechanical properties of muscles or motor units are appropriately relied upon by the central nervous system during performance of intended movements. By looking at the complexity and precision of human movements, however, one may wonder about the likelihood of identifying even the main possible schemes of activation, let alone the ways through which the motor command has access to these properties.

Motor unit recruitment is known to be nearly automatically achieved during an augmenting muscle contraction, thanks to the motoneurones' properties connected with size and/or specific resistivity (see Kernell, 1983, for a critical review). Graded force development derives as a consequence, since the motoneurone characteristics and the mechanical properties of their target muscle fibres are appropriately matched (Burke, 1981). This mechanism appears to be sufficient in order to control isometric contractions (Milner-Brown, Stein & Yemm, 1973*a*), and also ramp shortening contractions (Thomas, Ross & Calancie, 1987). Increasing velocities of shortening are obtained by recruitment of a progressively higher number of large motoneurones, according to the 'size principle' (Henneman & Mendell, 1981; Desmedt, 1983), in this way calling into action also fast-twitch motor units. The unavoidable activation of the slow-twitch motor units may not substantially counteract the economical advantages of automatic recruitment, since slow-twitch muscle units would become unloaded during the fast shortening contraction, under which condition (pulling no load) they undergo minor energy consumption (Hill, 1964). Furthermore, the discharge rate of these motor units tends to saturate during large and/or fast movements (Walmsley, Hodgson & Burke, 1978; Bellemare, Woods, Johansson & Bigland-Ritchie, 1983).

Graded motoneurone recruitment, however, may not in itself assure perfect performance of *any* intended movement. In fact, it may be conceived that the recruitment order of motor units is modified and updated during the evolution of a given movement, in order to match the neural command to the continuously changing mechanical characteristics of muscle. This would apply even more to the lengthening contractions. Easing down a load at a given controlled velocity, with a smooth movement trajectory (as for example when slowly extending a flexed load-bearing forelimb by controlled relaxation of the biceps brachii), must rely upon motor units with an appropriate relaxation time. Braking the fall of a load at a very slow velocity can be performed simply by derecruitment of slow-relaxing motor units, which should have been active during holding. But, easing down the load quickly enough (without simply letting it drop) may require activation of motor units with fast relaxation times, since slow-relaxing ones would give rise to a too slow descent, unless the antagonist muscle contracts to speed it up by pulling in the other direction.

As a corollary, it can be observed that this activation protocol would be useless in the case of dropping a very heavy load, since the load would exert by itself such a stretch of the muscle that the decay time of the motor units' force would become irrelevant. On the other hand, with no load, the intended movement trajectory would be solely imposed by the weight of the limb to be moved, and by the antagonist contraction, if the mechanical viscous properties of muscles and joints have to be overcome to reach the intended velocity.

Thus, recruitment of motor units having short relaxation times may be appropriate in order to better control the movement trajectory in an intermediate range of loads and velocities. A theoretical disadvantage of such an event would be represented by the larger force output of the fast-twitch motor units, which, in addition, would increase during lengthening owing to the muscle force–velocity relationship (Katz, 1939). This could be overcome: (1) by activating these units in a limited number and at a slow frequency of discharge, such that a favourable trade-off between motor units' total force and relaxation time would be achieved (Ducati, Parmiggiani & Schieppati, 1982), (2) by switching off the background activity of the slow-twitch units whose contribution, when stretched while active, would be anything but negligible (Joyce, Rack & Westbury, 1969), and which would hamper muscle lengthening with their slow relaxation times, as considered above. Both mechanisms appear to be within the reach of the CNS. In fact (1) high-threshold units can fire only once or a small number of times in each cycle during normal walking (Grimby, 1984), although they may well discharge at higher frequency in maximum voluntary isometric contractions, even if for only brief periods of time (Hannerz, 1974; Grimby & Hannerz, 1977); (2) previously activated motor units can decrease their frequency of discharge on beginning of firing of a newly recruited (higher-threshold) motor unit (Broman, De Luca & Mambrito, 1985).

It is the hypothesis of this work that fast-twitch motor units, presumed to be normally recruited at high levels of force output, become active during lengthening contraction on the basis of other factors in addition to their position in the rank order of recruitment holding for isometric or shortening contractions. It has been shown recently that, while shortening contractions of the triceps surae muscles (plantar flexion of the foot) are performed primarily by activation of the soleus muscle, lengthening contractions (dorsal flexions performed by gradually yielding to a dorsiflexing load) can imply activation of the fast gastrocnemii and deactivation of the slow soleus (Nardone & Schieppati, 1988). Evidence will be presented that, in addition to the shift in activity between muscles, substitution of high- for low-threshold motor units occurs within either muscle during active lengthening. A preliminary report of the data has been published in abstract form (Schieppati, Nardone & Romanò, 1987).

METHODS

Five volunteers (one female and four males) between 22 and 39 years of age participated in this study. All gave informed consent to the experimental procedure. The experimental set-up and the motor tasks required, as well as methods of EMG surface recording from leg muscles, and principles of data analysis, were previously published (Nardone & Schieppati, 1988). Briefly, the subjects sat in a chair, the knee flexed at 110 deg, the foot strapped to a mould allowing plantar–dorsal rotation of 25 deg (85–110 deg of tibio-tarsal joint angle) against a load opposing plantar flexion of 100 N (i.e. high enough to overcome the force developed by the elastic elements of the triceps surae in the dorsiflexed position, cf. Romanò & Schieppati, 1987). Under these conditions, the foot torque was about 15 N m and corresponded to 15–20% of the torque exerted during a maximum voluntary contraction. The torque remained approximately constant independent of tibio-tarsal joint angle, owing to the parallel direction of the force of the weight and of the triceps surae. In the maximally dorsiflexed position (85 deg) the action of the load was blocked by a mechanical stop. With this arrangement, the load was lifted, and its fall prevented or braked, by appropriate activation of the triceps surae muscles, without activation of its antagonists. The dorsal flexion was carried out in fact by gradually decreasing the activation of the extensor muscles, but not by activation of the pretibial muscles, whose EMG remained silent throughout the task in all the subjects. The thigh muscles EMGs were silent as well, in the three subjects which were recorded.

The subjects had to perform foot movements at various controlled velocities (ranging from 10 to 70 deg/s), on visual feed-back of the foot position. To this aim, the signal from a potentiometer centred on the tibio-tarsal joint was displayed on an oscilloscope at a slow sweep speed, in a free-run mode, and the subjects were asked to follow a path drawn on the screen, producing a track as smooth as possible. The tasks consisted in a ramp plantar flexion (shortening contraction), a holding phase of a few seconds duration, and a ramp dorsal flexion (lengthening contraction). The subjects initiated the movements at their own will, being simply required to rest (foot in dorsiflexed position), as well as to hold the contraction at the end of the plantar flexion, at least some seconds between successive movements. Plantar and dorsal flexions were also performed consecutively, once more in a self-paced mode, so as to produce a series of periodic quasi-sinusoidal changes in angular foot position. In this case, superimposition of the sequential traces on the storage screen provided the subjects with a means to check the regular rhythm and amplitude of foot rotation. Under these conditions the foot torque is not constant: while during slow ramp contractions the amplitude of the force modulation due to inertia of the load (calculated at the point of application) is negligible, it varies from about 15 N for the slowest to about 40 N for the fastest periodic movements. In all the subjects, pretibial muscles were silent also during the different rates of periodic movement. Alternatively, the foot mould could be fastened and the torque exerted by the triceps, under isometric conditions, could be recorded by means of a strain gauge.

