

CHANGES IN THE RECRUITMENT THRESHOLD OF MOTOR UNITS PRODUCED BY CUTANEOUS STIMULATION IN MAN

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SUMMARY

1. The effect of cutaneous stimulation on the recruitment of motor units has been studied during slowly increasing voluntary contractions of human first dorsal interosseous muscle.

2. Continuous electrical stimulation of the index finger at $4\times$ threshold for perception caused an increase in the recruitment threshold of units normally recruited at contraction strengths < 1.5 N and a decrease in the recruitment threshold of units normally recruited at contraction strengths > 1.5 N.

3. It is concluded that the recruitment order of motor units during gradually increasing voluntary muscle contraction is not fixed but depends in part on cutaneous input.

INTRODUCTION

It is widely agreed that the recruitment order of motor units recorded during voluntary muscle contraction in man is fixed in that it cannot be altered at will, nor is it different during different sorts of fast ballistic or slow ramp contractions (Denny-Brown & Pennybacker, 1938; Tanji & Kato, 1973; Büdingen & Freund, 1976; Desmedt & Godaux, 1977*a*, 1978). In spite of the known specialization of motor unit mechanical properties within individual muscles, the controlling motoneurone pool and its input would appear to be organized in such a way as to prevent rather than allow the potentially useful selective activation of units according to mechanical type. In support of this view, Henneman and his collaborators found that motoneurons in cat triceps surae were always recruited in the same sequence no matter what source of excitation or combination of excitation and inhibition they used to drive the motoneurone pool (Henneman, Somjen & Carpenter, 1965; Somjen, Carpenter & Henneman, 1965; Clamann, Gillies & Henneman, 1974; Henneman, Clamann, Gillies & Skinner, 1974). This rather clear result led to the attractive hypothesis that an elegantly simple principle governed the organization of synaptic input to a given motoneurone pool namely that every motoneurone within the pool shared qualitatively identical inputs and that the ratio of any given source of inhibition to any given source of excitation was the same for each cell (Henneman *et al.* 1965). During experimental tests using intracellular recording, this hypothesis has been found to hold true for

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some afferent inputs such as from muscle spindle primary endings (Mendell & Henneman, 1971; Burke, Rymer & Walsh, 1976) but not for others. Stimulation of the sural nerve, for example, produces largely inhibitory post-synaptic potentials in cat MG motoneurons innervating slow twitch muscle fibres (type S) but largely excitatory post-synaptic potentials in motoneurons innervating fast twitch highly fatigable muscle fibres (Type FF) (Burke, Jankowska & Bruggencate, 1970). Unlike group Ia muscle afferent input, cutaneous afferent input is not distributed in qualitatively the same way to all motoneurons; for some its effects are excitatory while for others its effects are inhibitory. Indeed, considering only excitatory effects, the pattern for cutaneous input is roughly the reverse of that found for Ia input whose excitatory effect is most marked for type S cells, and least effective for type FF cells (Burke, 1978). With this in mind, stimulation of cutaneous afferents could be expected to reverse the order of recruitment of motor units produced by muscle stretch. This turns out to be the case as has been shown recently by Kanda, Burke & Walmsley (1977) in the decerebrate cat.

The question is immediately raised as to whether similar effects could be demonstrated during normal voluntary contractions. This has also proved to be the case, during carefully controlled isometric contractions carried out by human subjects, as will now be described. Preliminary accounts of this work have already been presented (Buller, Garnett & Stephens, 1978; Stephens, Garnett & Buller, 1978; Garnett & Stephens, 1978).

METHODS

Experiments were performed on six apparently healthy volunteers aged between 21 and 35 years.

Mechanical recording. The hand and forearm were held in the pronated position with the elbow flexed at a right-angle. With fingers extended the hand was packed between two layers of modelling clay (Plasticine) and firmly held by a pressure plate. The thumb was secured fully extended in a separate Plasticine packed clamp. The force of abduction of the index finger produced by the first dorsal interosseous muscle was recorded by the pressure of the lateral side of the proximal interphalangeal joint against a plate borne by a strain gauge force transducer (Stratham Type UC3 with UL4-2 Load Cell) and displayed to the subject on an oscilloscope screen. The force transducer assembly was carefully directed so that its axis lay in the plane of action of first dorsal interosseous muscle. Under these conditions very little movement of the hand occurred and muscle action was nearly isometric.

