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THE EFFECTS OF DIGITAL NERVE STIMULATION ON THE FIRING OF MOTOR UNITS IN HUMAN FIRST DORSAL INTEROSSEOUS MUSCLE

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SUMMARY

1. The effect of cutaneous stimulation on the firing of single motor units has been studied during voluntary contractions in human first dorsal interosseous muscle.

2. Electrical stimulation of the index finger at 3 × threshold for perception reduced the firing rate of most units recruited at voluntary contraction strengths < 1·5 N and increased the firing rate of all units recruited at contraction strengths > 1·5 N. The firing rate of all slow twitch units (contraction time > 75 msec) was reduced. The behaviour of fast twitch units was mixed but at this stimulus strength all units recruited at contraction strengths > 1·5 N had their firing rate increased.

3. Tested at different stimulus strengths, the stronger the stimulus the more the firing rate of low threshold units was reduced. The firing rate of units recruited at high contraction strengths was increased by weak stimuli but reduced by strong stimuli.

4 It is concluded that stimulation of the index finger shifts the weighting of synaptic input associated with a voluntary contraction to favour the activity of the more powerful fast twitch motor units in first dorsal interosseous muscle.

INTRODUCTION

Cutaneous stimulation has been shown to alter the pattern of recruitment of motor units, during both reflex contractions in cat (Kanda, Burke & Walmsley, 1977) and voluntary contractions in man (Stephens, Garnett & Buller, 1978; Buller, Garnett & Stephens, 1978). During controlled ramp contractions of human first dorsal interosseous muscle, for example, continuous stimulation of the digital nerves of the index finger reduces the recruitment threshold of units normally recruited at high contraction strengths (> 1·5 N) and raises the recruitment threshold of units normally recruited at low contraction strengths (< 1·5 N) (Garnett & Stephens, 1978, 1981). One mechanism that could account for this result would be that cutaneous stimulation has an over-all excitatory effect on high threshold units but an inhibitory effect on low threshold units (Garnett & Stephens, 1980). To test this hypothesis we have examined the effect of cutaneous stimuli delivered to the index finger on the mean interval between single motor unit spikes in first dorsal interosseous muscle. If the over-all effect of a stimulus is excitatory then the mean interval between spikes

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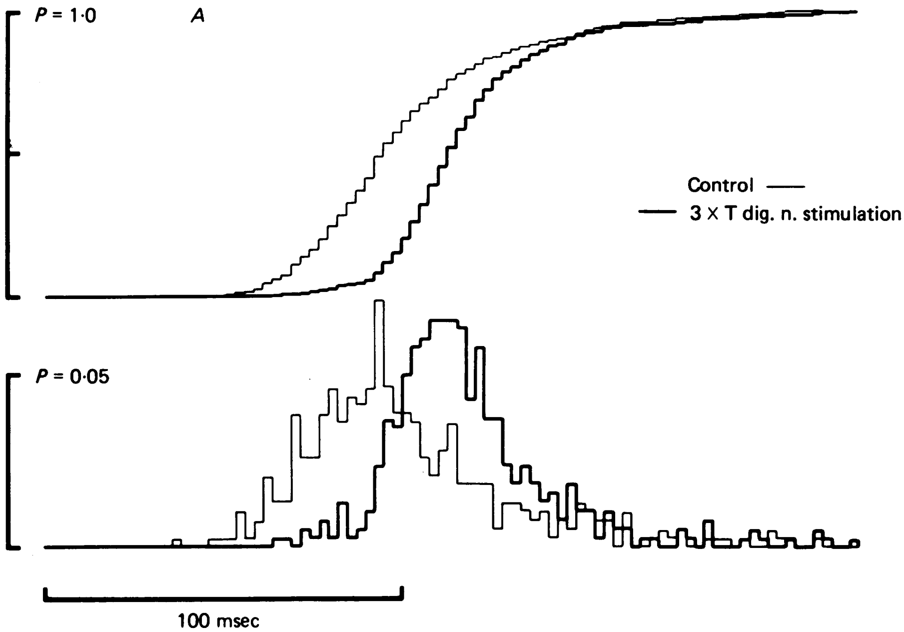