Recording from single motor units in soleus, gastrocnemius lateralis, or medialis was performed by means of a multipolar electrode. This was made of up to six varnish-coated Nichrome wires 50 μm in diameter (A-M Systems, USA), about 15 cm in length, twisted together and soldered to shielded wires for connections to the amplifier. The other end of the thread was introduced into an injection needle for insertion into the muscle. The wires jutted out of the needle tip, were cut at different lengths (from 0·5 to 2 mm) to increase the probability that at least one of them would come close enough to a muscle fibre, and bent to form a hook to assure stable recordings during movement. After electrode insertion, the needle was withdrawn from the muscle but not from the wires. The electrodes were very well tolerated by the subjects, were free from movement artifacts and assured a consistent recording for long periods of time, regardless of the muscle movement. Recording was made monopolarly, against a ground electrode applied to the skin over the shin or the knee. The potentials were amplified (up to ×25000), band-pass filtered (300–2500 Hz) and recorded on tape. The results obtained were checked by repeated playbacks and film recordings. Only those recordings, in which the unit potentials could be identified by their characteristic shape throughout the experimental session, were subjected to further analysis. When the selectivity of the recording was satisfactory, the unit potentials were fed into a variable-threshold discriminator, whose output was used for constructing frequency histograms of the unit's discharge. This was done automatically (Olivetti M24, DT2801 A/D board), by counting the number of spikes occurring during successive epochs centred on the phase to be analysed, and whose duration depended on the duration of the task. Additional inputs to the computer were the rectified and integrated (time constant 10 ms) EMG of the soleus and gastrocnemius muscles, and the position (or force) trace, a given level of which was the signal for the (peri-trigger) computer acquisition.

The characterization of the recorded motor units was attempted in various ways: (1) The force level at which the unit began firing was investigated by asking the subject to exert a gradually increasing isometric plantar torque against the strain gauge, up to the level at which lower limb and body position changed due to the intense effort. To this aim, the velocity of the ramp was kept between 10 and 40 N m/s (mean value 16·2 N m/s) (Büdingen & Freund, 1976). (2) For the units discharging during isotonic plantar flexion, the degree of tibio-tarsal joint angle at which they began discharging was observed. Since in subsequent repetitions of the task the degree at which the motor unit began discharging was influenced by slight variations in rotation velocity, we simply assigned the motor units to three groups according to when they appeared for the first time (first, second or third part of the plantar flexion). Most units not discharging during isotonic plantar flexion (or ramp torques) were also studied during ballistic plantar flexion or rapid isometric contraction. When these efforts were in vain, and only after checking that the unit appeared again on performance of a subsequent dorsal flexion, the unit was considered as a very high-threshold unit. (3) Reflex activation of the motor unit by electrical stimulation (1 ms in duration) of the tibial nerve in the popliteal fossa was frequently attempted. Successful reflex activation of the unit by stimulus strengths just above the threshold for Ia fibres (as monitored by the soleus or gastrocnemius H reflex) was considered a criterion for assuming a high excitability and low axonal conduction velocity of the parent motoneurone (Bawa, Binder, Ruenzel & Henneman, 1984), and therefore for regarding the corresponding muscle unit as a slow-twitch unit. (4) In the case of gastrocnemius medialis motor units, an attempt at measuring the conduction velocity of the motor axon was done systematically. To this aim, a second stimulating electrode was positioned on the nerve directed to the gastrocnemius muscle, medially on the upper part of the leg, at a known distance from the electrode in the popliteal fossa (8–10 cm, along the presumed path of the nerve, drawn on the basis of the maximal direct response recorded from the muscle on stimulation at various points of the medial part of the upper leg). On the two occasions in which both stimuli directly activated the same unit, and recording was not altered by field potentials, the axon conduction velocity was calculated. On the other hand, when only one stimulus position was effective, direct activation of the unit by very low stimulus strength was none the less a sign of a large motor axon, and suggested a high threshold for excitation of the parent motoneurone. (5) Spike-triggered averaging of the motor unit twitch was performed occasionally, but no reliable results could be obtained since: (i) only very few of the units active during lengthening contraction could be made to discharge steadily with a voluntary effort, (ii) when this happened, the unit-bearing muscle was rather active and stiff, and co-contraction of other leg muscles was also present, such that the unit twitch was superimposed on a high background of force, which would therefore have required a too high number of averages to detect the unit's twitch.

RESULTS

The discharge of ninety-nine motor units (forty-one in the soleus, forty-six in the gastrocnemius lateralis (GL) and twelve in the gastrocnemius medialis (GM)) was studied under the following conditions: (a) isotonic shortening and (b) isotonic lengthening contractions, corresponding to plantar and dorsal flexions respectively, (c) the two subsequently performed so as to yield quasi-sinusoidal foot rotations, (d) tonically maintained plantar flexions of a few seconds duration, (e) isometric ramp plantar efforts, and (f) ballistic isometric or isotonic contractions.

The forty-one units in the soleus belonged to two subjects in whom the muscle was consistently active during the dorsal flexion, as judged by the surface EMG recording. The fifty-eight units in the gastrocnemii belonged both to the above subjects, and to three others, in one of whom the soleus activity dropped to very low levels during the dorsal flexion. The units in the two gastrocnemii will be considered together, since no appreciable differences in their behaviour were found either within or between subjects and muscles.

The motor units will be referred to henceforth on the basis of the phase(s) during which they were active, namely as S (plantar flexion, shortening contraction), S+L (plantar and dorsal flexion) and L (dorsal flexion, lengthening contraction). In addition, some of the above units were active during the tonic contraction subserving the holding phase: they are included either within the S or the S+L units, according to their behaviour in those phases. In fact, no unit was active during only the tonic phase. Moreover, L units were *never* found to be active during the tonic phase, either in the soleus or gastrocnemii. The units studied were then distributed as follows.

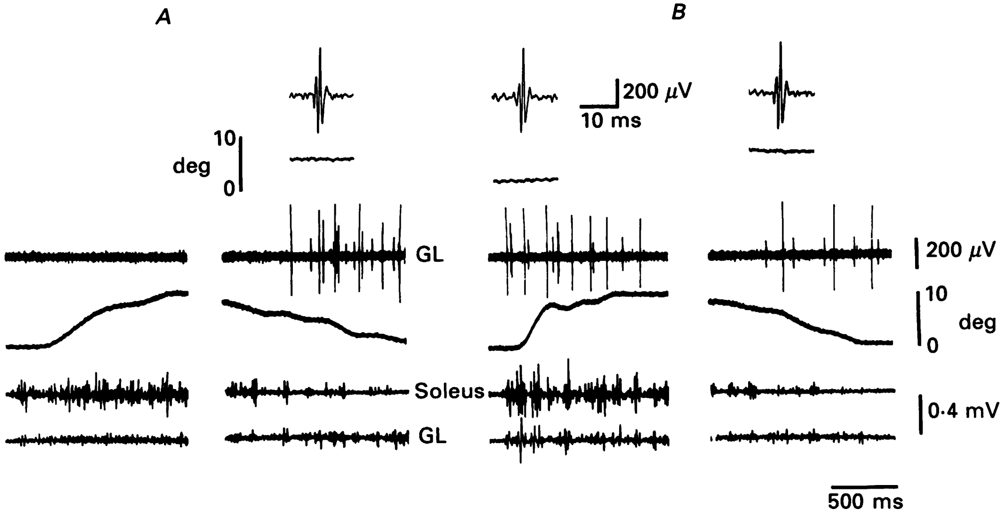

Fig. 1. Pattern of discharge of a gastrocnemius lateralis (GL) motor unit during isotonic shortening and lengthening contractions, performed in a ramp and in a ballistic mode. From top to bottom, wire recording, foot position, raw EMG of soleus and GL muscles. Insets at the top are recordings of the motor unit action potential and foot position on an expanded time scale. The unit was not active during slow plantar flexion (*A*, left), but was consistently recruited during the lengthening contractions subserving dorsal flexions at a velocity of foot rotation of about 8 deg/s (*A* and *B*, right). It could be voluntarily activated only by ballistic contraction (*B*, left). In this and in the following figures, 0 deg corresponds to a tibio-tarsal joint angle of 85 deg.