First dorsal interosseous is the only muscle to produce abduction of the index finger. Other muscles attached to the finger are active during voluntary abduction but by their anatomical arrangement do not contribute force in this direction. Activity in extensor digitorum, serves to counteract the flexion component of the force developed by first dorsal interosseous which if left unopposed would tend to cause flexion at the metacarpophalangeal joint of the index (Warwick & Williams, 1973). Electrical stimulation of the appropriate part of extensor digitorum was found to produce simple extension of the metacarpophalangeal and interphalangeal joints of the index. Stimulation of the superficial and deep flexor muscles was found to produce flexion of the proximal, middle and distal phalanges. Neither the flexors nor extensors attached to the index finger were found to exert force in the direction of action of first dorsal interosseous recorded by the strain gauge. The second palmar interosseous arises from the ulnar side of the second metacarpal and is attached to the ulnar side of the digital expansion of the index finger. This muscle is the only muscle to produce adduction of the index and is the functional and anatomical antagonist for first dorsal interosseous.

Electrical recording. Motor unit electrical activity was recorded and displayed simultaneously from first dorsal interosseous muscle and its anatomical antagonist second palmar interosseous using conventional monopolar concentric needle electrodes.

Electrical stimulation. Two spring type ring electrodes were smeared with electrode jelly and

placed around the index finger one on each side of the proximal interphalangeal joint. Electrodes were covered with waterproof adhesive tape. Stimuli were delivered by a constant voltage stimulator (50 shocks/sec; pulse width 0.1 msec). Stimulus strength was set at $4 \times$ threshold for perception. It should be noted that in these experiments threshold strength was determined using 50 shocks/sec stimulation. Threshold strength for perception of single shocks was considerably higher, frequently by as much as 100%. Stimulation used in this study was not painful but elicited a sensation similar to having the finger firmly gripped.

Experimental procedure. Once a single motor unit action potential had been isolated, the mechanical properties of the unit were measured using the spike triggered force averaging technique (Milner-Brown, Stein & Yemm, 1973a). The subject was then required to make repeated isometric contractions following a target on the oscilloscope screen. The task was so arranged that the force of abduction exerted by the subject increased linearly for a period of about 10 sec and then the subject relaxed. The rate of rise of force was never greater than 0.5 N/sec and the whole task was repeated every 18 sec. For each contraction the recruitment threshold of the unit was defined as that level of force at which the unit first fired continuously (Freund, Budingen & Dietz, 1975).

After at least six control contractions the index finger was stimulated electrically for 4–6 min. The subject was instructed to continue the test contractions throughout this time and for some 5–10 min afterwards.

The subject was allowed to relax for at least 15 min before starting a new experimental run.

Occasionally in the relaxed subject, continuous electrical stimulation of the index finger produced an effect which might be termed a 'tonic skin reflex'. After about 2–3 min stimulation, spontaneous electrical activity would appear in both first dorsal and second palmar interosseous muscles. Although no systematic recordings were made our impression was that other muscles in the hand and forearm were also involved. This effect appears to be similar to the tonic finger flexion reflex recently described by Torebjork, Hagbarth & Eklund (1978) following vibratory stimulation of digital mechanoreceptors. In view of this phenomenon electrical activity in second palmar interosseous was carefully monitored during the present experiments. Any activity in this muscle would, of course, tend to reduce the force of abduction recorded at the index finger and therefore result in an apparent lowering of the recruitment threshold of units in first dorsal interosseous.