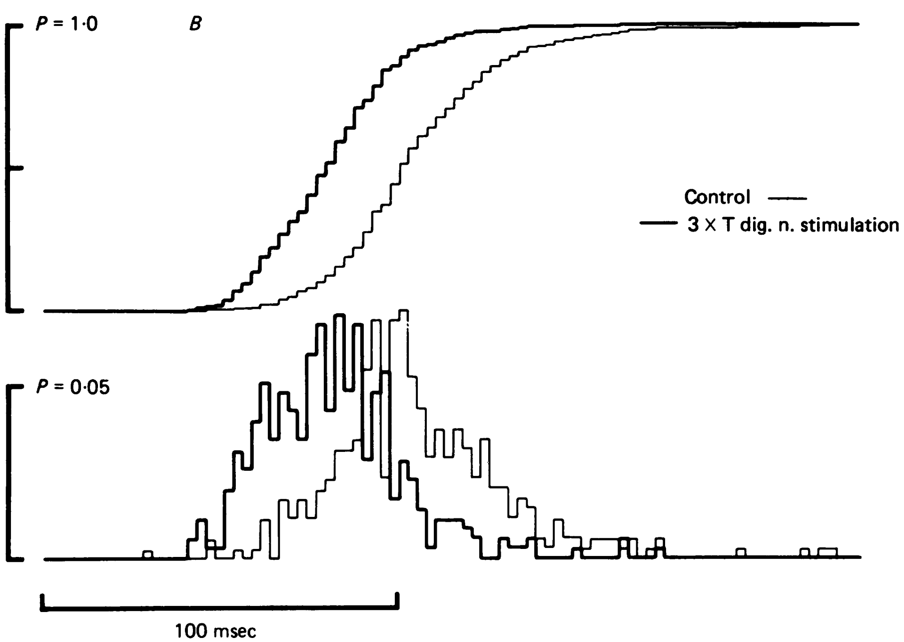

Fig. 1. The effects of 3 × threshold electrical stimulation of the digital nerves (dig. n.) of the index finger on the firing of two different motor units in human first dorsal interosseous muscle. For the unit shown in *A*, the effect of stimulation is to shift the histogram of measured interspike intervals to the right (heavy line) compared to control. For the unit shown in *B*, the effect is the reverse. The mean interspike interval is shortened

can be expected to be shortened. If, on the other hand, the effect is inhibitory, then the interval between spikes is lengthened (Kranz, Adorjani & Baumgartner, 1973). A preliminary account of this work has already appeared (Datta & Stephens, 1979).

METHODS

Experiments were performed on fourteen apparently healthy human volunteers aged between 20 and 32 yr.

Mechanical recording. The hand was immobilized palm downwards in modelling clay (Plasticine) with the thumb fully extended. The force of abduction of the index finger produced by first dorsal interosseous muscle was recorded with a strain gauge positioned against the radial side of the proximal interphalangeal joint.

Motor unit recording. Single motor unit action potentials were isolated for recording using a conventional monopolar concentric needle electrode inserted into first dorsal interosseous muscle.

The threshold of motor unit recruitment was taken to be that level of voluntary contraction strength at which the motor unit under study first began to fire steadily while the subject slowly increased his force of contraction over a period of several seconds. Twitch contractions of a single motor unit were recorded by averaging the total force of abduction of the index finger produced by first dorsal interosseous muscle while triggering from that unit's action potential (Milner-Brown, Stein & Yemm, 1973*a*, *b*; Stephens & Usherwood, 1977). Skin temperature over first dorsal interosseous muscle was measured, and maintained at 30 ± 2 °C using a reading lamp directed over the hand.

Electrical stimulation of the digital nerves. Two ring electrodes smeared with electrode jelly were placed around the index finger, one on each side of the proximal interphalangeal joint. Stimuli were delivered by a constant voltage stimulator (pulse width 100 μsec), the proximal ring electrode acting as cathode. The stimuli used in this study were graded in multiples of stimulus strength at threshold for perception. Before each experimental run, sensory threshold was measured by stimulating at 2 per second while gradually changing the stimulus voltage. Threshold was taken to be the stimulus voltage needed for the subject to feel each stimulus distinctly.

Experimental procedure. Once the threshold of recruitment and mechanical properties of a motor unit had been measured, the subject was instructed to maintain a voluntary contraction such that the unit under study fired steadily at 10 per second. He was aided in this by an auditory monitor and frequency meter display of the firing of the unit. Meanwhile, electrical stimuli were delivered to the index finger and timed to occur 80 msec after every third motor unit action potential. Histograms with bin widths of 320 μsec were constructed of the interval between the two motor unit spikes immediately following each stimulus. Intervals were only recorded if the preceding interval, in which the stimulus was given, was between 95 and 105 msec. Given a total afferent plus efferent conduction delay of 30 msec, this procedure ensured that the afferent volley reached the motoneurone between 5 and 15 msec after the start of the measured interspike interval. The over-all reflex effect of stimulation was estimated by expressing the mean of 200 test interspike intervals measured in the presence of cutaneous stimulation as a percentage of the mean of the same number of intervals logged in the absence of stimulation.