Soleus: S = 22 (54% of all soleus units), S+L = 13 (32%), L = 6 (15%). Gastrocnemii: S = 15 (26% of all the units in the two gastrocnemii), S+L = 14 (24%), L = 29 (50%). Apart from the differences in the percentages of the various types of motor units within the soleus or gastrocnemius muscle, no appreciable difference was found between the behaviour of the units belonging to either muscle and firing in a given phase of the task.

Figure 1 shows an example of a GL motor unit, classified as an L unit, discharging during controlled lengthening contraction (*A* and *B*, right panels), but not during shortening contraction (*A*, left panel). Other units active during the dorsal flexion can be identified in the trace, whereas no unit is active during plantar flexion. Accordingly, the gastrocnemius EMG recorded by surface electrodes is rather poor during plantar flexion. On the other hand, a shift of the EMG activity from the soleus to the gastrocnemius muscle occurred during the dorsal flexion. As shown in part *B*, this unit could also be active during plantar flexion, provided however that the latter was performed in a ballistic manner (left panel).

A GM type L unit recorded in another subject is shown in Fig. 2. It was silent during ramp plantar flexion (not shown), but displayed a burst of activity at the beginning of a ballistic plantar flexion (left column), and discharged at a slower frequency during dorsal flexion (right column). This task was accomplished by large activation of the GM muscle, while the soleus was virtually silent, as indicated by the average of the rectified and integrated surface EMG of the two muscles. Unlike the unit in Fig. 1, this started firing just before and at the beginning of the dorsal flexion. This unit could be directly activated on electrical stimulation of the tibial nerve in the popliteal fossa (top left), at a very low stimulus strength, as indicated by the synchronous small-amplitude deflection on the EMG recording corresponding to the M response. The high excitability of the motor axon is an indirect sign of a large diameter of the fibre innervating this muscle unit.

The pattern of discharge of a soleus L unit not firing during plantar flexion (not even a ballistic one), is reported in Fig. 3 (*A*, left panel). The unit was instead active during dorsal flexion (*A*, right panel). Under this condition, it fired only once, although consistently during various repetitions of the task, at the beginning of the dorsal flexion. It is evident that, in this period, the background activity picked up by the wire electrode, and connected with the discharge of the motor units active during plantar flexion and holding phase, comes to an end. It remains absent throughout the completion of the dorsal flexion. The soleus EMG also decreases during the dorsal flexion, showing however a segmented, bursting aspect, which is rather common for this muscle (Nardone & Schieppati, 1988). The unit fires in correspondence to one EMG peak; the other peaks appear to be synchronous with the activity of other units active in this phase. The unit could be recruited during a ramp isometric contraction of the triceps surae (Fig. 3*B*), but only on reaching a high level of torque. It was not active during the decreasing part of the isometric contraction.

Figure 4 shows the pattern of discharge of two GL type L units, simultaneously recorded. Both were silent during plantar flexions and the holding phase, but were active during dorsal flexions. The histogram of the discharge of either unit was constructed for three velocities of foot rotation (performed repetitively so as to yield a periodic movement), and compared to the average of the movement trajectory and the integrated EMG of the GL and soleus muscle. The two units' discharges appear correlated in different ways to the velocity of lengthening contraction, in so far as the frequency of firing of the former (second row from the top) is higher for the slow rotations and virtually absent for the fastest rotations, while the latter (third row) fired more at the intermediate velocities of rotation and was still active at the highest. A second difference consists of their discharge frequency timing, which reaches a peak at mid-position during the dorsal flexion for the former, and at the very beginning of dorsal flexion for the latter. When the rotations were made even faster (not shown), and not controlled any more but issued as a series of ballistic plantar flexions followed by free relaxations, both units became silent, and accordingly no EMG could be recorded during the phase of dorsal flexions in either muscle. The units, and the whole muscle, were silent as well during very slow dorsal

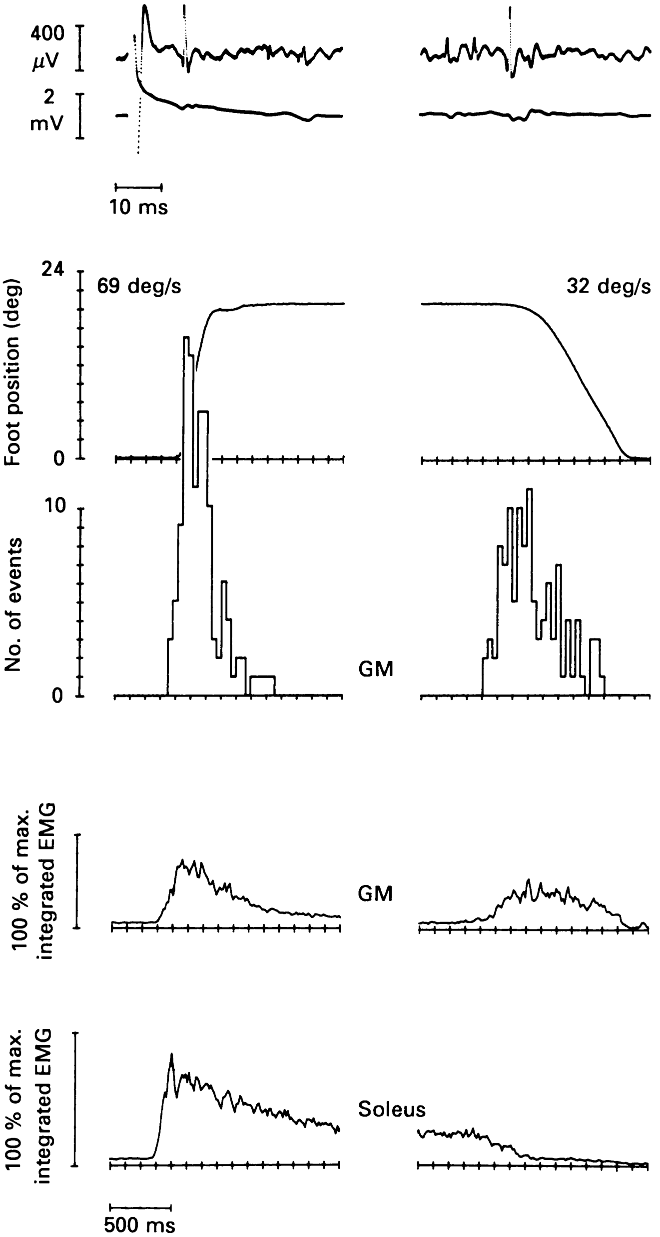

Fig. 2. Pattern of discharge of an L unit in the gastrocnemius medialis (GM) during ballistic shortening contractions (left panel) and controlled lengthening contractions (right panel). The traces on the top represent the direct response of the unit on low-intensity electrical stimulation of the nerve to the GM (left) and its discharge at the beginning of the dorsal flexion (right), and the raw GM EMG. In the lower part of the figure are reported, from top to bottom, foot position, frequency histogram of unit's discharge, GM and soleus integrated EMGs (averages of twenty trials).

flexions. Neither unit could be activated by ballistic plantar flexion or ramp isometric torques. It is interesting to note that the integrated EMG of the soleus and GL muscles are out of phase during the slower tasks, and become in phase during the fastest rotations. Contrary to the behaviour of the surface EMG, the units are active only during the phase of lengthening contraction. In particular, during the fastest rotations, the behaviour of these L units does not follow that of the parent muscle; in other words, during shortening contraction, the GL is indeed active (and more than during dorsal flexion) but the corresponding neural command does not succeed in activating the motoneurones innervating the recorded units. On the other hand, activation of these units during lengthening occurs despite a decreased level of GL EMG, which one would expect, instead, to be proportional to the neural drive to the motor pool.