In each experiment, activity in second palmar interosseous was monitored using a conventional monopolar concentric recording needle electrode (Medelec, Type ENS1), resting in the belly of the muscle. The position of the tip of the recording electrode was carefully adjusted so that the slightest voluntary effort by the subject to adduct his index finger resulted in an obvious increase in recorded electrical activity. This procedure ensured that the needle tip lay close to muscle fibres innervated by motoneurons recruited at low levels of contraction strength. The amplifier settings used were chosen to be optimum for recording from as large a volume of muscle as is possible with a conventional monopolar concentric e.m.g. electrode. The useful pick-up range under these conditions is about 1 mm from the leading off surface of the electrode (Stalberg & Trontelj, 1979). Assuming a mean muscle fibre diameter of $25 \mu\text{m}$ (Sissons, 1974), about 6000 fibres would be in range, approximately one third of the total for second palmar interosseous. If the number of muscle fibres per motor unit in second palmar interosseous is similar to that in first dorsal interosseous then we may calculate that second palmar interosseous has about sixty motor units (half the number estimated for first dorsal interosseous by Feinstein, Lindgard, Nyman & Wohlfart, 1955). If the muscle fibres of each motor unit are intermingled randomly with those of other units then a sample of sixty adjacent muscle fibres would on average contain one muscle fibre from each motor unit. This number of muscle fibres would be encompassed within a radius of about $100 \mu\text{m}$ of the leading off surface of the e.m.g. needle. About 100 muscle fibres from *each* motor unit would be within 1 mm of the needle. Under these conditions no motor unit activity in second palmar interosseous muscle can be expected to escape detection by the recording electrode. This is an important consideration as it allows us to exclude antagonist activity in second palmar interosseous from playing any significant part in the present experiments designed to investigate the effects of cutaneous stimulation on the recruitment of motor units in first dorsal interosseous muscle. To this end test contractions of first dorsal interosseous were excluded from the data if accompanied by more than a few isolated potentials recorded from second palmar interosseous.

RESULTS

Fig. 1 shows the effect on the recruitment of motor units in first dorsal interosseous muscle of stimulating the digital nerves of the index finger at a strength $4 \times$ threshold for perception. The recruitment threshold of a relatively high threshold unit (large e.m.g. spike) is reduced while the threshold for firing of a low threshold unit (small e.m.g. spike) is increased by the same stimulus. Twenty-five units have been examined in this way. Seven units had their recruitment threshold lowered and eighteen their recruitment threshold raised by digital nerve stimulation.

Fig. 2 shows the distribution of time intervals between the start of cutaneous stimulation and the onset of a change in recruitment threshold for the different motor units in this study. In the majority of cases, recruitment threshold had changed by the first or second test ramp contraction. The time resolution for the data is limited, however, because the test ramp contractions were slow and repeated only once every 18 sec. A change in recruitment threshold was said to have occurred if the measured value differed by more than two standard deviations from the mean control value.

Once started, changes in recruitment threshold were progressive reaching some final value between two and four minutes after the onset of stimulation. For most motor units, this new level of recruitment threshold was maintained for as long as the stimulus was applied. In seven cases, however, the recruitment threshold returned towards the control value during the later part of the period of stimulation, though it always remained significantly different from the control value. The changes in recruitment threshold with time for a low and high threshold unit are shown in Fig. 3.

With one exception, units normally recruited at contraction strengths > 1.5 N had their recruitment threshold lowered by digital nerve stimulation. Units recruited at contraction strengths < 1.5 N had their recruitment threshold raised by the same stimulus. This result is illustrated in Fig. 4*A*. The recruitment threshold of some high threshold units was reduced by more than 3.0 N. On the other hand, some low threshold units were recruited at contraction strengths 1.0 N or more above control. When the change in recruitment threshold is expressed as a proportion of control value (Fig. 4*B*) this change appears to be most marked for the low threshold units.

In most cases, recruitment threshold had returned to control by the first or second ramp contraction after the end of stimulation. It was often some minutes, however, before the variability between successive measurement returned to within normal limits.

During normal gradually increasing voluntary muscle contractions, motor units are recruited in order of increasing twitch contraction strength (Milner-Brown, Stein & Yemm, 1973*b*; Stephens & Usherwood, 1977). This is shown for the present data in Fig. 5*B*. This is not, however the case if contractions are made in the presence of skin stimulation (Fig. 5*A*). Under these circumstances, some units with small twitch tensions (< 0.02 N) normally recruited at contraction strengths < 0.25 N are now not recruited until the force of contraction reaches about 1.0 N or more. Conversely, some units with large twitch tensions (> 0.05 N) normally recruited at contraction strengths > 2.0 N are now amongst the first units to be recruited at contraction strengths < 1.0 N.

