RESEARCH ARTICLE

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The "size principle" and synaptic effectiveness of muscle afferent projections to human extensor carpi radialis motoneurones during wrist extension

Abstract The question of whether muscle spindle afferents might control human motoneurone activity on the basis of the "size principle" during voluntary contraction was investigated by recording the discharge of single motor units (n=196) in wrist extensor muscles while stimulating the homonymous muscle spindles by means of tendon taps. The mechanical stimuli were delivered with a constant post-spike delay of 80 ms so that the resulting afferent volleys could be expected to reach the motoneurones towards the end of the inter-spike interval (mean±SD duration: 124.7±11.9 ms). In the six subjects tested, the response probability was found to be significantly correlated with the motor units' functional parameters. Differences in twitch rise times, twitch amplitudes, recruitment thresholds and macro-potential areas were found to account for 18%, 9%, 6% and 2% of the differences in the response probability observed within the whole population of motor units tested. These differences could not be due to differences in firing rate for two reasons: first, the motor units were found to discharge with a similar range of inter-spike intervals whatever their functional characteristics; secondly, the weak positive correlation observed between the response probability and the motor unit firing rate showed parallel regression lines between the late-recruited fast-contracting motor units and the first-recruited slowly contracting motor units, but the y-intercept was significantly higher in the latter case. This confirmed that the responses of the first-recruited slowly contracting motor units tended to be larger whatever the firing rates. In most of the pairs tested in the same experiment, the motor units which had the lowest recruitment thresholds, longest contraction times, smallest contraction forces or smallest motor unit macro-potentials tended to produce the largest responses, which also had the longest latencies. Taking the response latency to be an index of a motoneurone's conduction velocity and therefore of its size, the data obtained with this index – and with other functional indices such as the twitch rise times and amplitudes, the macro-potential areas and the recruitment thresholds – can be said to be fully consistent with the "size principle", as previously found in anaesthetized animals. It can be inferred that the presynaptic inhibition which is liable to take action during voluntary contraction does not seem to alter the graded distribution of the muscle afferent projections to human wrist extensor motoneurones.

Key words Motor units · Muscle spindle · Size principle · Wrist extensor muscles · Humans

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Introduction

During voluntary contraction, the muscle spindles – specialized stretch-sensitive endings which monitor the muscle length – generate a continuous flow of inputs which are thought to contribute to the regulation of motoneurone discharge (Vallbo 1973; Burke 1981; Roll and Vedel 1982). The mono- and polysynaptic actions of these inputs have been thoroughly documented in animal experiments (Matthews 1972). For instance, the amplitude of homonymous Ia monosynaptic excitatory postsynaptic potentials (EPSPs) has been found to depend on both the size and the intrinsic membrane properties of the motoneurone (Eccles et al. 1957; Lüscher et al. 1983; Gustaffson and Pinter 1985) and on the biomechanical properties of the motor units (Burke 1968; Burke et al. 1976; Dum and Kennedy 1980; Fleshman et al. 1981). On the basis of these data, small motoneurones, which are associated with slowly conducting axons and slowly

contracting muscle fibres producing small forces, can be expected to receive larger Ia EPSPs than the larger motoneurones, which are associated with faster conducting axons and faster contracting muscle fibres producing larger forces. This gradient in the EPSP amplitude is thought to contribute to or at least assist the order of recruitment or "size principle" described by Henneman (1977), according to which the motor units consisting of small, slowly conducting motoneurones and slowly contracting muscle fibres are recruited before those consisting of large, fast-conducting motoneurones and fast-contracting muscle fibres (cf. Henneman and Mendell 1981; Pinter 1990; Heckman and Binder 1990; Mendell et al. 1990).

These data were largely obtained on anaesthetized animals lacking the normal patterns of activity in the supraspinal and peripheral pathways, which exert a presynaptic inhibitory control on the transmission of Ia monosynaptic projections (cf. Rudomin 1990, 1994). In humans, the existence of such a presynaptic inhibition has been clearly established (cf. Hultborn et al. 1987). The amount of presynaptic inhibition exerted was also found to vary, depending, for instance, on the muscle and on the motor task (Capaday and Stein 1986; Katz et al. 1988) and on the activity of cutaneous afferents (Berardelli et al. 1987). The question therefore arises as to what becomes of the distributed action of the Ia afferents on the various types of motoneurones during voluntary contraction, when presynaptic inhibitory processes are going on. Animal data have suggested that the degree of presynaptic inhibition might be directly correlated with the amplitude of the Ia EPSPs (Zengler et al. 1983). If the same principle holds in humans, the graded action of Ia afferents following the "size principle" might be preserved during voluntary contraction.

Only a few studies have addressed the possible existence of a gradient relating the amplitude of the monosynaptic Ia projections to the properties of single motor units in humans. The results obtained on the first dorsal interosseous muscle (Buller et al. 1980), the soleus muscle (Awiszus and Feistner 1993) and the tibialis anterior muscle (Ashby et al. 1986; Semmler and Türker 1994) have shown the existence of some discrepancies which suggest that the "size principle" might not apply uniformly, depending on the muscle and/or on the parameter used to characterize the motor unit type.

The present study was therefore undertaken to investigate further the distribution of Ia muscle spindle projections in terms of the "size principle" during voluntary contraction in another group of muscles, namely the extensor carpi radialis longus and brevis muscles. The responsiveness of wrist extensor motoneurones to homonymous Ia volleys elicited by tendon taps was studied in relation to each of the mechanical and electrical parameters which are relevant to classifying the motor unit functional types, i.e. the twitch rise time and amplitude, the force recruitment threshold, the macro-potential area and the conduction velocity. Since complete convergence between the data based on all these criteria was observed

here for the first time in humans, the distributed action of the Ia muscle spindle afferents on the wrist extensor motoneurones can be said to follow the "size principle" during voluntary contraction.

Material and methods

Experiments were performed on both arms of six healthy male subjects aged 18–30 years, with the approval of the ethics committee of the local Medical University (CCPPRB, Marseille I, approval no. 92/74). All subjects gave their informed consent to the experimental procedure, as required by the Helsinki Declaration (1964).

Instructions to subjects

The subjects were seated in an adjustable arm-chair. Their right or left forearm was placed in a cushioned groove so as to ensure that the same stereotyped position was adopted from one experiment to another. The distal end of the forearm was immobilized in a device leaving the wrist joint free and maintaining the hand in a semi-prone position, flexed at an angle of 10°, with the back of the hand in contact with an isometric force transducer. Auditory and visual feedback of the single motor unit activity was constantly provided to the subject on a loudspeaker and an oscilloscope.

The subjects were asked to perform selective contractions of the wrist extensor muscles by pushing on the force transducer device with the back of their hand, while keeping their fingers relaxed. The contraction level had to be adjusted so that the motor units kept firing tonically during two recording sequences, each lasting 5–6 min.

Each motor unit was tested in an initial sequence, during which about 1000 mechanical taps were applied to the tendons of the extensor carpi radialis muscles during voluntary contraction (see Stimulation paradigm). After a 3-min rest period, the same unit was tested with the same paradigm during a second sequence without any mechanical stimulation. During both sequences the subjects were asked to maintain the motor unit firing at the rate which could be sustained effortlessly for several minutes, with the help of visual and auditory feedback.

Muscle force recording

The net force produced by the wrist extension was calibrated in newtons and recorded as direct (DC) and filtered (AC; band-pass 0.1 Hz–1 kHz) signals. The AC force recorded without any mechanical stimulation was used off line to extract the motor unit twitch by means of the spike-triggered averaging method (Stein et al. 1972).

Muscle activity recording

A pair of single-use surface electrodes (non-polarizable Ag-AgCl, diameter 0.7 mm) was placed 2 cm apart, longitudinally over the extensor carpi radialis brevis and longus muscles in order to record the surface electromyographic (EMG) activity associated with their contraction during wrist isometric extension.

The action potentials generated by single motor units were recorded at random in either the extensor carpi radialis brevis or longus muscles by means of stainless steel single-use semi-microelectrodes (impedance 12 MΩ tested at 1000 Hz, Frederick Haer, Brunswick, ME, USA), previously sterilized in formaldehyde vapour.

The subject was connected to the ground through an electrode placed on the upper arm, close to the elbow. The microelectrode and the surface electrodes were connected to amplifiers (Grass P11, Grass Instruments, USA) through probes with an isolated

ground to ensure optimum subject protection (current leakage less than 3 µA). The bandwidths of the amplifiers were set at 30 Hz–10 kHz and 300 Hz–3 kHz for the surface and intramuscular recording, respectively.

Stimulation paradigm

The tendons of the extensor carpi radialis muscles were stimulated using a spike-triggered paradigm (Fig. 1A). The discharge from the voluntarily activated motor units was used to trigger a pulse generator (Grass S88 stimulator, USA), which delivered constant-voltage pulses activating an electromagnetic hammer (LDS 201 Vibration generator, UK) via a power amplifier, after a delay of 80 ms. The hammer was positioned over the distal part of the tendons of the extensor carpi radialis muscles. The magnitude (0.5 mm) and duration of indentation (2 ms) of the taps as well as the pressure exerted by the hammer were monitored and kept constant by means of an infra-red emitting-detecting photocell fixed to both the electromagnetic coil and the vibrating rod. After each triggering pulse, the pulse generator was automatically turned off for 300 ms in order to maintain the stimulation frequency at around 3 Hz (mean±SD:2.74±0.25 Hz).