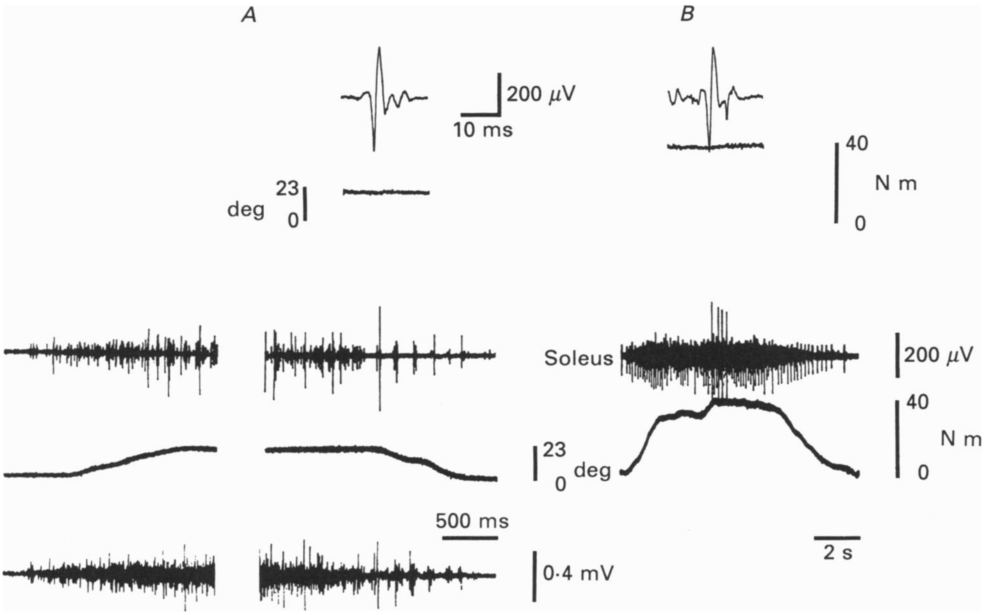

Fig. 3. Pattern of discharge of a soleus L unit during isotonic controlled shortening and lengthening contractions (*A*) at a mean velocity of 25 and 29 deg/s respectively, and during slow isometric contraction and relaxation (*B*). *A*, from top to bottom, wire recording, foot position and raw EMG of soleus. *B*, wire recording and foot torque. The unit could be voluntarily recruited only on attaining high levels of foot torque. Insets at the top represent the unit's action potential under both conditions.

Some L units in the GM and GL muscles, which were not activated during isometric plantar effort, were able to fire instead during isometric flexion of the leg, during which task either or both muscles are readily activated (Gravel, Arsenault & Lambert, 1987). However, it must be noted that, also in this case, the amplitude of the EMG at which the units started discharging was much larger (close to that of a maximum voluntary effort) than that observed during lengthening contractions.

The velocity of lengthening contraction influenced the firing frequency of the L units. This was a common finding for all units subjected to dorsal flexions of different

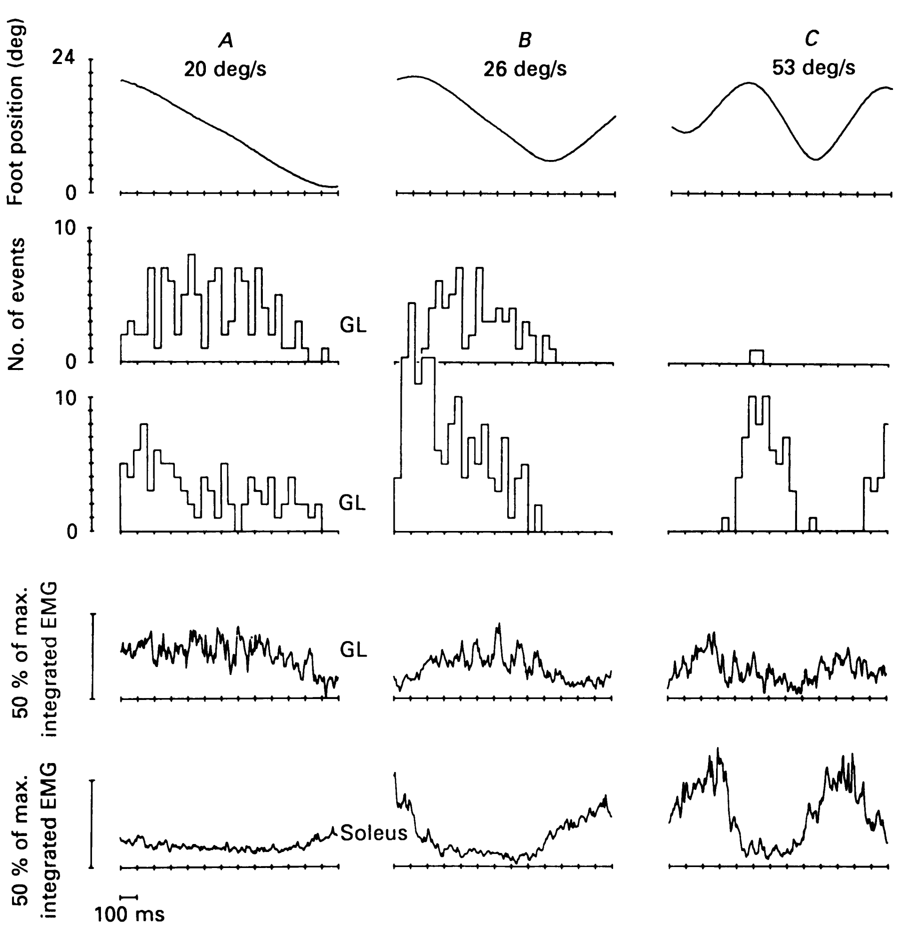

Fig. 4. Patterns of discharge of two GL type L units simultaneously recorded during periodic foot movements, performed at three different velocities. From top to bottom, foot position, frequency histograms of units' discharge, integrated EMGs of GL and soleus muscles (averages of sixteen trials). It is shown that the frequency of discharge of the two units is differently influenced by the velocity of foot rotation. At intermediate velocities of foot rotations (*A* and *B*), GL and soleus integrated EMGs are out of phase, the activity of the former occurring during lengthening contractions and being paralleled by the discharge of the two units. At the fast velocity (*C*), the GL EMG displays two periods of activity, one during lengthening contraction in time with the unit's discharge, the other in-phase with that of soleus during the shortening contraction.

velocities, but no consistent linear relationship was found between the two parameters. Rather, it seemed that each unit fired maximally in correspondence to a given velocity, different for different units. Figure 5 shows the behaviour of an L unit in the GM muscle, whose firing frequency peaks about at the middle of the lengthening contraction (top right recordings). The height of the histogram peak is larger for fast than for slow velocities of foot rotation. This unit was activated by stimulation of both the tibial and the GM nerve, as shown by the left and centre top recordings, respectively. The calculated conduction velocity of the motor axon was