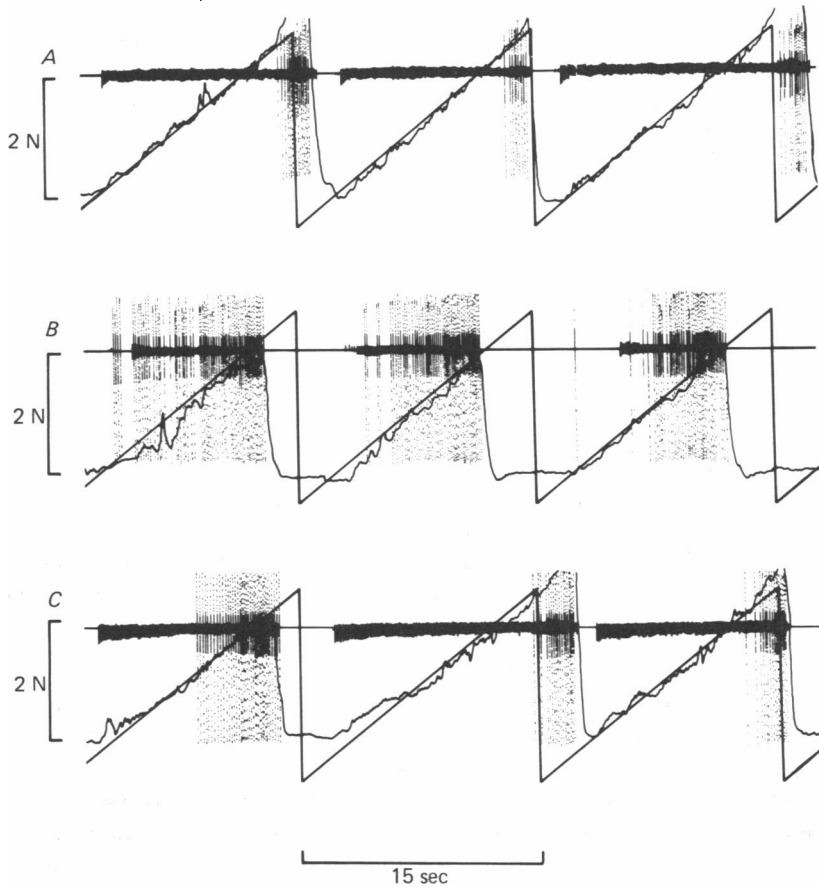


Fig. 1. Changes in the recruitment threshold of motor units recorded during controlled voluntary ramp contractions of first dorsal interosseous muscle produced by electrical stimulation of the digital nerves of the index finger (50 pulses/sec, pulse width 0.1 msec, strength $4 \times$ threshold for perception). In each section of the figure the top trace shows the e.m.g. signal recorded from a needle electrode in first dorsal interosseous muscle. The straight saw-toothed outline is the target ramp followed by the subject and the irregular line close to it is the force of abduction of the index finger recorded using a strain gauge placed against the lateral side of the proximal interphalangeal joint. The three sections were taken from the same continuous recording. The top trace (A) was taken during the control period at the start of the experiment and shows the regular recruitment of the unit under study (large e.m.g. spike) at about 2.5 N (10% of maximum voluntary contraction strength). Trace (B) was recorded 30 sec after the start of digital nerve stimulation. Notice that the unit under study was now recruited at lower levels of contraction strength than before. Trace (C) was recorded 10 sec after the end of stimulation and the recruitment threshold of the unit under study gradually returned to control. Also in Fig. 1 can be seen the behaviour of a low threshold motor unit seen as the small e.m.g. spike in each recording. The effect of digital nerve stimulation in this case was to cause an increase rather than a decrease in recruitment threshold (compare last contractions in A, B and C).

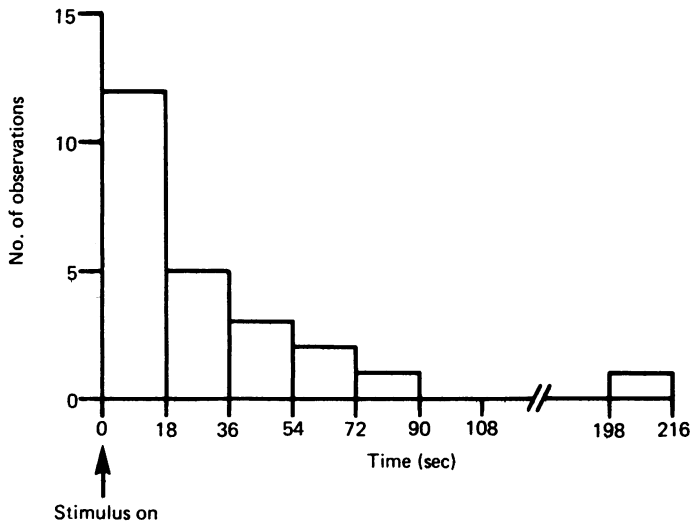


Fig. 2. The distribution of time intervals between the start of digital nerve stimulation and the onset of a change in recruitment threshold. Each observation from a different motor unit.