The delay of 80 ms was chosen so that the afferent volley induced by the tendon taps could be expected to reach the recorded motoneurone approximately 100–110 ms after each triggering action potential, given the conduction times from the motoneurone to the muscle and from the muscle receptors to the motoneurones, i.e. the reflex loop (80 ms+20–30 ms). The inter-spike intervals in the motor unit discharges had a mean duration of 124.7±11.9 ms in the present experiments. Under these conditions, most of the afferent volley could be expected to reach the motoneurones after the triggering action potentials at the most favourable time for triggering the subsequent firing, i.e. when the membrane potential was approaching its firing threshold at the end of the post-spike hypo-excitability period.

To determine the motor unit twitch and macro-potential, the above paradigm was repeated with the electromagnetic hammer turned off, during the period when the recordings were carried out with no mechanical stimulation.

The force signals (DC and AC), the surface EMG recording, the microelectrode recordings, and the pulses which triggered the tendon taps were stored on a digital tape recorder (Biologic DTR 1800) for off-line analysis.

Discrimination of single motor unit activity

Dual time-amplitude window discriminators (BAK Electronics, USA) were used to discriminate the action potentials recorded by the microelectrode and to generate TTL pulses. These pulses were subsequently used to analyse the single motor unit activity using conventional computer procedures. An autocorrelogram of each motor unit's discharge was systematically computed in order to check that no spurious firing of other motor units had occurred, which might have led to abnormally short inter-spike intervals during the period of post-spike hypo-excitability.

Motor unit recruitment threshold

The subjects were asked to perform stereotyped ramp contractions (0.25 N·s⁻¹) at the beginning of each recording session with and without mechanical stimulation. The force level at which the motor unit started to fire was measured in each ramp and the mean of the two values obtained with each motor unit was taken to be its force recruitment threshold. Since the extensor carpi ulnaris and the extensor digitorum communis muscles contribute to the maximal wrist extension force, it was impossible, however, to express the motor unit recruitment threshold in terms of the percentage of the maximal force produced by the selective contraction of the extensor carpi radialis muscles.

In addition to the threshold measurement, the DC force associated with the wrist isometric extension was averaged 200 ms before and after each of the motor unit action potentials (Fig. 1D,E) during the whole duration of the two sequences performed with and without mechanical stimulation.

Motor unit contractile properties

To evaluate the motor unit contractile properties, the force change (twitch) selectively associated with the activity of each motor unit was extracted by applying the spike-triggered averaging procedure (Fig. 1B,C) to the net filtered extension force (band-pass 0.1 Hz–1 kHz), as described by Stein et al. (1972). To minimize the distortion resulting from the partial fusion of successive twitches, any spikes occurring with an inter-spike interval of less than 130 ms (both before and after the spike) were excluded from the analysis (Nordstrom et al. 1989). This exclusion criterion was applied successfully in about 80% of all the cases tested. In the remaining 20% of cases where the units fired at frequencies higher than 7 imp·s⁻¹, the minimum inter-spike interval was set at 100 ms.

The rise time and force (Fig. 1B,C) of the twitch extracted for each motor unit were measured and taken as indexes of its contractile properties.

Motor unit bioelectrical characteristics

The motor unit macro-potential, or macro-MUP (Fig. 1F,G), which reflects the activity of all the muscle fibres of a given motor unit, was derived by applying the spike-triggered averaging procedure to the surface EMG activity recorded during the two sequences when the motor unit was tested (first, associated with tendon taps, and secondly, without any mechanical stimulation). The shapes and amplitudes of the macro-MUPs obtained during these two periods were carefully compared to make sure that the same motor unit had been tested during the two periods.

The size of each macro-MUP was assessed in terms of its area (mV·ms). To assess the earliest sign of a motor unit's electrical activity, the time elapsing between the onset of the macro-MUP and the TTL pulse generated by the muscle fibre action potential recorded by the microelectrode was measured (time elapsing between 0 and arrow in Fig. 1F,G). The values observed ranged from 2 to 18 ms (mean±SD: 8.32±3.01 ms). The variability of these values could be attributed to differences either in the position of the microelectrode within the field occupied by the muscle fibers of the motor unit tested and/or in the position of the window discriminators in relation to the time course of the action potential recorded by the microelectrode.

Analysis of motor unit responses induced by tendon taps

The motoneurone reflex activation was analysed during each sequence of stimulation by computing peri-stimulus time histograms giving the firing probability of the motor units in bins of 0.5 ms, 200 ms before and after the tendon tap. The motor unit response was characterized by an increase in the bin counts forming a peak with a latency compatible with monosynaptic activation (Fig. 1H,I). The amplitude of the peaks was assessed in terms of motor unit "response probability per trigger", which was given by the number of impulses in the peak above the baseline divided by the number of stimulus pulses. The baseline was positioned symmetrically in latency and duration as regards the peak response with respect to the triggering action potentials in the left part of the peri-stimulus time histogram which, due to the spike-triggered stimulation paradigm used, was similar to the autocorrelogram of the motor unit discharge without any stimulation.

In order to assess accurately the peak onset, a cumulative sum (Ellaway 1978) was computed which gave the variation in the content of the successive bins of the peri-stimulus time histogram

with respect to the mean value computed over a period of 200 ms before the stimulation. The onset of the response was identified by the occurrence of a sharp rise in the cumulative sum after the tendon tap pulses. The latency and duration of the post-stimulus rise in the cumulative sum were used for the final delimitation of the baseline positioned symmetrical to the peak response with regard to the triggering impulses, in a region of the peri-stimulus time histogram representing the firing of the motor unit expected without stimulation.

The peak onset reflected the activation of only a small fraction of the motor unit muscle fibres, i.e. those whose action potentials were recorded by the microelectrode. The latency of the motor unit response as a whole was therefore evaluated as described by Awiszus and Feistner (1993), by taking the earliest sign of motor unit electrical activity, i.e. the macro-MUP onset time measured as explained above (Fig. 1F,G). The latency of the whole motor unit response (subsequently referred to as the "corrected latency") was obtained by subtracting the macro-MUP onset time from the latency of the response measured from the peri-stimulus time histogram.

At each stimulation session, the tendinous reflex was systematically averaged from the surface EMG using the tendon taps as triggers.

Motor unit firing rate

The motor unit firing rates were characterized in terms of the mean duration of inter-spike intervals of the tonic discharges (discarding any intervals longer than 300 ms). The possible dependence of the response probability on the inter-spike interval duration was investigated by analysing the responses of motor units tested during two to four successive periods of stimulation lasting about 80 s and including 250 tendon taps.

Quantitative and statistical analyses

In each experimental session only the motor unit activity providing auditory and visual feedback to the subjects was analysed. The various bioelectrical and biomechanical parameters of the motor units, their discharge frequencies and their response latencies and amplitudes were analysed by performing simple linear regressions in order to determine what relationships existed consistently between these parameters among the subjects. Whenever necessary, the slopes and the y-intercept of the regression lines were compared using an F-test developed by Snedecor and Cochran (1989).

Paired comparisons were performed on the discharge and response characteristics with an ANOVA procedure for repeated measures (Statview 4 Macintosh software, Abacus Concept) by selecting at each experiment the two motor units which displayed the highest and lowest values of each of the relevant functional parameters, i.e. recruitment threshold, twitch rise time, twitch amplitude, macro-MUP area, response latency and mean inter-spike interval.

Results

A total of 236 motor units were tested, each of which was characterized by the mean duration of the inter-spike intervals, the level of its force recruitment threshold, the rise time and amplitude of its twitch, the area of its macro-potential, and the latency and amplitude of its response to the tendon taps.

To reduce the likelihood of spontaneous firing occurring between the triggering action potential and the tendon tap, 40 motor units which discharged with mean inter-spike intervals shorter than the time required for the Ia afferent volleys to reach the motoneurone (80 ms+the duration of myotatic loop assessed by the latency of the motor unit response) were rejected. The remaining 196 motor units discharged with mean inter-spike intervals ranging from 103 to 152 ms (mean±SD: 124.72±11.92 ms), while the time taken by the afferent volleys to reach the motoneurones was estimated to range from 98 to 116 ms (mean±SD: 105. 31±3.43 ms). The Ia EPSPs could therefore be expected to affect the motoneurone membrane most when it was nearing the firing threshold, at the end of the ramp of repolarization followed by the membrane potential after each action potential (Schwindt and Crill 1982; Ashby and Zilm 1982).

Table 1 gives the descriptive statistics (mean and standard deviation, range) on each of the functional parameters which characterized the motor units selected in each subject.