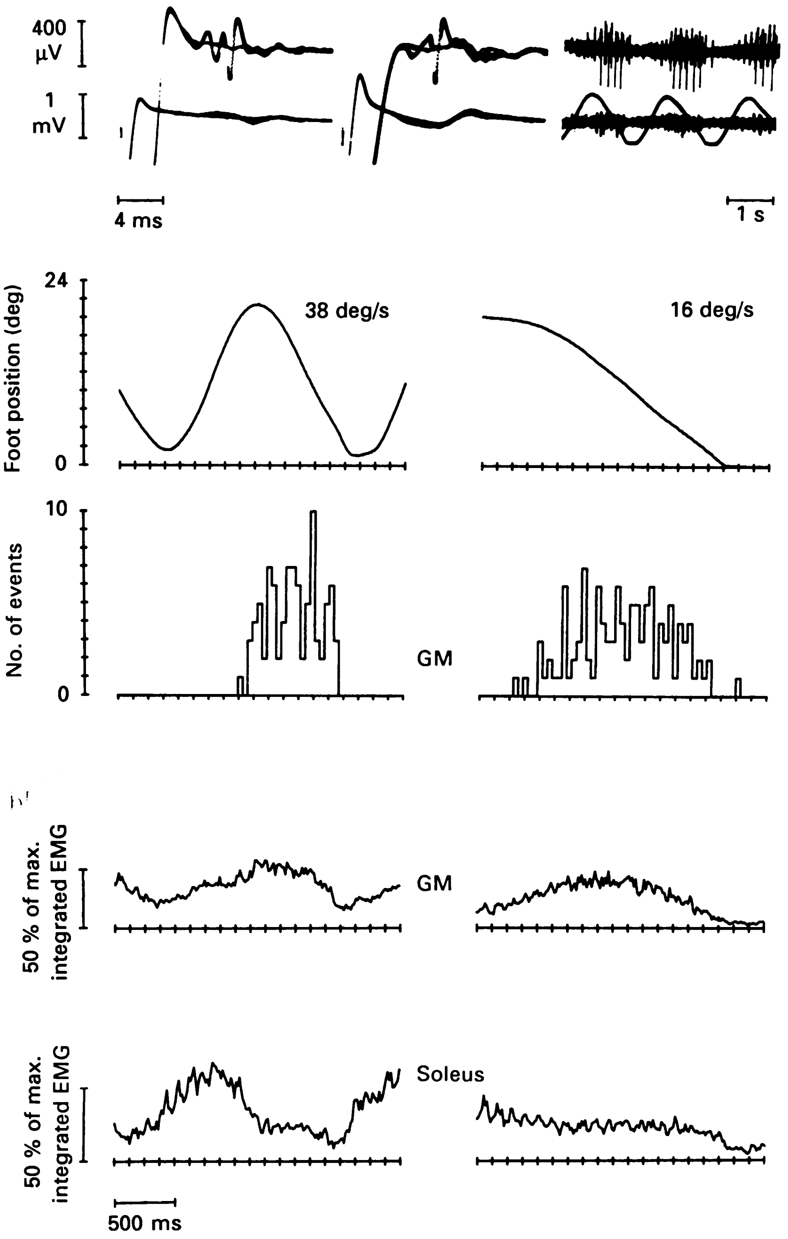

Fig. 5. Pattern of discharge of a GM type L unit, innervated by a fast-conducting axon (53 m/s, cutaneous temperature 32 °C). The top panels show the unit's action potential in response to low-amplitude stimulation of the posterior tibial nerve at the popliteal fossa (left) and of the nerve to GM (middle), along with the raw GM EMG. It is shown by superimposition of five sweeps that the stimulus strength was liminal for axon activation. On the right is reported an example of the pattern of discharge during periodic isotonic contractions. In the lower part of the figure, foot position, frequency histogram of unit's discharge, GM and soleus integrated EMGs (averages of twenty trials) are reported from top to bottom.

53 m/s (for another GM type L unit, showing a similar pattern of discharge, the conduction velocity was 49 m/s).

The mean frequency of firing of the units active during dorsal flexion was calculated for a selected sample of ten units, whose activity was recorded for at least twenty repetitions of the task. It was 6·2 ± 2·2 Hz (S.D.) for a mean velocity of foot rotation of 21·2 ± 2·7 deg/s. The mean amplitude of the action potential of the units of this group was 665 ± 273 μV. The mean threshold torque could not be calculated, since only two units were recruitable during plantar torque, four were active on ballistic contraction and four were not recruitable during either manouevre.

A representative example of an S + L unit is shown in Fig. 6. This is a soleus unit, which starts being active at about two-thirds of the plantar flexion, remains active throughout the holding phase, and accompanies dorsal flexion. Its derecruitment during dorsal flexion is gradual from the beginning, and is not correlated with the bursting activity in the soleus integrated EMG (*C*); its frequency of discharge is even larger during slow than fast dorsal flexion (*B* and *C*). This unit was activated during a ramp isometric contraction at a torque level of about 20 N m (average of the threshold levels of twelve trials). Electrical stimulation of the tibial nerve at very low stimulus strength, just above the threshold for the H reflex, induced a discharge of this unit with a fixed latency compatible with a reflex activation (top inset). The unit could not be activated directly on increasing stimulus strength, at least up to when a large field potential encroached upon the trace. It can be noted that, also in this case, GM activation increased during the fast dorsal flexion (*C*) above the level occurring during the tonic phase, with the same time course of the soleus EMG. This bursting activity is not correlated with the discharge of the recorded low-threshold unit, and is therefore probably connected with the firing of high-threshold units. The general characteristics of the pattern of activity of this unit are shared by all other S + L units, found either in the soleus or in the gastrocnemii muscles, and resemble the pattern of activity occurring during increasing or decreasing isometric plantar torques (compare columns *B* and *E* in Fig. 6).

In S + L units, the firing frequency was usually larger during plantar than dorsal flexion (see also Denier van der Gon, ter Haar Romeny & van Zuylen, 1985). The mean frequency of firing was calculated for a sample of ten units studied during a period of time comprising almost twenty repetitions of the task, and having known threshold torque and spike amplitude (mean values for the group 27 ± 31 N m (S.D.) and 345 ± 83 μV, respectively). It was 6·8 ± 5·3 Hz during plantar flexion (mean velocity of rotation 19·6 ± 7·8 deg/s) and 4·1 ± 2·8 Hz during dorsal flexion (mean velocity 20·5 ± 8 deg/s). In the latter phase the frequency of firing decreased gradually and almost linearly with foot position, at variance with the behaviour of the L units, and the discharge stopped about at the same position at which it began during plantar flexion.