DISCUSSION

In a previous study (Garnett & Stephens, 1980), we have shown that stimulation of the digital nerves of the index finger has mixed short latency excitatory and inhibitory reflex effects on the probability of firing of first dorsal interosseous motoneurons active during a steady voluntary contraction. At short latency, the predominant effect for fast twitch high threshold motor units is an increased probability of firing while for low threshold slow twitch units, single cutaneous stimuli produce predominantly a reduction in firing probability. A similar differential reflex effect for cutaneous stimulation has been found using intracellular recording in cat. Stimulation of the sural nerve produces predominantly hyperpolarizing responses in MG motoneurons innervating slow twitch muscle units and depolarising responses in cells innervating fast twitch units (Burke *et al.* 1970). In both this and our earlier human study the result is the same; cutaneous stimulation has a predominantly inhibitory effect on slow twitch, low threshold motor units and an excitatory effect on high threshold fast twitch units. Spinal interneurons mediating the reflex effects of cutaneous stimulation appear to be largely inhibitory for units recruited at low contraction strengths and excitatory for units recruited at high contraction strengths (Kanda *et al.* 1977). The fact that the same result has been obtained in such different situations suggests to us that this weighting of excitatory and inhibitory interneurons along the cutaneous reflex pathway according to motor unit type might also be responsible for the present results. Continuous electrical stimulation of the digital nerves of the index finger can be expected to hyperpolarize those motoneurons in first dorsal interosseous normally recruited at low contraction strengths and to depolarize those normally recruited later. As a result, the intensity of excitatory input necessary to drive high threshold motoneurons is reduced and for low threshold motoneurons is increased. As the subject follows the target ramp, increasing

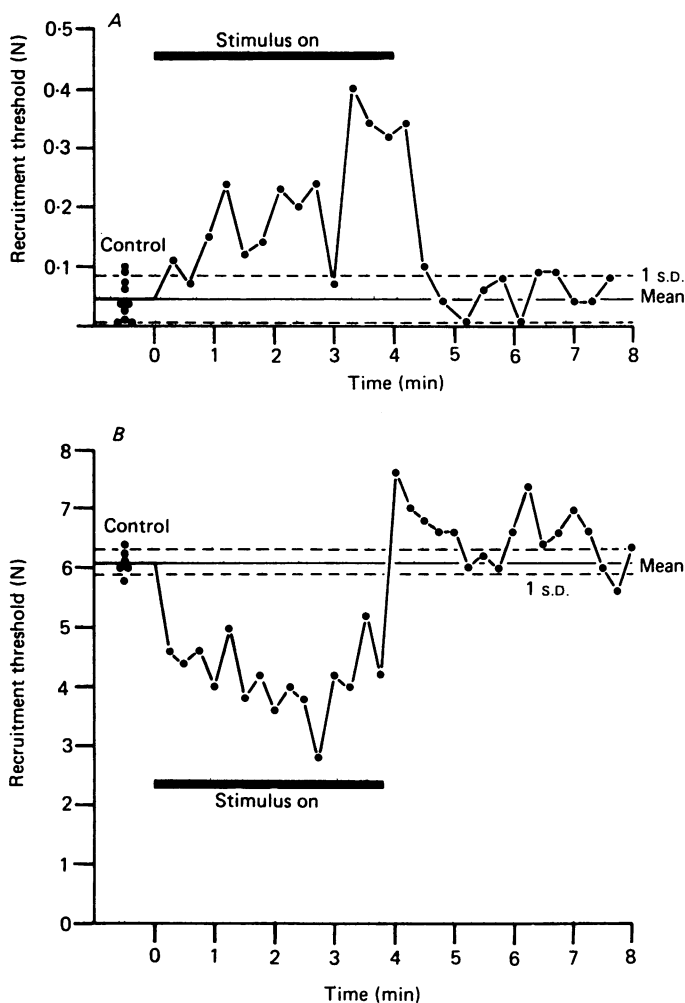


Fig. 3. Time course of the changes in recruitment threshold observed for two motor units in first dorsal interosseus muscle during $4 \times$ threshold continuous electrical stimulation of the digital nerves of the index finger (50 pulses/sec, pulse width 0.1 msec, strength $4 \times$ threshold for perception). The recruitment threshold of a unit with a low mean control value (0.04 N) is raised (A) while the unit with the high mean control value (6.1 N) has its threshold lowered by the same stimulus.