Characteristics of the motor unit responses to tendon taps

The two motor units shown in Fig. 1 are typical examples of those tested during the same experiment in subject 1 (Table 1). One motor unit (Fig. 1B) produced a small twitch force (2.55 mN) with a fairly long rise time (77.23 ms), while the second motor unit (Fig. 1C) produced a much larger force (15.61 mN) and a faster twitch rise time (28.83 ms). Accordingly, the slowly contracting motor unit was recruited at a low level of extension force (0.22 N), as confirmed by the low value of the averaged DC force (0.33 N, Fig. 1D), while the fast-contracting motor unit had a much higher force recruitment threshold (2.32 N), as confirmed by the high value (2.83 N) reached by the averaged DC force (Fig. 1E). The two motor units also differed markedly as regards their macro-potentials: the slowly contracting, low-threshold motor unit showed quite a small macro-MUP (Fig. 1F) with an area of 0.36 mV·ms, while the fast-contracting, high-threshold motor unit showed a much larger macro-MUP (Fig. 1G) with an area of 1.14 mV·ms.

Similar relationships between the motor unit's electrophysiological and biomechanical characteristics (macro-MUP area, twitch amplitude, twitch rise time, recruitment threshold) were observed consistently in each of the six subjects, as shown in Table 2, which summarizes the correlation coefficients observed between these various parameters.

The peri-stimulus time histograms (Fig. 1H,I) illustrate the motor unit's firing probability before and after the tendon taps. As the stimulation was time-locked to the motor unit action potentials with a latency of 80 ms, the peri-stimulus time histograms also give the distribution of the discharge before and after the motor unit action potentials which triggered the tendon taps (i.e. the motor unit autocorrelogram). The responses to the tendon taps took the form of sharp increases in the probability of the motor unit discharge occurring 23.5 and 22.5 ms (corrected latencies in relation to macro-MUP

Table 1 Motor unit characteristics, firing patterns and reflex responses in each subject [mean±SD (range)]

Subjects	Motor unit characteristics				Firing properties	Reflex response			Peak duration (ms)
	Twitch rise time (ms)	Twitch amplitude (mN)	Recruitment threshold (N)	Macro-MUP area (mV.ms)	Inter-spike interval (ms)	Latency (ms)	Corrected latency (ms)	Response probability (imp./trigger)	
Subject 1 n=32	40.5±17.1 (18.8–78.4)	5.1±4.6 (0.04–17.1)	0.9±0.8 (0.04–3.6)	0.33±0.25 (0.04–1.0)	121.5±10.5 (104–145)	27.9±3.5 (21.5–34.0)	17.5±0.7 (16.2–19.2)	0.34±0.15 (0.09–0.71)	4.3±1.0 (3.0–6.5)
Subject 2 n=36	43.1±17.3 (19.6–81.6)	3.3±3.3 (0.04–10.3)	2.0±1.5 (0.17–5.6)	0.30±0.19 (0.02–0.7)	127.2±11.7 (106–151)	28.6±2.4 (24.5–32.5)	18.8±1.1 (16.8–21.2)	0.39±0.18 (0.02–0.67)	4.1±0.9 (2.5–6.5)
Subject 3 n=31	44.6±14.8 (21.9–74.5)	11.2±20.8 (0.05–68.1)	1.4±1.4 (0.12–5.3)	0.41±0.31 (0.09–1.2)	122.4±10.6 (104–141)	23.3±3.5 (18.0–30.5)	14.1±0.7 (12.5–15.5)	0.44±0.15 (0.09–0.79)	3.5±0.8 (2.0–6.0)
Subject 4 n=31	46.4±16.4 (18.0–76.8)	4.9±8.7 (0.6–29.9)	1.3±1.7 (0.03–6.9)	0.34±0.22 (0.03–0.8)	123.8±12.4 (103–143)	24.2±1.6 (22.0–27.5)	18.0±0.7 (16.5–19.2)	0.29±0.10 (0.12–0.51)	4.1±0.8 (2.0–6.0)
Subject 5 n=20	53.4±19.7 (20.4–86.2)	2.4±4.4 (0.07–14.4)	0.8±0.7 (0.16–2.5)	0.26±0.17 (0.03–0.54)	118.9±11.5 (103–143)	23.0±1.1 (21.5–26.0)	17.1±0.5 (15.5–18.9)	0.35±0.12 (0.19–0.62)	4.1±0.9 (3.0–6.5)
Subject 6 n=46	39.8±14.5 (19.6–75.3)	6.0±11.5 (0.1–66.1)	1.7±2.1 (0.08–9.5)	0.45±0.25 (0.10–1.2)	129.7±11.8 (103–152)	23.7±2.0 (20.0–28.0)	17.2±0.7 (16.2–19.1)	0.38±0.16 (0.16–0.90)	4.0±0.9 (2–6)

onset: 19.4 and 17.6 ms) after the tendon taps in the case of the slowly contracting, low-threshold motor units and in that of the fast-contracting, high-threshold motor units, respectively (Fig. 1H,I). The response probabilities of the slowly contracting, low-threshold motor unit (Fig. 1H) and the fast-contracting, high-threshold motor unit (Fig. 1I) were 0.411 and 0.282 imp·/trigger, respectively.
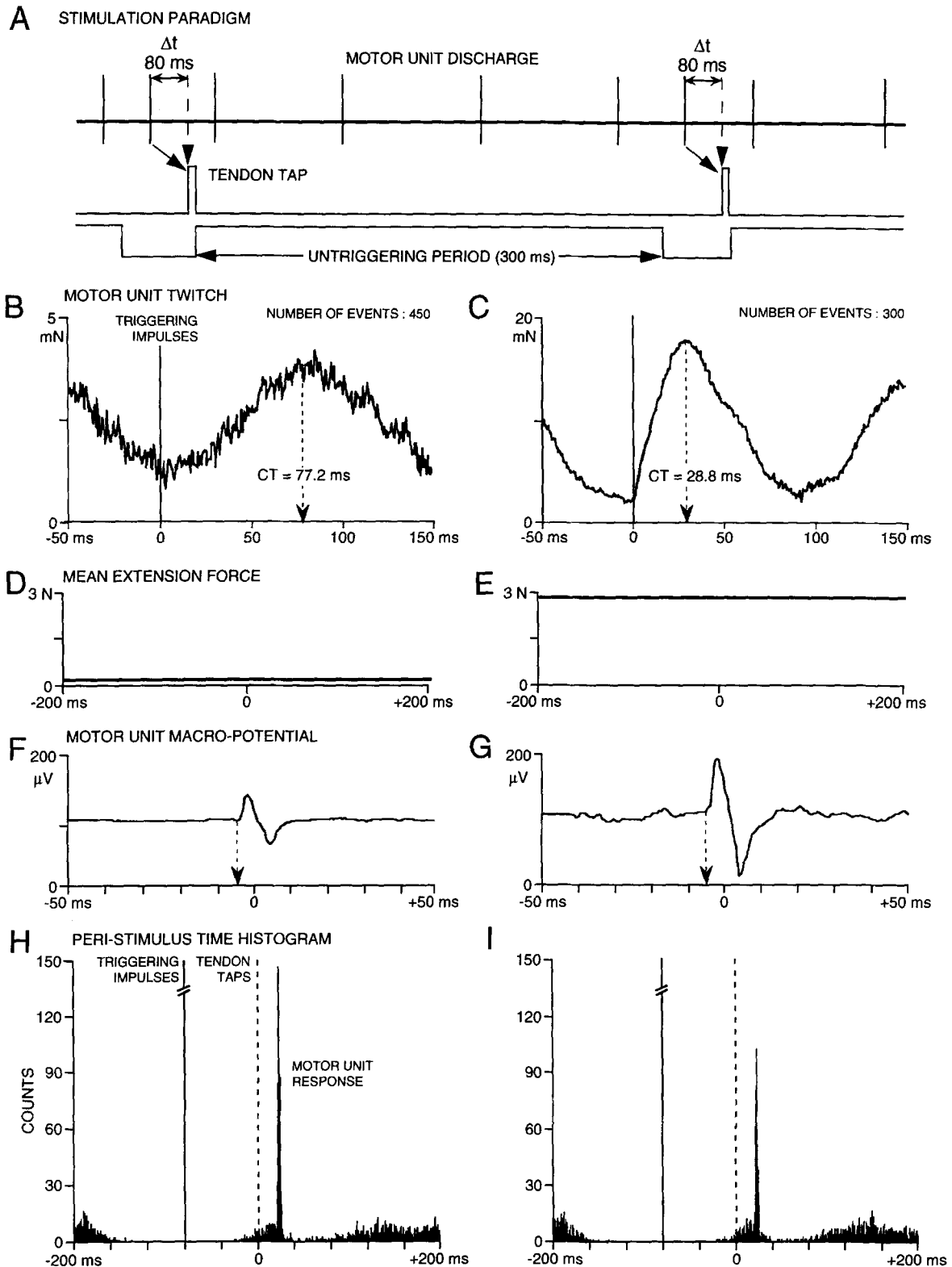
In these two examples, as in all the cases studied, the motor units' responses were concurrent with the tendinous reflex detected by averaging the surface EMG recording. The mean latency of the tendinous reflex versus the mean corrected latency of the motor unit responses was 17.6 versus 17.5 ms (subject 1), 18.7 versus 18.7 ms (subject 2), 14.1 versus 14.2 ms (subject 3), 18.4 versus 18.0 ms (subject 4), 17.4 versus 17.1 ms (subject 5) and 17.0 versus 17.2 ms (subject 6). These latencies are compatible with the idea that a monosynaptic pathway was involved.