The amplitude of the action potential of the motor units was plotted against the level of torque at which the units began firing. The graph in Fig. 7 shows that a significant regression was found between the two parameters. The units recruitable only on ballistic contraction have been plotted together in correspondence of the first interrupted segment in the abscissa. Their average threshold torque calculated from the equation of the regression line, in the hypothesis that they belong to the same

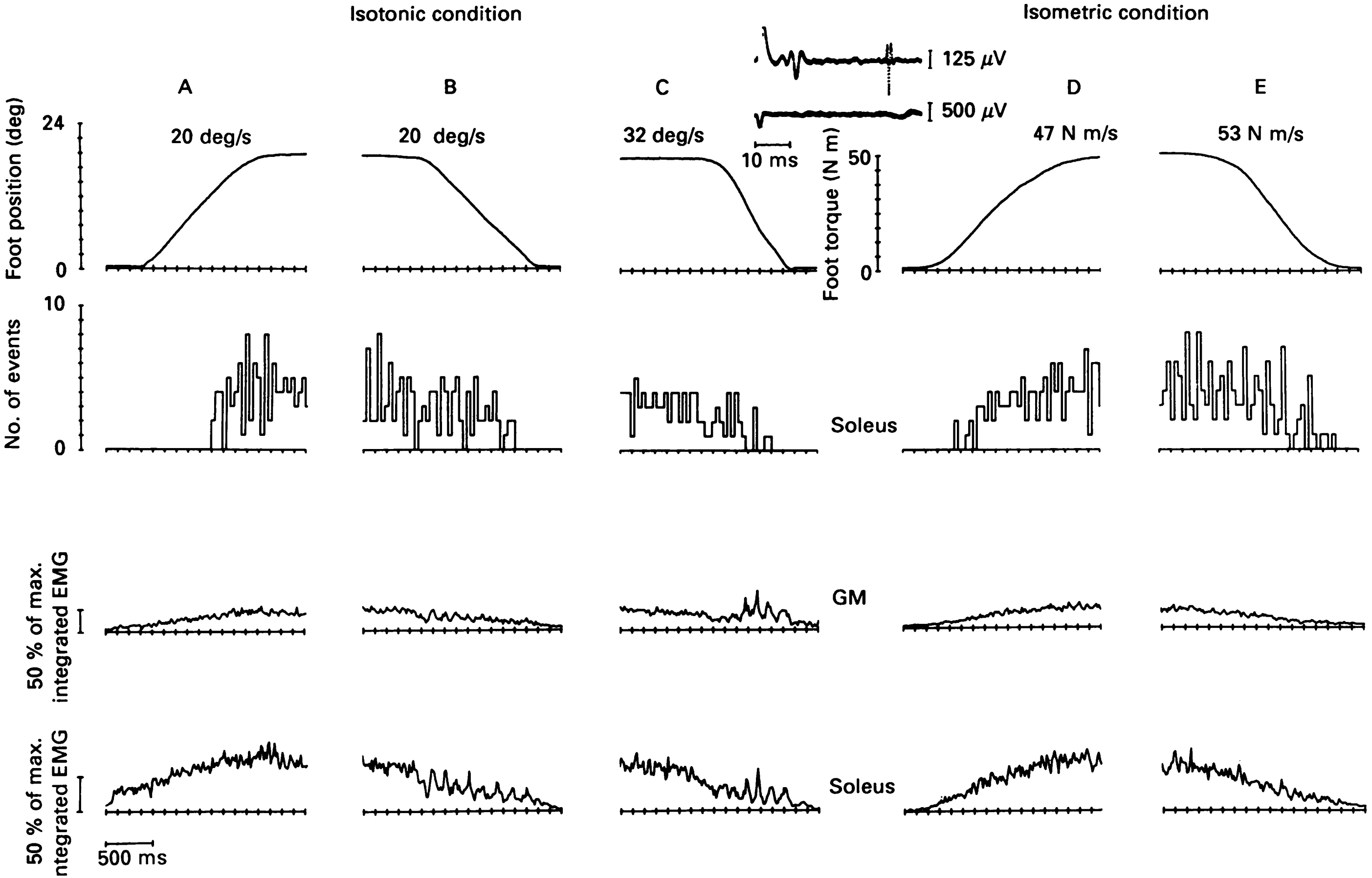

Fig. 6. Pattern of discharge of a soleus S+L unit during controlled shortening (*A*) and lengthening contractions at two different velocities (*B* and *C*), and during isometric contractions (*D*) and relaxations (*E*). From top to bottom: foot position (*A*, *B* and *C*) or torque (*D* and *E*), frequency histogram of unit's discharge, GM and soleus integrated EMGs (averages of twenty trials). This unit is gradually recruited and derecruited during shortening and lengthening contractions, as well as in the case of isometric increase and decrease of torque. Its firing frequency is not influenced by the velocity of foot rotation (compare *B* and *C*). Inset at the top shows the unit's action potential, along with raw soleus EMG (three superimposed traces). The unit is reflexively recruited on low-intensity stimulation of the tibial nerve at the popliteal fossa. The threshold strength for activating the unit was just supraliminal for the H reflex (small deflection on the right).

population of the units recruitable during ramp isometric contraction, was 92·4 N m. The last group of data points on the right belongs to units not voluntarily recruitable on either plantar ramp or ballistic contraction. On extrapolation of the regression line, the average threshold torque of this group of units would be 169·5 N m; all units of this group were L units.

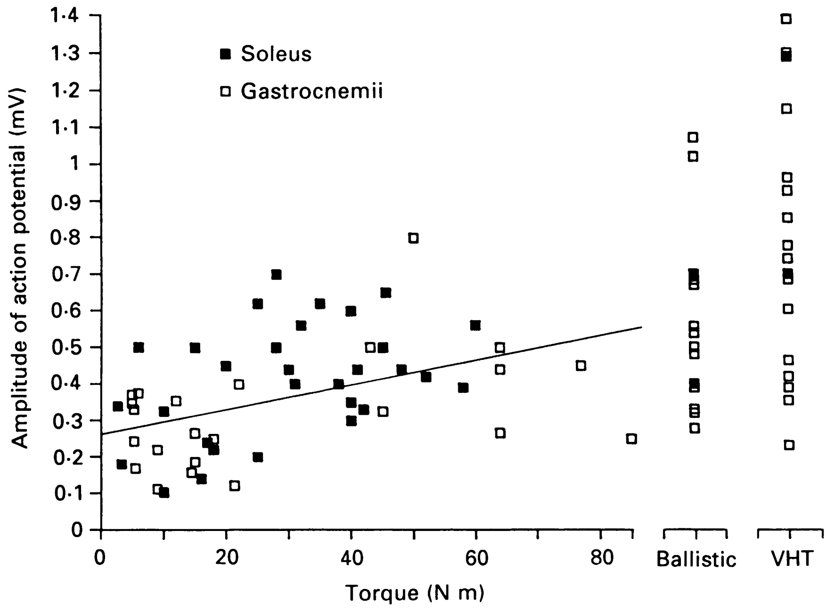

Fig. 7. Relationship between amplitude of motor unit action potential and torque threshold. The graph shows pooled data from S, S+L and L units from soleus and both gastrocnemii. The regression line ($y = 3{\cdot}1\ x + 283{\cdot}8$; $P < 0{\cdot}05$) has been fitted through the data points belonging to motor units recruited during ramp isometric contractions. On the right are reported the amplitudes of the action potentials of the units recruited in ballistic contractions and of those units classified as very high-threshold (VHT) units, i.e. not recruitable at all with a voluntary shortening or isometric effort.

If the spike amplitude and torque data are split into three parts according to the phase in which the units are active (pooling that data from soleus and gastrocnemii), the following results are obtained. Neither the mean amplitudes of the potentials, nor the mean torque levels (at which the motor units are recruited under ramp isometric effort) are significantly different between the units active during either S (spike amplitude 350·1 ± 180·7 μV (S.D.); torque 34·8 ± 22·6 N m) or S+L (spike amplitude 393·7 ± 204·6 μV; torque 27·7 ± 27·4 N m). On the other hand, the same parameters are significantly different ($P < 0{\cdot}05$) between the units of these two groups and the units active during L (spike amplitude 693·6 ± 261·3 μV; torque 55·2 ± 6·1 N m). If the allocation of the units in soleus or gastrocnemii is considered (Fig. 8), no significant difference is found, between muscles and within each condition, either for the mean spike amplitude or for the mean threshold torque (note, however, that the threshold torque was measured for only four of the units discharging during dorsal flexion, all the others being very high-threshold units).