descending drive with increasing voluntary effort brings some motoneurons to firing threshold earlier and others later than in control. Indeed in the relaxed human subject (unpublished observations) and in the decerebrate cat where descending drive is absent, cutaneous stimulation alone can cause sufficient reflex excitation to cause a muscle to contract and motor units to become active in a sequence different from that associated with a voluntary contraction in man or the tonic stretch reflex in cat (Kanda *et al.* 1977).

The over-all effect of continuous electrical stimulation of the index finger is to promote the recruitment of more powerful higher threshold units in first dorsal interosseus muscle and to delay the recruitment of lower threshold less powerful

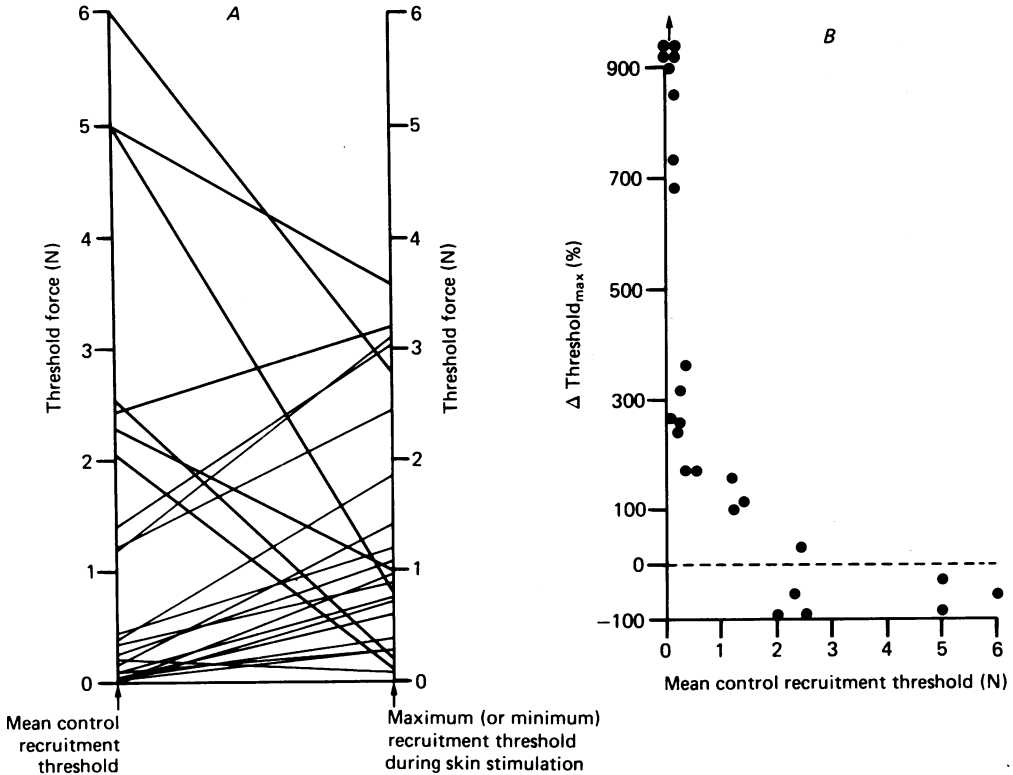


Fig. 4. Changes in the recruitment threshold of motor units recorded during controlled ramp contractions of first dorsal interosseous muscle produced by electrical stimulation of the digital nerves of the index finger (50 pulses/sec, pulse width 0.1 msec, strength $4 \times$ threshold for perception). *A*, pooled results from all experiments. With one exception units recruited at contraction strengths > 1.5 N had their recruitment thresholds lowered by digital nerve stimulation. Those recruited at contraction strengths < 1.5 N had their recruitment thresholds raised by the same stimulus. The same result is shown in *B* which plots the maximum change in recruitment threshold observed for each unit as a percentage of control values.