Under the present conditions, only 24 of the 196 motor units tested (12%) showed late responses 5–20 ms after the early increases in firing, which suggests that polysynaptic spinal and/or supraspinal pathways may have been involved. In the present study, only the early peaks consistently produced by all the motor units with a latency compatible with a monosynaptic pathway were examined.

Correlations between the response probability and the motor units' biomechanical and electrophysiological parameters

Upon pooling the data obtained on the whole population of 196 motor units, weak but consistent trends were observed between the response probability and each of the motor unit's biomechanical and electrophysiological parameters (Fig. 2).

Fig. 1 A Experimental paradigm used to studied the motor units' responsiveness to Ia afferents in the extensor carpi radialis muscles. Percussion applied to the distal tendons of the muscles was triggered by single muscle fibre action potentials after a delay of 80 ms. A refractory period (300 ms) imposed on the pulse generator led to a limitation of the stimulation frequency to around 3 Hz. B, C Motor unit twitch extracted from the AC muscle force using the triggered averaging procedure. The triggering muscle fibre action potentials occurred at time 0 on the abscissa. Twitch rise times are marked by arrows with durations of 77.2 ms (B) and 28.8 ms (C), respectively. D, E Extension DC force averaged throughout the motor unit recording. F, G Averaged motor unit macro-potential (macro-MUP) extracted from the surface EMG recording by applying the spike triggered averaging procedure. Macro-MUP onset times are marked by arrows with values of 4.1 ms (F) and 4.9 ms (G) in relation to the triggering action potentials (time 0 in the diagram). H, I Motor unit discharge probability before and after the tendon taps triggered 80 ms after the muscle fibre action potentials. The increase in firing rate induced by the stimulation (motor unit response) occurred at latencies of 23.5 ms (H) and 22.5 ms (I). The earliest sign of the motor unit response was determined by subtracting the macro-MUP onset time from the response latency, giving corrected latencies of 19.4 ms and 17.6 ms, respectively

A STIMULATION PARADIGM

Δt 80 ms — MOTOR UNIT DISCHARGE — Δt 80 ms

TENDON TAP

UNTRIGGERING PERIOD (300 ms)

B MOTOR UNIT TWITCH
5 mN — TRIGGERING IMPULSES — NUMBER OF EVENTS : 450
CT = 77.2 ms
0
-50 ms   0   50   100   150 ms

C 20 mN — NUMBER OF EVENTS : 300
CT = 28.8 ms
0
-50 ms   0   50   100   150 ms

D MEAN EXTENSION FORCE
3 N
0
-200 ms   0   +200 ms

E 3 N
0
-200 ms   0   +200 ms

F MOTOR UNIT MACRO-POTENTIAL
200 μV
0
-50 ms   0   +50 ms

G 200 μV
0
-50 ms   0   +50 ms

H PERI-STIMULUS TIME HISTOGRAM
150 — TRIGGERING IMPULSES — TENDON TAPS
120
90 — MOTOR UNIT RESPONSE
COUNTS 60
30
0
-200 ms   0   +200 ms

I
150
120
90
60
30
0
-200 ms   0   +200 ms

The regression analysis of the motor unit response probability with respect to the twitch rise time is illustrated in Fig. 2A. The responses tended to increase with the twitch rise times ($r=0.42$, $P<0.0001$). Similar trends were observed in all six subjects, and the differences in contraction times were found to account for 15–32% of the differences in response probability.

The regression analysis of the response probability with respect to twitch amplitude (expressed on a logarithmic scale) is illustrated in Fig. 2B. The responses

Table 2 Correlation coefficients between the motor unit's biomechanical and electrophysiological properties

Motor unit properties	Subject 1 $n=31$	Subject 2 $n=27$	Subject 3 $n=31$	Subject 4 $n=27$	Subject 5 $n=31$	Subject 6 $n=39$	Total $n=186$
Twitch rise time vs twitch amplitude	**-0.67** ***	**-0.75** ***	**-0.63** ***	**-0.67** ***	**-0.56** ***	**-0.6** ***	**-0.51** ***
Twitch rise time vs recruitment threshold	**-0.61** ***	**-0.73** ***	**-0.73** ***	**-0.57** **	**-0.7** ***	**-0.67** ***	**-0.62** ***
Recruitment threshold vs twitch amplitude	**0.64** ***	**0.81** ***	**-0.63** ***	**0.6** ***	**0.67** ***	**0.62** ***	**0.62** ***
Macro-MUP area vs twitch rise time	**-0.52** **	**-0.64** ***	**-0.61** ***	**-0.38** *	**-0.59** ***	-0.3 $P=0.06$	**-0.45** ***
Macro-MUP area vs twitch amplitude	0.22 $P=0.2$	**0.57** **	**0.69** ***	0.27 $P=0.17$	**0.53** **	0.04 $P=0.8$	**0.45** ***
Macro-MUP area vs recruitment threshold	0.29 $P=0.1$	**0.61** ***	**0.77** ***	**-0.49** **	**0.65** ***	0.18 $P=0.2$	**0.46** ***
Reflex response latency vs twitch rise time	**0.61** ***	**0.43** *	**0.52** **	**0.53** **	**0.48** **	**0.55** ***	
Reflex response latency vs twitch amplitude	-0.28 $P=0.13$	**-0.43** *	-0.17 $P=0.35$	**-0.49** **	-0.21 $P=0.25$	-0.23 $P=0.1$	
Reflex response latency vs recruitment threshold	**-0.44** *	-0.26 $P=0.18$	**-0.4** *	**-0.49** **	**-0.53** **	**-0.42** **	
Reflex response latency vs macro-MUP area	**-0.41** *	**-0.4** *	**-0.35** *	**-0.49** **	**-0.42** *	-0.29 $P=0.07$	

* $0.01<P<0.05$, ** $0.001<P<0.01$, *** $0.0001<P<0.001$

tended to decrease as the twitch amplitudes increased ($r=-0.31$, $P<0.0001$). Similar trends were observed in the six subjects and the differences in twitch amplitude were found to account for 5–16% of the differences in response probability.

The regression analysis of the response probability with respect to the force recruitment threshold (expressed on a logarithmic scale) is illustrated in Fig. 2C. The responses tended to decrease as the level of recruitment thresholds increased ($r=-0.24$, $P<0.001$). Similar trends were observed in all six subjects and the differences in recruitment threshold were found to account for 3–15% of the differences in response probability.

The regression analysis of the response probability with respect to the macro-MUP is illustrated in Fig. 2D. The responses tended to decrease as the macro-MUP area increased ($r=-0.15$, $P=0.05$). Similar trends were observed in five of the six subjects, and in these five subjects the differences in macro-MUP area were found to account for 3–12% of the differences in response probability.

To reduce the possible effects of any variations in the position of the electromagnetic hammer from one experiment to the other that might have altered the response probability, the analysis was then restricted to the two motor units tested during the same experimental session which yielded the maximal and minimal values of each of the motor unit parameters observed at this session, respectively. The paired comparisons, which are summarized in Table 3, fully confirmed the trends observed in the regression analyses. Namely, the motor units with the lowest recruitment thresholds, the longest twitch rise times, the smallest twitch forces and the smallest macro-MUP areas produced larger responses than those with
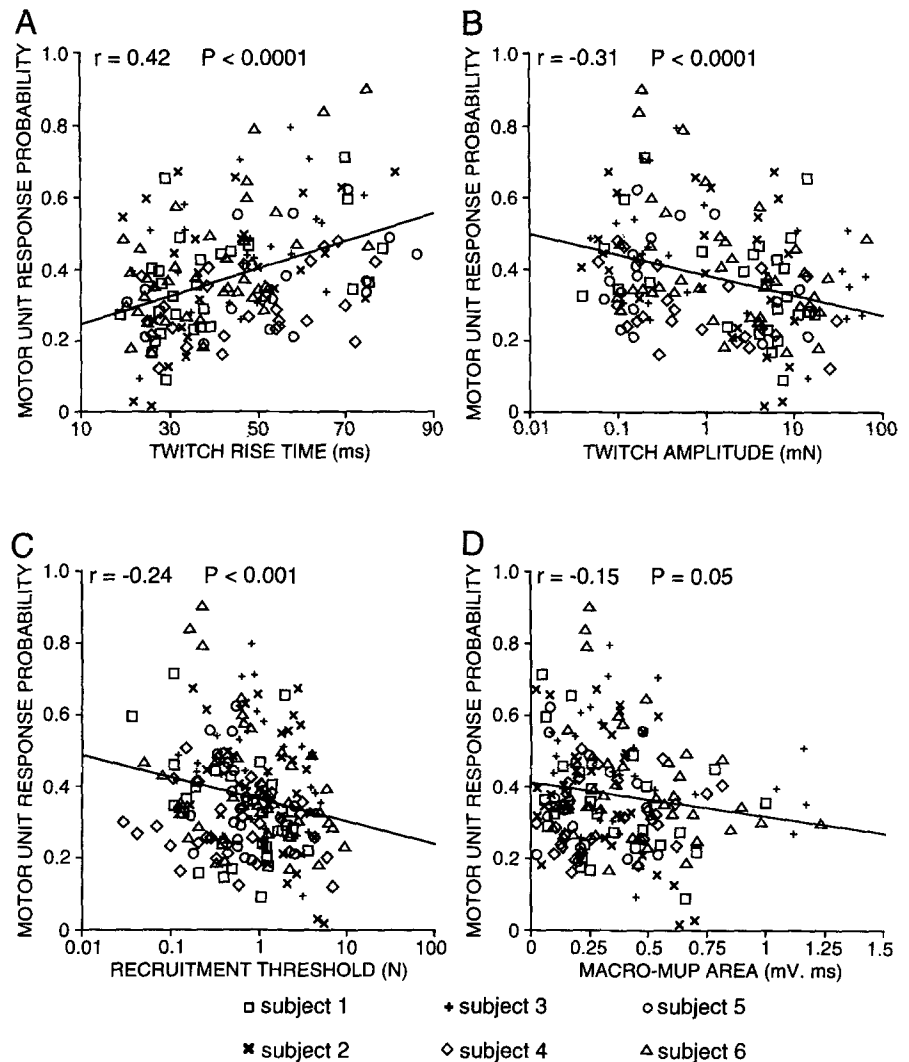
the highest recruitment thresholds, the shortest twitch rise times, the largest twitch amplitudes and the largest macro-MUP areas.