As far as the units active during plantar flexion (S) or plantar and dorsal flexion (S + L) are concerned, a significant regression was found between the degree of foot rotation in plantar flexion at which they started firing and both the amplitude of their potentials ($y = 12{\cdot}9\,x + 236$; $P < 0{\cdot}05$) and the threshold torque ($y = 2{\cdot}1\,x + 6{\cdot}1$; $P < 0{\cdot}05$) (not shown in figure). This result has the same meaning as the regression between spike amplitude and isometric torque, since the active force developed by the triceps muscle must increase during plantar flexion, regardless of constant torque, owing to the force–length relationship.

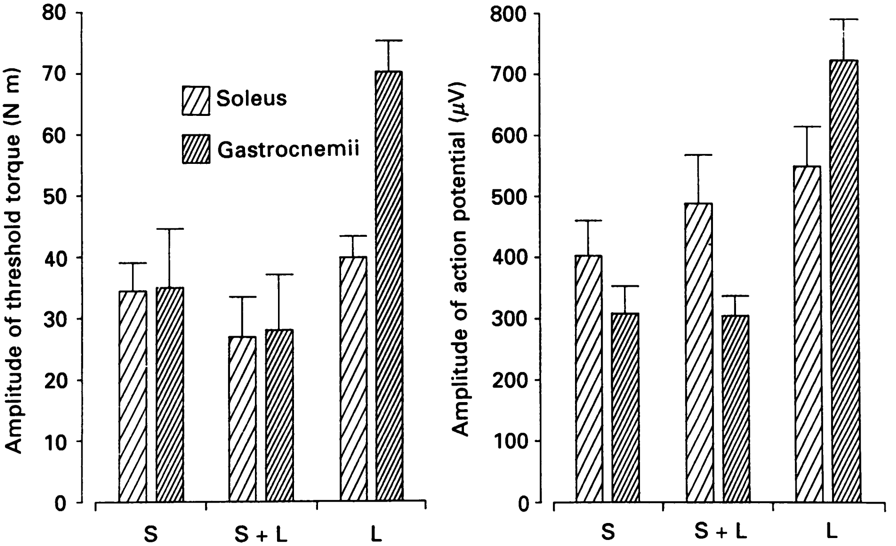

Fig. 8. Threshold torque (left) and action potential (right of soleus and gastrocnemii motor units pooled on the basis of the isotonic phase in which they are active. A significant difference is present (both for torque and spike amplitude) between conditions (L *versus* both S and S + L, pooled data from the two muscles), but not between muscles, within each condition. Each bar represents the mean + S.E.M.

DISCUSSION

A considerable number of motor units exist which are silent during shortening and sustained contractions, and fire during lengthening of the active muscles, as when braking a dorsiflexing load and gradually yielding to it. The L units are present both in the gastrocnemii and the soleus muscle, although they were picked up more frequently in the former than in the latter, in spite of repeated attempts.

These units have the following characteristics: (1) They are activated either (a) at a medium to high level of muscle force, when performing a voluntary, gradual increase in plantar torque under isometric conditions or (b) during quick, ballistic plantar efforts, either under isometric or isotonic conditions, or (c) they are non-recruitable under any of the above conditions. As far as the units in the gastrocnemii are concerned, they may be activated also (d) during a voluntary isometric ramp flexion of the leg, but in this case again their firing begins only on attainment of large forces, as witnessed by the level of integrated EMG. (2) It is very difficult to keep these units active for an extended period of time, as was previously described for muscle units assigned to type II (Grimby & Hannerz, 1977). This proved possible only in a very few cases, paying particular attention to the sound generated by the spike and by continuously performing small adjustments in the foot or leg position. This fact strongly suggests their assignment to fast-fatiguing units (Burke, Levine, Tsairis & Zajac, 1973; Garnett, O'Donovan, Stephens & Taylor, 1978). (3) The mean amplitude of the action potentials of the units discharging only during active lengthening is significantly larger than that of the units discharging during the phase of shortening contraction. This suggests that these motor units are made up of a high number of large muscle fibres (Olson, Carpenter & Henneman, 1968). (4) The conduction velocity of the two motor axons, which could be measured through stimulation of the gastrocnemius medialis nerve in two points, falls in the upper range of conduction velocities measured for the motor nerves of the leg in humans (Thomas, Sears & Gilliatt, 1959; Mayer, 1963; Mavor & Atcheson, 1966; Behse & Buchthal, 1971; Ingram, Davis & Swash, 1987). The parent axon of ten more motor units in this group was also excited by the very low stimulus strengths in either stimulating site, indicating a large diameter of the fibre. No L unit was ever activated at a latency compatible with the delay of the monosynaptic reflex.

We therefore feel confident that the above units can be classified as high-threshold units, most likely units innervated by large motoneurones furnished with a large axon and a low-excitability soma, and whose mechanical properties are presumably those of a short contraction time and a short relaxation time (Fleshman, Munson, Sypert & Friedman, 1981). During active lengthening, these units come into play, but they don't do so on the basis of their position in the expected rank order of recruitment. In fact, in this phase the active muscle force must decrease from the level achieved in the holding phase, or in the phase of plantar flexion during periodic foot rotation. This is because: (a) at the beginning of the dorsal flexion, less force is needed to sustain the weight, the force due to the inertia of the load being of opposite phase to the actual movement, (b) as long as the dorsal flexion goes on, the elastic elements of the triceps muscle take on part of the weight themselves (Romanò & Schieppati, 1987), and (c) the active muscle units, whichever they be, develop more force during the lengthening phase than under isometric (holding phase) or shortening contraction (plantar flexion), all things being equal.

Therefore, the recruitment of these units must occur at the expense of derecruitment of other motor units during the lengthening contraction, to allow easing down of the load. This is indeed what happens, as indicated by: (1) The not so negligible percentage of units found to fire only in plantar flexion (both in the soleus and gastrocnemii), whose number is certainly underestimated since most of our attention was devoted to identifying the motor units active during lengthening (which were also the largest). (2) The observation of the integrated EMG in the soleus, whose amplitude is larger during shortening than during lengthening contraction (see also Romanò & Schieppati, 1987). (3) The observation of an analogous EMG pattern in the gastrocnemii, when they are active also during shortening, as occurs during rapid foot rotations. In this case (see Fig. 4), the amplitude of the EMG can be larger during plantar than dorsal flexion, in spite of the appearance in the latter phase of the newly recruited high-threshold unit(s). On the other hand, even when the EMG in the gastrocnemii is larger during lengthening than shortening contractions, such as occurs at intermediate velocities of rotation, the wire records show poor background activity during lengthening (see Fig. 5).

A substantial proportion of the units studied discharged both during lengthening and during shortening contractions (S + L units), and most of these were active also in the holding phase. These units, however, do not share the same properties with the units active exclusively during lengthening, because: (1) the torque level at which they were first recruited during a ramp plantar effort is significantly lower; (2) the amplitude of the unit's action potential is significantly smaller, (3) stimulation to the muscle nerve never evoked direct activation of the motor axon of these units, while it could activate them reflexively, at a very low stimulus strength (cf. Calancie & Bawa, 1985). Within this group, the mean values of threshold torque and amplitude of action potential were not, in turn, significantly different from those of the units found to be active during plantar flexion only.