units. Extrapolating from this result to a more physiological situation leads us to consider the functional implications of our findings. We can suppose that the cutaneous input arising from holding an object between forefinger and thumb has an overall excitatory effect on the first dorsal interosseous muscle thereby helping to reinforce the grip. It is presumably the loss of this facilitatory effect which accounts in part for the difficulty experienced in holding objects when the fingers are anaesthetized. Loss of this facilitatory effect presumably also explains the subjective loss of power and increased perceived heaviness of weights lifted by the fingers when anaesthetized (Gandevia & McCloskey, 1977*b*). In the same study Gandevia & McCloskey (1977*a*) also showed that a weight lifted by flexing the index finger feels lighter when the thumb is electrically stimulated and similarly that a weight lifted by flexing the distal joint of the thumb feels lighter when the index finger is stimulated. In both these situations we can imagine that cutaneous stimulation has altered the pattern of recruitment in the prime movers just as in the present study.

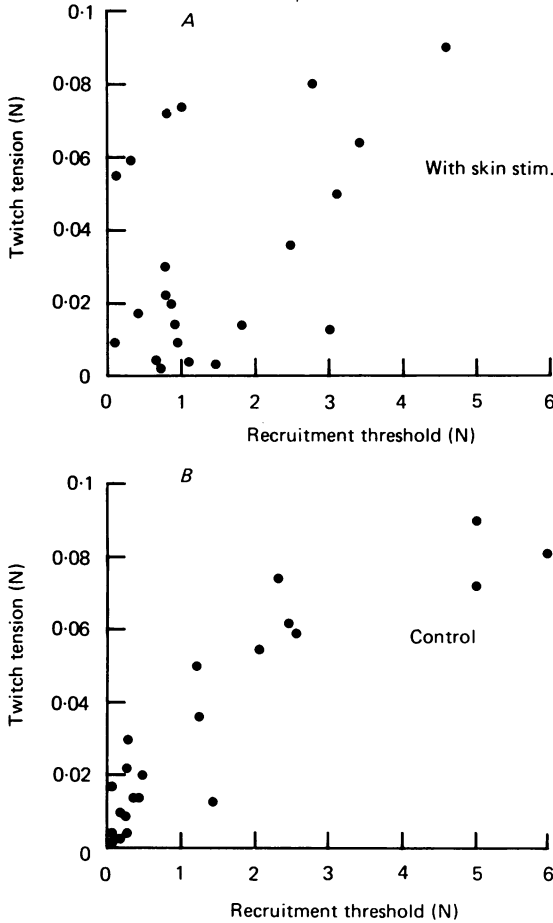


Fig. 5. The effect of continuous electrical stimulation of the digital nerves of the index finger (50 pulses/sec, pulse width 0.1 msec, strength $4 \times$ threshold for perception) on the relationship between motor unit twitch tension amplitude and recruitment threshold measured during slow voluntary ramp contractions of first dorsal interosseous muscle. In the absence of stimulation (*B*), units recruited at progressively higher contraction strengths have progressively larger twitch amplitude. In the presence of stimulation (*A*), the sequence is different. Digital nerve stimulation promotes the early recruitment of units with large twitch tensions and delays the recruitment of units with small twitch tensions.

The facilitatory effect of cutaneous stimulation on the recruitment of more powerful motor units results in less descending drive to the lower motoneurone pool being necessary to produce a given force. Less voluntary effort is required and the object feels lighter.

Since the discovery that individual muscles contain motor units with a surprisingly wide range of motor unit mechanical properties, many authors have been attracted by the idea that the different motor unit types might be used in different tasks. Most common has been the idea that powerful fast twitch units might be used selectively for fast ballistic contractions. The available evidence however, does not support this view (Desmedt & Godaux, 1977 *a, b*). In most studies in man the order of motor unit

recruitment has turned out to be disappointingly inflexible and the same no matter what the nature of the descending voluntary command (Tanji & Kato, 1973; Büdingen & Freund, 1976; see however Grimby & Hannerz, 1977). It would appear that the descending pathways involved are connected to the motoneurone pool in a particular way and that simply changing the dynamics of the impulse traffic along these pathways with different voluntary commands does not alter the final relative distribution of excitatory drive to motoneurons of different type. It is not changes in voluntary command that alter the process of recruitment but rather changes in the pattern of afferent input. Context, not command, determines the type of motor unit active in a particular task. It is with this idea that we should seek the functional correlation between motor unit type and activity in normal movements.

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