Correlations between the response latency and the motor unit characteristics

The latency of the response could be expected to depend on the motoneurones' conduction velocity, which in turn was presumably correlated with the motor units' biomechanical and electrophysiological characteristics.

This correlation was assessed by means of regression and correlation analyses. Significant correlations were observed consistently between a motor unit's corrected response latency and the level of its force recruitment threshold, the characteristics of its contractile force and the size of its macro-MUP area. The corresponding correlation coefficients obtained with each subject are given in Table 2. The regression analyses are shown in Fig. 3A–D for subject 1 and in Fig. 3E–H for subject 6. In both subjects, the response latency was negatively correlated with the recruitment threshold, as expressed on a logarithmic scale (Fig. 3A,E), with the twitch amplitude as expressed on a logarithmic scale (Fig. 3C,G) and with the macro-MUP area (Fig. 3D,H), and positively correlated with the twitch rise time (Fig. 3B,F). The paired comparisons (Table 3) fully confirmed that the motor units which had either the highest recruitment thresholds, the largest twitch amplitudes, the shortest twitch rise times or the largest macro-MUP areas tended to show shorter response latencies than the motor units which had the lowest recruitment thresholds, the smallest

Fig. 2 Regression analysis of the motor unit response probability to tendon taps in relation to the twitch rise time (A), the twitch amplitude (B), the recruitment threshold (C) and the macro-potential area (macro-MUP, D). The response probability was significantly correlated with the motor unit contractile properties, increasing when the twitch rise time increased (A), and decreasing when the twitch force (B), the recruitment threshold (C) and the macro-potential area (D) increased(D). These data confirm the existence of a gradient in the motor units' responsiveness to reflex activation, depending on their functional properties: the slowly contracting, low-threshold motor units producing small forces and characterized by small macro-potential areas were the most sensitive to Ia afferent inputs

□ subject 1   + subject 3   o subject 5

✱ subject 2   ◇ subject 4   △ subject 6

twitch amplitudes, the longest twitch rise times or the smallest macro-MUP areas in the same experiment. It was also observed that the differences between the shortest and the longest corrected response latencies observed in a given experiment tended to increase as the motor units showed greater differences in their recruitment thresholds ($r=0.31$, $P=0.02$), twitch rise times ($r=0.30$, $P=0.05$), twitch amplitudes ($r=0.31$, $P=0.05$) or macro-MUP areas ($r=0.25$, $P=0.08$).

Relationships between the response probability and the response latency

A significant positive correlation between the response probability and the latency was observed in subjects 1 and 6 ($r=0.50$, $P=0.0001$ and $r=0.47$, $P=0.001$, respectively). Upon pooling the data obtained on all six subjects, the paired comparisons between the motor units which showed the longest and the shortest latencies in each experiment (Table 3) yielded highly significant results, which confirmed that the longest response latencies tended to be associated with the largest response probabilities.

Figure 4A shows the covariation of the response latency (abscissa) and the response probability (ordinate) of the pairs of motor units which showed the longest and the shortest latencies, respectively, in each of the experimental sessions performed by the six subjects. In most of the pairs, the motor unit which showed the longest latency had the largest response probabilities. Figure 4B gives the regression analysis between the difference in response probability and the difference in latency of each pair. The differences in latency were found to account for 17% of the difference in response probability between the motor units of each pair ($r=0.41$, $P=0.001$).

Motor unit firing rate and responsiveness

No consistent relationships were observed in the regression analyses between the motor units' firing rates and any of their functional characteristics (not illustrated). This was confirmed in the paired comparisons summarized in Table 3, which showed the lack of significant differences between the mean inter-spike intervals of the motor units which produced either the longest versus the

Table 3 Paired comparisons between the response and firing characteristics and the motor unit's biomechanical and electrophysiological properties

Motor unit pairs	Recruitment threshold (N)	Twitch rise time (ms)	Twitch amplitude (mN)	Macro-MUP area (mV·ms)	Inter-spike interval (ms)	Corrected latency (ms)	Response probability (imp/trigger)
Recruitment threshold							
Lowest	0.6±0.6	51.9±13.3	1.2±2.3	6.7±4.7	124.5±12.4	17.3±1.8	0.43±0.17
Highest	2.8±2.2	33.2±13.8	12.8±18.1	9.4±9.3	127.4±11.6	16.7±1.7	0.31±0.13
d.f. (1–47)	F=48.5 ****	F=35.8 ****	F=15.3 ***	F=10.4 **	F=1.6 NS	F=23 ****	F=22.8 ****
Twitch rise time							
Longest	0.7±0.8	57.7±14.9	1.1±2.1	6.2±4.4	125.4±10.8	17.5±1.7	0.46±0.16
Shortest	2.1±1.9	31.9±10.8	10.4±13.6	8.2±5.3	125.1±13.0	16.8±1.6	0.32±0.13
d.f. (1–49)	F=23.5 ****	F=164.8 ****	F=24.9 ****	F=6.5 **	F=0.24 NS	F=17.9 ****	F=35.0 ****
Twitch amplitude							
Smallest	0.6±0.7	54.5±15.5	1.1±2.1	6.4±4.6	125.3±11.9	17.5±1.8	0.44±0.17
Largest	2.2±1.7	32.9±12.2	10.8±13.9	7.9±5.0	124.9±12.9	16.7±1.8	0.31±0.14
d.f. (1–49)	F=35.7 ****	F=88.9 ****	F=26.6 ****	F=4.0 *	F=0.06 NS	F=16.2 ***	F=16.6 ***
Macro-MUP area							
Smallest	0.9±0.9	50.3±18.4	2.9±5.5	4.8±3.4	123.5±13.3	17.4±1.7	0.40±0.16
Largest	2.1±2.2	38.3±15.9	9.2±15.0	9.9±5.3	126.2±11.5	16.9±1.6	0.32±0.14
d.f. (1–49)	F=10.4 **	F=10.1 **	F=6.1 *	F=10.4 **	F=1.4 NS	F=14.8 ***	F=8.5 **
Response latency							
Longest	0.9±1.1	52.5±17.5	3.5±7.6	5.8±4.3	127.5±11.4	17.8±1.6	0.45±0.17
Shortest	2.1±1.9	35.3±14.5	9.7±14.5	8.6±5.4	125.9±12.5	16.7±1.5	0.29±0.12
d.f. (1–53)	F=15.7 ***	F=22.5 ****	F=6.8 **	F=16.1 ***	F=0.7 NS	F=166 ****	F=48.1 ****

* $0.01<P<0.05$, ** $0.001<P<0.01$, *** $0.0001<P<0.01$, **** $P<0.0001$

shortest twitch rise times, the smallest versus the largest twitch amplitudes, the lowest versus the highest force recruitment thresholds, the smallest versus the largest macro-MUP areas and the longest versus the shortest corrected response latencies.

Nor were any consistent correlations observed between the response probability and the discharge frequency ($r=0.13$, $P=0.08$; not illustrated). Among the six subjects, only one (subject 6) showed a weak positive correlation between the motor units' discharge frequencies and their response probability ($r=0.38$, $P=0.01$).

The dependence of the response probability on the motor unit firing rate might have been obscured because each motor unit was tested only once. This dependence was therefore further investigated by analysing the responses of 63 motor units tested during three or four successive sequences of 250 tendon stimulations during which the units fired at different frequencies. Upon pooling the data a weak but significant correlation was detected, showing that the response probability tended to increase as the inter-spike intervals became longer ($r=0.23$, $P=0.0003$). This trend became more clearly apparent, however, upon differentiating between the motor units in terms of their biomechanical properties. A group of 22 slowly contracting, low-threshold motor units (twitch rise time >40 ms, twitch amplitude <2 mN, recruitment threshold <1 N) and a group of 23 fast-contracting, high-threshold motor units (twitch rise time <40 ms, twitch amplitude >2 mN, recruitment threshold >1 N) were identified on the basis of previous data on

the same muscles (Schmied et al. 1994). This ruled out 18 motor units which could not be identified as belonging to either group because their twitch characteristics and their recruitment thresholds did not meet with the criteria applied.