As to the pattern of discharge, the S+L units appear to behave, during foot plantar and dorsal flexion, very much as in increasing and decreasing isometric effort, which manoeuvre admittedly implies a 'normal' recruitment and derecruitment of motor units (Milner-Brown, Stein & Yemm, 1973*b*; Denier van der Gon *et al.* 1985; De Luca, 1985). In fact, they increased and decreased gradually their frequency of firing under plantar and dorsal flexion, respectively, and the mean frequency of discharge was lower during dorsal than plantar flexion, at comparable velocities of foot rotation. The ample scatter in the amplitude of the action potential of the units in this group can be connected with the demonstrated recruitment of both slow-twitch and fatigue-resistant units at low force levels in the human gastrocnemius medialis (Garnett *et al.* 1978). Since a large proportion (86%) of the S+L units fire during the sustained contraction subserving the holding phase, we suggest that their discharge during plantar and dorsal flexion corresponds to the increasing neural drive required to reach the appropriate frequency of discharge needed to hold the load in position, and to the diminution of the same to allow the derecruitment, respectively. In this sense, these units assure the background activity (both electrical and mechanical) on top of which the discharge of the high-threshold units is superimposed during the lengthening reaction.

In addition, as far as it can be deduced from the soleus data, these units do not appear to be causally correlated with appearance of the bursts in the surface EMG of the corresponding muscle (see for example Fig. 6), which are characteristic of the lengthening reaction and are possibly generated instead by those few units discharging only during lengthening (Fig. 3). In this regard, it may be noted that the bursting activity in the soleus muscle occurs at about the same velocities of dorsal flexion at which the gastrocnemius becomes active (see for example Figs 1 and 6). Although we have no direct evidence of simultaneous activation of high-threshold units in both muscles during this phase, it is tempting to attribute this behaviour to the 'common drive' mechanism (De Luca, 1985), whereby more motor units, in the same or different muscles (De Luca & Mambrito, 1987), receive the same descending command in parallel. If this is plausible, then the motor units, target of the common command, might well belong to the same type.

These results appear to be in favour of the hypothesis arrived at previously, and recalled in the Introduction, that fast-twitch, and therefore fast-relaxing motor units, may be selectively brought into action during a voluntary task implying controlled lengthening of active muscle. The frequency of discharge of these units in this act is accordingly rather low, certainly much lower than during a maximal ballistic or sustained contraction. At these low frequencies of discharge, the unfused tetanus of the fast-twitch motor units should correspond to about 20% only of their maximal tetanic tension (Ducati *et al.* 1982), so that a favourable exchange between force and velocity of relaxation is not unlikely. It should be noted that L units are active only at intermediate ranges of load weight and velocity, since slow velocities of lengthening of the active muscle do not need fast-relaxing motor units to be recruited. Conversely, small weights can be eased down mostly by relying upon the passive components of the muscle, or, if they are too small and/or the required velocity of dorsal flexion too high, the subjects use the alternative strategy of activating the pretibial muscles. Within these limits, the firing of the L units is modulated by the required velocity of lengthening, in a way different for different units, probably as a function of the mechanical characteristic of the units. In addition, for all high-threshold units there was at least a range of velocities within which a positive correlation was found between velocity and frequency of firing. S + L units never showed such a correlation, whereas they did sometimes (see Fig. 6) show a negative correlation between the same parameters, as expected if the active muscle develops more force at higher than at slower velocity of stretch (Joyce *et al.* 1969). These findings also corroborate the results obtained by studying whole-muscle activity during lengthening (Nardone & Schieppati, 1988), and allow the attribution of most of the surface EMG of lengthening muscles to the activity of high-threshold, fast-twitch motor units.

Failure to detect consistently selective recruitment of fast muscles or high-threshold motor units during human movement (see Thomas *et al.* 1987, for a review of the recent literature) may simply be attributed to the particular tasks investigated, which never included controlled lengthening of active muscles. In this connection, we should emphasize that the lengthening reactions described in this investigation appear to be a rather skilled task, for the correct performance of which attention is required. The short period of time necessary for learning to produce a smooth movement trajectory (a few repetitions were enough for all subjects) only indicates that control of lengthening of muscles while active is not an unusual burden to the central nervous system. Another notable observation is that on several occasions the high-threshold motor units were recruited just *before* onset of lengthening (see for example the units of Figs 2 and 4). It might therefore be envisaged that, at least in a predictable task as that employed here, subjects can funnel the motor commands to the appropriate motor units, without recourse to afferent feed-back, as has been recently demonstrated for the intrinsic muscles of the hand under different experimental circumstances (Gandevia & Rothwell, 1987). The observation of the changes in recruitment (anticipation, time to peak firing) which occur both within and between units in relation to the velocity of lengthening, and therefore to the force modulation necessary to overcome the inertia of the load, suggests that the motor system can control subtly both the timing and the targets of the excitatory command to the motor pool, and possibly to the spinal interneurones, in order to cope with the constraints of the task. That the motor units voluntarily called into action are fast-twitch ones appears not unlikely also in the light of early results of Clough, Kernell & Phillips (1968) in the baboon, showing larger corticomotoneuronal EPSPs for cells with rapidly conducting axons than for those with more slowly conducting axons, at least among motoneurones of the median nerve (see Discussion in Clough *et al.* 1968).

Our results shed no light on the possible neural pathways responsible for this phenomenon. They do not oppose, however, the hypotheses put forward and discussed earlier (Schieppati, Nardone & Musazzi, 1986; Romanò & Schieppati, 1987; Schieppati, 1987) that recurrent and presynaptic inhibitions can contribute to changing the order of recruitment of the motor units. In fact, in order to put together the present findings with that of the literature, one could speculate that the motor command to perform a lengthening contraction would be sufficiently intense to activate the largest motoneurones. The simultaneous activation (both direct and reflex, through the γ-loop) of the small, most excitable ones would be minimized by the descending enhancement of both the recurrent inhibition from the large to the small motoneurones, and the presynaptic inhibition of the Ia terminals, which are known to be distributed mostly to the small motoneurones (see Nardone & Schieppati, 1988). This notion would also explain the lack of reflex, unwanted muscle contraction, due to autogenetic motoneurone excitation from spindle stretch, expected during the performance of the lengthening task. However, it does not exclude other possibilities, as for example those envisaged by Hoffer, Loeb, Sugano, Marks, O'Donovan & Pratt (1987). They found functional segregation of motor units in the sartorius muscle during locomotion in the cat, and proposed the existence of task-related motoneurone groups within a motor pool having different central connections and recruitment characteristics. In this regard, it may be observed that one group of their units was recruited during active lengthening, and that these units co-existed with those active during shortening, within a single anatomical subdivision of the muscle. As to the connectivity of the motoneurones belonging to different functional groups one of the inputs more relevant in order to allow selective recruitment of fast-twitch motor units may be indeed the Ia synaptic projections, known to be distributed differently within the sartorius motoneurone pool (Eccles & Lundberg, 1958). This is in turn a necessary condition for the differential control of groups of motoneurones by descending presynaptic modulation. For the time being, and whatever the responsible neural networks may be, we should limit ourselves to suggesting the likelihood that more muscles are multifunctional (Hoffer *et al.* 1987; see Loeb, 1987), possibly all muscles independent of their anatomy, at least when shortening and lengthening contractions are considered to be two different tasks (see Stuart, Hamm & Vanden Noven, 1988). This is not unlikely in the light of the striking differences in kinematic and dynamic features in the two conditions.

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