The regression analyses between the response probability and the inter-spike intervals measured during three or four successive periods of 250 stimulations are illustrated in Fig. 5A with black dots in the case of the slowly contracting, low-threshold motor units and white circles in the case of the fast-contracting, high-threshold motor units. In both groups, the differences in the mean inter-spike intervals accounted for 8% and 7% of the differences in the response probability, respectively (as compared with 5% when all motor units were pooled together). The regression lines computed for the two groups yielded similar slopes ($d.f.=1–74$, $F=0.40$), but the y-intercept was significantly higher in the case of the slowly contracting, low-threshold motor units ($d.f.=1–174$, $F=68.06$, $P<<0.005$).

Figure 5B illustrates the dependence of the response probability on the firing rate in the case of nine pairs of motor units tested in different experiments during successive sequences of 250 stimulations. In each of these pairs, the slowly contracting, low-threshold motor unit (black dots) showed a larger response than the fast-contracting, high-threshold unit (open circles), whatever their firing rates.

The differences observed in the motor unit response probability in terms of the motor units' mechanical and
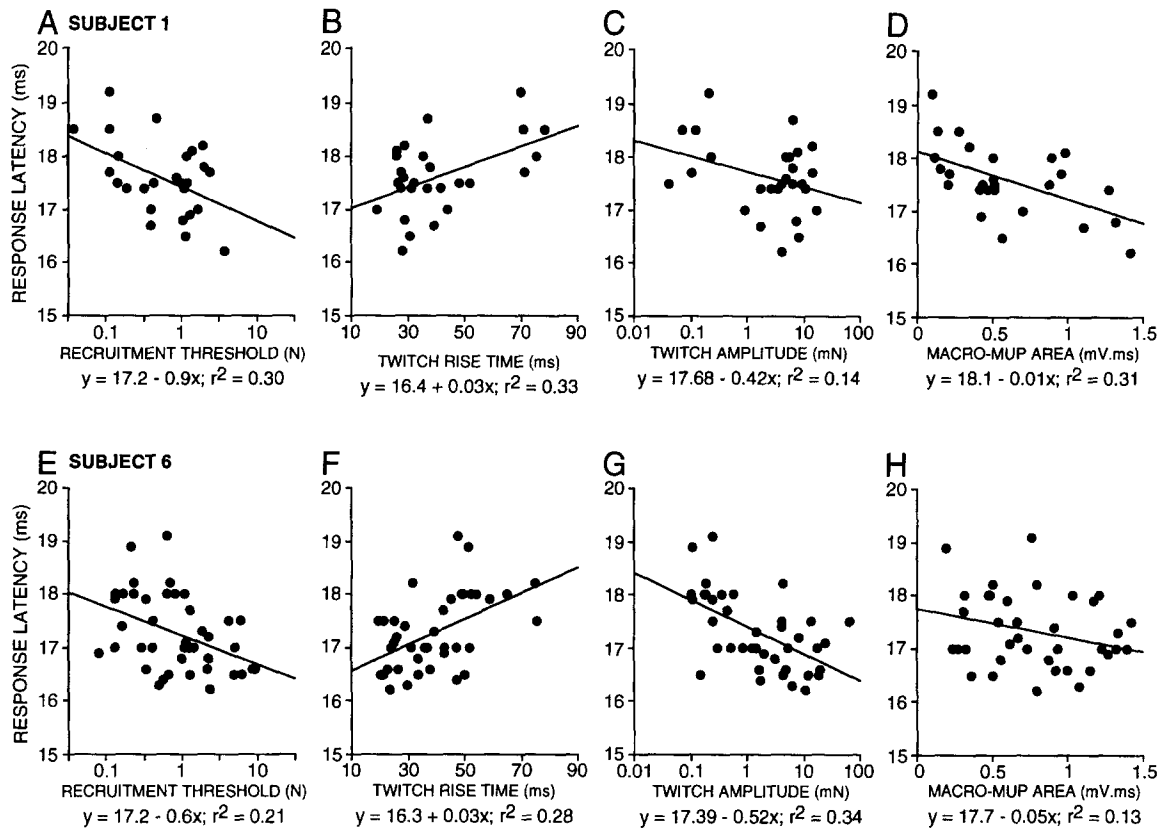
Fig. 3 Correlations between the motor unit response latency corrected with respect to the macro-MUP onset (*ordinate*) and the motor unit mechanical or electrical characteristics (*abscissa*) in subject 1 (**A–D**) and subject 6 (**E–H**). The motor units with the lowest recruitment thresholds (**A, E**), the longest twitch rise times (**B, F**), the smallest twitch amplitudes (**C, G**) and the smallest macro-MUP areas (**D, H**) were consistently found to have the longest response latencies

electrical properties therefore do not seem to be attributable in any way to the discharge rate.

Discussion

The strength of the monosynaptic excitatory pathways which carry muscle spindle inputs to wrist extensor motoneurones was investigated during voluntary isometric contraction as a function of the motor unit type. Despite the existence of various supraspinal and peripheral pathways which are liable postsynaptically to modulate motoneurone excitability and presynaptically to modulate the efficiency of Ia monosynaptic inputs during voluntary contraction, the results showed that in the wrist extensor muscles, motoneurone responsiveness to tendon taps apparently depends on the mechanical and electrical properties of the motor units, with a gradient consistent with the "size principle".

Contribution of the Ia monosynaptic inputs to the motor unit responses

The transient muscle stretches induced by tendon taps have classically been used as a tool to stimulate the muscle spindles in order to elicit a reflex activation of the homonymous motoneurones. The possibility that cutaneous afferents may have been involved can be ruled out in view of the fact that whenever the hammer was not positioned exactly on the tendon, it was completely ineffective, although cutaneous receptors were probably still activated. Although possible contributions from other proprioceptive inputs, such as those mediated by spindle secondary afferents and tendon organ afferents, cannot be completely ruled out (Burke et al. 1983), data obtained in animal experiments (Stuart et al. 1970; Matthews 1972; Fetz et al. 1979) as well as in human microneurographic recordings (Vallbo 1973; Vallbo et al. 1979; Roll and Vedel 1982; Burke et al. 1978, 1983) have indicated that the muscle spindle primary afferents are those most readily activated by this type of stimulation. The Ia afferent volleys can induce both monosynaptic and polysynaptic excitatory responses (Watt et al. 1976; Malmgren and Pierrot-Deseilligny 1988; Romaiguère et al. 1991). With the paradigm used in the present study, however, the responses of the motor units to tendon taps were observed during the earliest part of the reflex response (tendinous reflex) extracted by averaging the surface EMG recording, with a latency compatible with the contribution of a monosynaptic pathway.

Fig. 4 A Paired comparisons on the response probabilities (*ordinate*) of motor units tested in the same experiments (identified by *symbols* connected by *lines*), showing the shortest versus the longest corrected response latencies, respectively (*abscissa*) in the six subjects. In most pairs, the motor units with the shortest latencies were found to be the least responsive. **B** The regression analysis computed between the differences in the response probability (*ordinate*) and the differences in the response latency (*abscissa*) of each pair. The greater the difference in the latency, the larger the difference in response probability was found to be
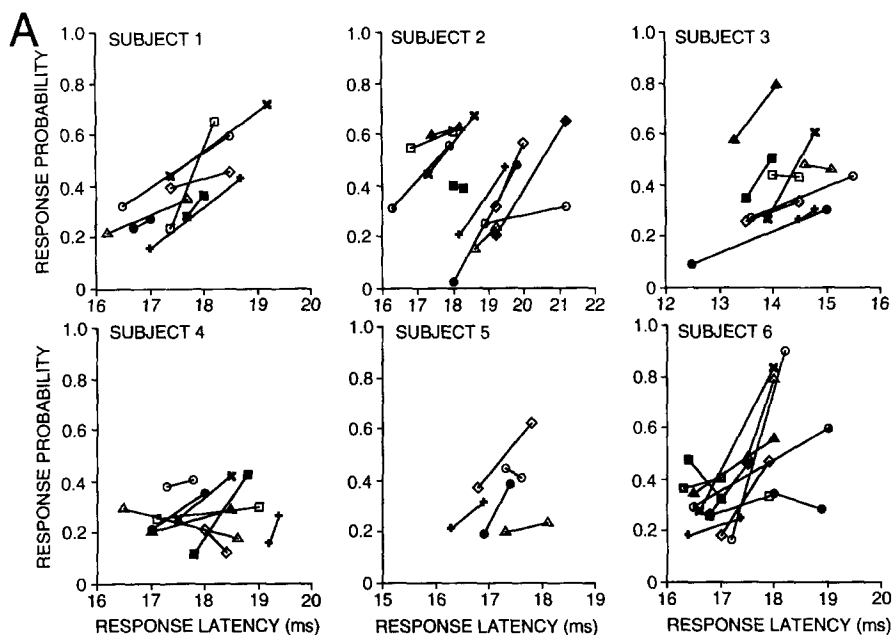
Possible influence of the firing rate on the motor unit response probability

The possibility that a motoneurone's responsiveness to monosynaptic inputs might depend on its firing rate has been addressed in several studies on humans where electrical stimulations of muscle afferents with frequencies ranging from 0.5 to 3 Hz were delivered either randomly as regards to motoneurone discharge, or with a controlled post-spike delay in order to investigate motoneurone responsiveness at different times throughout the post-spike hyperpolarization period. In some of these studies, the firing rate was not found to have any marked effect on motoneurone responsiveness (Ashby and Labelle 1977; Ashby and Zilm 1982; Ashby et al. 1986; Miles et al. 1989; Awiszus and Feistner 1993), while in other studies a tendency was observed for the motor unit monosynaptic responses to become smaller at higher frequencies (Kudina 1988; Miles et al. 1989; Piotrkiewicz et al. 1992).
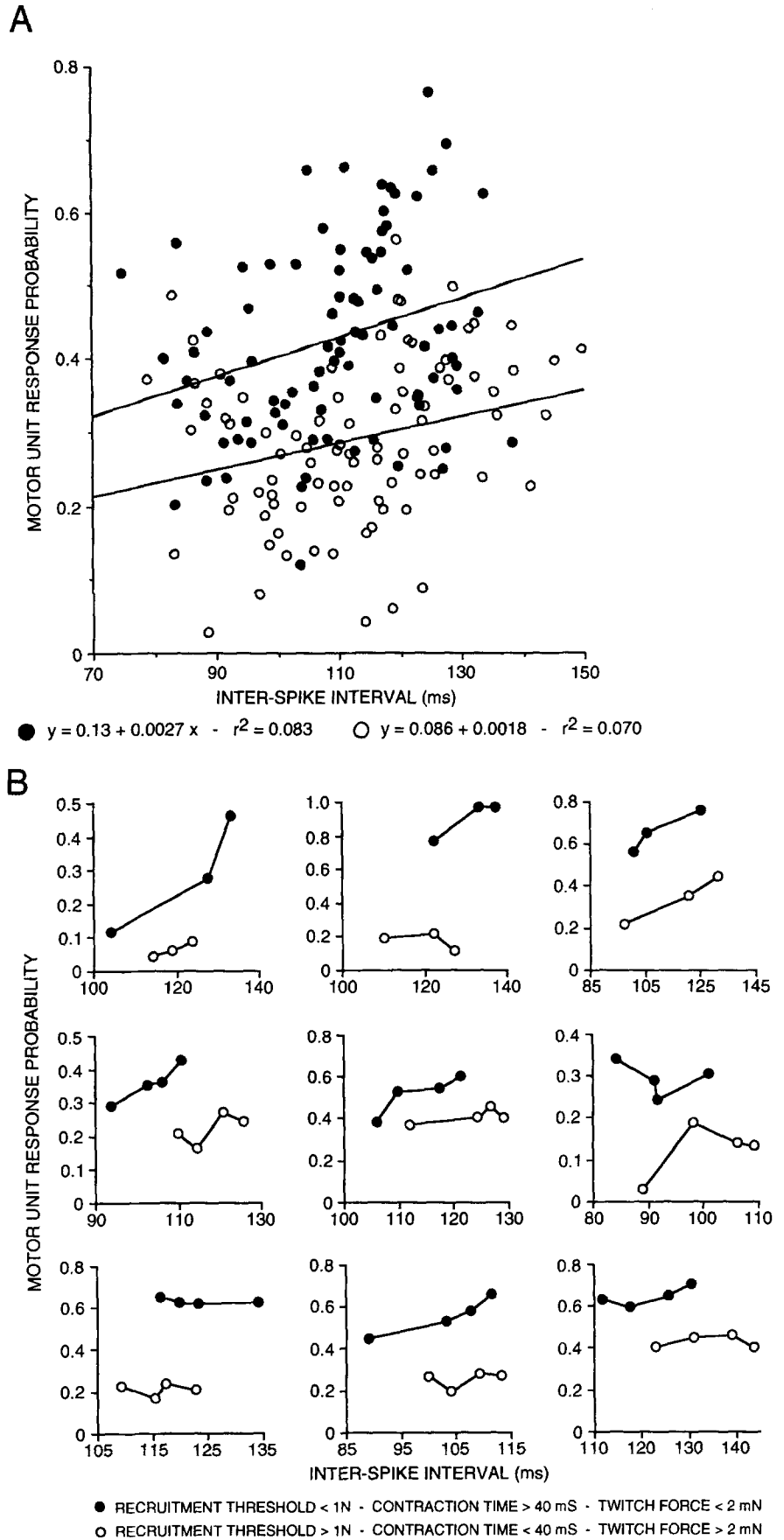
This issue has been reinvestigated recently by Jones and Bawa (1995) in the flexor carpi radialis muscle. When electrical stimulations of the muscle afferents were delivered with post-spike delays longer than 60 ms or at random, the responses became smaller as motor unit firing frequency increased. These findings are fully consistent with our own observations. When the tendon taps were delivered with a post-spike delay of 80 ms, we observed a weak correlation between the response probability and the motor unit's firing rate. This correlation, however, became significant only when the same motor units were tested with different firing frequencies during three or four recording periods.

At a given amplitude of the compound EPSPs generated by the tendon taps, motoneurone responsiveness depends mainly on the timing of the stimulation relative to the previous action potential and on the membrane potential level at the various stages in its post-spike after-

hyperpolarization in relation to its firing threshold. Under these conditions, the firing rate might influence motoneurone responsiveness in several ways leading to opposite effects. On the one hand, high firing frequencies are likely to reflect a strong amount of net excitatory drive which might keep the membrane closer to its firing threshold than lower frequencies. On the other hand, high firing rates might also lead to a summation of the post-spike after-hyperpolarizations keeping the membrane potential farther from its firing threshold. This would at least partly explain why the responsiveness tends to be lower at higher frequencies when the stimulation is delivered either randomly or towards the end of the post-spike hyperpolarization period, as observed in the present data and in previous studies (cf. Jones and Bawa 1995). If, however, the firing frequency increases in such way that the inter-spike intervals tend to become shorter than the time required for the afferent volleys to reach the motoneurone after the triggering spike (post-
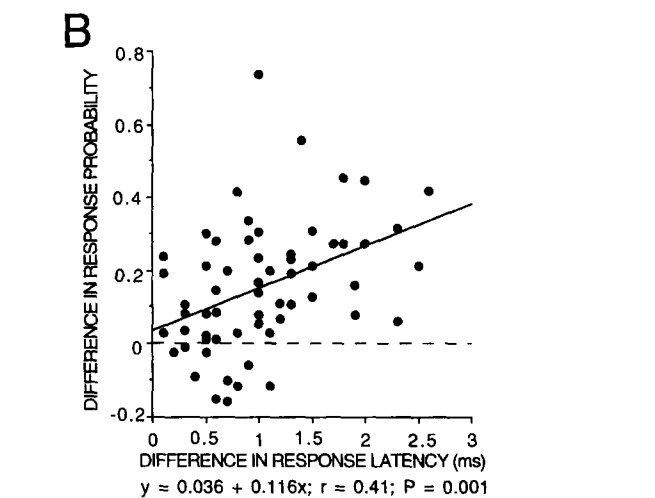
Fig. 5 A Regression analysis between the response probabilities and the mean inter-spike intervals of motor units tested during three or four successive sequences of 250 tendon taps, during which they fired at different frequencies. A group of 22 (*black dots*) were slowly contracting, low-threshold motor units (twitch rise time >40 ms, twitch amplitude <2 mN, recruitment threshold <1 N) and a group of 23 (*open circles*) were rapidly contracting, high-threshold motor units (twitch rise time <40 ms, twitch amplitude >2 mN, recruitment threshold >1 N). The regression lines of the two groups had similar slopes (F=0.4), and the marked difference in the y-intercept ($d.f.$=1–74, F=68.1, $P \ll 0.005$) shows that the slowly contracting, low-threshold motor units had larger response probabilities, whatever their firing rates. **B** The covariation of the response probability and the firing frequency for nine pairs of motor units both of which were tested in the same experiment during three or four successive periods. In each pair, the motor unit identified as low-threshold, slowly contracting (*black dots*) consistently showed a higher response probability than the motor unit identified as high-threshold, fast-contracting (*open circles*), regardless of their firing rates

A

$y = 0.13 + 0.0027\,x$ - $r^2 = 0.083$ $y = 0.086 + 0.0018$ - $r^2 = 0.070$

B

MOTOR UNIT RESPONSE PROBABILITY

INTER-SPIKE INTERVAL (ms)

● RECRUITMENT THRESHOLD < 1N - CONTRACTION TIME > 40 mS - TWITCH FORCE < 2 mN
O RECRUITMENT THRESHOLD > 1N - CONTRACTION TIME < 40 mS - TWITCH FORCE > 2 mN

spike delay+reflex loop latency), many of the EPSPs might be immediately preceded by spontaneous action potentials, and this would greatly reduce motoneurone responsiveness. We have reduced this possibility by excluding from our sample the motor units which fired with a shorter mean inter-spike interval than the time required for the afferent volleys to reach the motoneurone (80 ms+motor unit response latency). Under these conditions, the afferent volleys were expected to reach the motoneurones with a mean delay of 105 ms, when about four-fifths of the duration of the mean inter-spike interval (125 ms) had elapsed, i.e. when the motoneurone membrane was nearing its firing threshold. During this period, motoneurone responsiveness to monosynaptic inputs of cortical or peripheral origin has been found to reach maximal values (Jones and Bawa 1995; Olivier et al. 1995).

The fact that the firing frequency could not be taken to be responsible for the differences between the motor units' responsiveness was established by the regression analyses between response probability and mean inter-spike interval performed on a group of slowly contracting, low-threshold motor units and a group of fast-contracting, high-threshold motor units tested at various frequencies in the same experiments. Both groups showed the same slight tendency for the responsiveness to increase at longer inter-spike intervals. The y-intercept of the regression line computed from the group of slowly contracting, low-threshold motor units was, however, much higher than that of the group of fast-contracting, high-threshold motor units. This confirmed without any doubt that whatever the firing frequency, the response probability of the slowly contracting, low-threshold motor units tended to be higher.

Motor unit response latency and the "size principle"

The motor units were functionally characterized in terms of the force levels at which they were recruited, the rise time and amplitude of the twitch associated with their discharge, and their electrophysiological activity in terms of the area of the macro-potential extracted from the surface EMG.

The reliability of the recruitment threshold, twitch and macro-MUP values was confirmed by the strong correlations observed between all these parameters in each of the six subjects tested. In line with most of the previous data obtained on various human muscles (Milner-Brown et al. 1973; Milner-Brown and Stein 1975; Stephens and Usherwood 1977; Goldberg and Derfler 1977; Monster and Chan 1977; Vogt et al. 1990), the higher the motor unit recruitment threshold, the shorter the twitch rise time, the larger the twitch amplitude and the larger the macro-MUP area turned out to be (Tables 2, 3). The good correlation observed between twitch amplitude and twitch rise time confirms previous data obtained in another extensive study of the same muscle (Schmied et al. 1994). This is in keeping with the structural observations

indicating that the extensor carpi radialis longus muscles fibres appear to extend from one tendon to the other over the entire length of the muscle (Lieber et al. 1990). Such a longitudinal distribution can be expected to greatly facilitate the assessment of the contractile force.

The present data show for the first time that, in humans, each of these parameters is correlated with the latency of the motor unit responses to tendon taps (Table 2). The fact that these correlations were of various strengths might be attributable to the distortions liable to differently affect first the recruitment threshold along with the possible contribution of other wrist extensor muscles, secondly, the twitch rise time and force along with the possible effect of synchronization (Thomas et al. 1990) and, thirdly, the macro-potential extracted from the surface EMG recording (Stalberg 1980).

All in all, the correlations observed in the regression analyses between the motor units' response latency and their biomechanical and bioelectrical parameters were fully confirmed by the paired analyses in which comparisons were made between the response latencies of the two motor units tested in the same experiment which showed, respectively, the highest and lowest values in terms of their twitch amplitude, recruitment threshold, macro-MUP area or twitch rise time.

The differences in the latency observed within these pairs tended to increase as the difference between the motor units' biomechanical and bioelectrical parameters increased. The greatest difference amounted to 2.6 ms. Assuming that the conduction distance between the spinal cord and the extensor carpi radialis muscles was about 60 cm, this difference in latency would correspond to a difference in axonal conduction velocity of about 17 m·s^{-1}. This is consistent with the conduction velocity range of 40–60 m·s^{-1} that has been observed in human arm muscle nerves (Betts et al. 1976; Dengler et al. 1988).

Assuming that the afferent conduction times and input processing times were similar at the motoneurone membrane, the present results indicate that the various biomechanical and electrophysiological characteristics of the motor units tested in the extensor carpi radialis muscles may be correlated with the apparent conduction velocity of the motoneurone, in line with the "size principle". This is consistent with results based on direct measurements of the motoneurone conduction velocity in human hand muscles (Freund et al. 1975; Dengler et al. 1988).

Gradient in motor unit responsiveness to tendon taps and the "size principle"

Upon pooling the whole population of motor units tested in the six subjects, the correlations between the amplitude of the responses induced by the tendon taps and the motor units' mechanical and electrical parameters were found to be rather weak. About 18% of the differences in motor unit response probability could be accounted for by differences in this parameter. Only 9%, 6% and 2% of

the differences in motor unit responsiveness could be accounted for by differences in twitch amplitude, recruitment threshold and macro-MUP area, respectively. The fact that weaker correlations were observed in the case of these three parameters is in keeping with the distortion which is liable to affect their assessement.

Much stronger evidence for the existence of a gradient in response probability in terms of the motor units' functional properties was obtained in the paired comparisons on the motor units tested in the same experiment. Under these conditions, larger response probabilities were consistently observed among the motor units which were either recruited at the lower force levels, or developed slower and smaller twitches or generated smaller macro-MUPs. Complementary to these data, it was observed that the longer response latencies likely to reflect slowly conducting axons were consistently associated with higher response probabilities.

If the main pathways involved in the motor unit responses are monosynaptic, as discussed above, the existence of a higher response probability suggests that the motoneurones recruited at lower thresholds, which are associated with slower conducting axons and with more slowly-contracting muscle fibres generating smaller forces and smaller macro-MUP areas, may receive larger EPSPs, which is in good agreement with the results of previous investigations on the "size principle" based on animal data (Burke et al. 1976; Dum and Kennedy 1980; Harrison and Taylor 1981; Fleshman et al. 1981; Bawa et al. 1984).

In a pioneer study on humans (Buller et al. 1980), the motoneurones tested in the second dorsal interosseous muscle were activated by taps applied to the first dorsal interosseous muscle belly, and their responses showed a gradient which was correlated with the motor unit recruitment threshold, as in the present study, consistent with the "size principle". No correlations were observed, however, in that study between the latency of the response and the force level at which the motor units were recruited. This may be attributable to the fact that the latencies measured in the peri-stimulus time histograms were not corrected by taking into account the first sign of motor unit electrical activity, namely the onset of the macro-MUP, as they were in the present study, using the method developed by Awiszus and Feistner (1993).

In a more recent study, the monosynaptic activation of motor units elicited by electrical stimulation of primary afferents was tested in the soleus muscle (Awiszus and Feistner 1993). The motor units which were activated at the shortest latencies had the smallest response probability, in keeping with the "size principle". No correlation was observed, however, between the motor axon conduction velocity and macro-MUP area. This negative result, based on a rather small sample of motor units, may have been partly due to the fact that the macro-MUP extracted from the surface EMG is liable to be greatly distorted (Stalberg 1980). In our study, this parameter was actually that which showed the weakest correlations with the response latency and probability.

Completely different data have been obtained on the human tibialis anterior muscle (Ashby et al. 1986; Semmler and Türker 1994). In both studies, the paired comparisons performed between motor units tested during the same experiment in the tibialis muscle showed that the largest probabilities of response to the electrical stimulation of primary afferents were associated with high-threshold motor units. Up to now, however, in all the muscles (including the tibialis anterior muscle) investigated by performing intracellular recordings on motoneurones in anaesthetized animals, the Ia monosynaptic EPSPs have been found to be distributed according to the "size principle" (Eccles et al. 1957; Burke 1968; Burke et al. 1976; Dum and Kennedy 1980; Harrison and Taylor 1981; Fleshman et al. 1981; Lüscher et al. 1983). One possible reason for the discrepancies between the data on animals and humans might be the existence of species-related differences in the distribution of the Ia EPSPs to the motoneurones of the tibialis muscle. A more complete functional characterization of the motor units in terms of their contractile force and response latency is required in order to test this hypothesis. Another hypothesis is that inhibitory Ib afferents may have been co-activated by the electrical stimulation of the nerve along with the Ia afferents. We propose a third hypothesis based on the contribution of a tonic presynaptic inhibition which might differentially affect the motor units depending on their type. During voluntary contraction in humans, presynaptic inhibition has been found to modulate in opposite ways the amplitude of the responses assumed to originate from Ia monosynaptic inputs, in the case of the soleus versus tibialis anterior muscles (Katz et al. 1988). This may at least partly account for the discrepancies existing between the data obtained on the soleus muscle (Awiszus and Feistner 1993) and the tibialis anterior muscle (Ashby et al. 1986; Semmler and Türker 1994).

During voluntary contraction, inputs such as those provided by cutaneous afferents are liable to modify the rank ordering of motoneurone excitability as determined by the "size principle" (Garnett and Stephens 1981; Nielsen and Kagamihara 1993). Moreover, presynaptic inhibition of various origins can be expected to play a prominent role in the modulation of the effectiveness of the Ia monosynaptic inputs during isometric contraction of human forearm muscles (Berardelli et al. 1987; Nakashima et al. 1990; Burke et al. 1992). If this occurs in the extensor carpi radialis muscles, it does not seem to alter the graded action of the afferent volleys evoked by tendon taps on wrist extensor motoneurones, which were found here to obey the "size principle".

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