RESULTS

Fig. 1 *A* and *B* shows examples of the effect of 3 × threshold for perception electrical stimulation of the digital nerves of the index finger on the firing of two motor units

and the histogram shifted to the left. Motor unit interspike intervals in *A* and *B* were only logged if the preceding interval lay between 95 and 105 msec. For both units, stimuli were timed in such a way that the corresponding afferent volley arrived at the spinal cord 5–15 msec after the onset of the measured interspike interval (see Methods). Subject instructed to maintain unit firing at 10 per second throughout. Above each histogram is drawn the corresponding cumulative sum.

in first dorsal interosseous muscle. Such stimulation is not painful and gives rise to the sensation of having the finger struck lightly by a pencil. In both *A* and *B* the subject was required to maintain a voluntary contraction such that the unit under study fired steadily at 10 per second. In the absence of stimulation, the histograms of motor unit interspike intervals (unshaded) are centred around 100 msec. In the presence of stimulation (shaded histograms), the distribution of intervals immediately following each stimulus is shifted to the right in Fig. 1*A* but to the left in Fig. 1*B*. Corresponding shifts can be seen in the cumulative probability distributions shown above each pair of interval histograms. Despite the subject's best efforts and despite the fact that each interval measured in Fig. 1 was preceded by an interval lying between 95 and 105 msec, the reflex effect of identical cutaneous afferent volleys timed to arrive at the spinal cord just after the start of the measured interspike interval is opposite for the units shown in *A* and *B*. In Fig. 1*A* the effect is to delay motoneurone firing while in Fig. 1*B* the effect is to facilitate the next motoneurone firing. Thus, the reflex effect of digital nerve stimulation is inhibitory for the unit in Fig. 1*A* but excitatory for the unit in Fig. 1*B*.

The effect of cutaneous stimulation on the distribution of motor unit interspike intervals was very reproducible. For any given unit, repeated measurements of the mean interspike interval made under either test or control conditions commonly varied by less than 2 % from trial to trial.

In general, units recruited at low contraction strengths (recruitment threshold < 1·5 N) fired more regularly than those recruited at higher contraction strengths (> 1·5 N), coefficients of variation of intervals for the two groups of units being 0·13–0·37 (mean 0·22, $n = 24$) and 0·24–0·45 (mean 0·32, $n = 7$) respectively. Such a difference in regularity of firing is significant (t test, $P < 0.001$). Taking the data as a whole, the coefficient of variation of measured interspike intervals for individual units was not significantly different under test when compared to control conditions (paired t test, $P > 0.2$).

Of fifty-five units examined in this study, thirty-one behaved like the unit in Fig. 1*A* and twenty-four like the unit in Fig. 1*B*. This difference in behaviour was found to be related to motor unit mechanical properties and recruitment threshold.

The behaviour of units recruited at different contraction strengths is compared in Fig. 2. For each unit the magnitude of the effect of cutaneous stimulation was measured by determining the mean of 200 interspike intervals logged in the presence of stimulation expressed as a percentage of the mean of a similar number of intervals logged in the absence of stimulation. As can be seen from Fig. 2, there is a clear tendency for the magnitude of the reflex response to be graded according to motor unit recruitment threshold irrespective of twitch type. It is of particular significance to note that this gradation includes a reverse in the *sign* of the reflex, changing from being inhibitory for most units recruited at contraction strengths < 1·5 N (mean test interspike interval > 100 % of control mean interval) to being excitatory for all units recruited at contraction strengths > 1·5 N.

A three-dimensional histogram displaying motor unit recruitment threshold, twitch contraction time and twitch tension for thirty-three units examined in this study is shown in Fig. 3. Units whose mean interspike interval was lengthened by 3 × threshold cutaneous stimulation are identified with filled circles, while units whose mean interspike interval was shortened by the same stimulation are shown with open circles. The population of slow twitch units (contraction time > 75 msec), recruited at low contraction strengths (< 1·5 N) and developing small twitch tensions (1·8–20 mN) stand out to have been universally inhibited (mean test interspike interval 100·1–124·2 % control interval, mean 108·4 %, $n = 15$). In contrast, the behaviour of the fast twitch population (contraction time < 75 msec) was mixed.

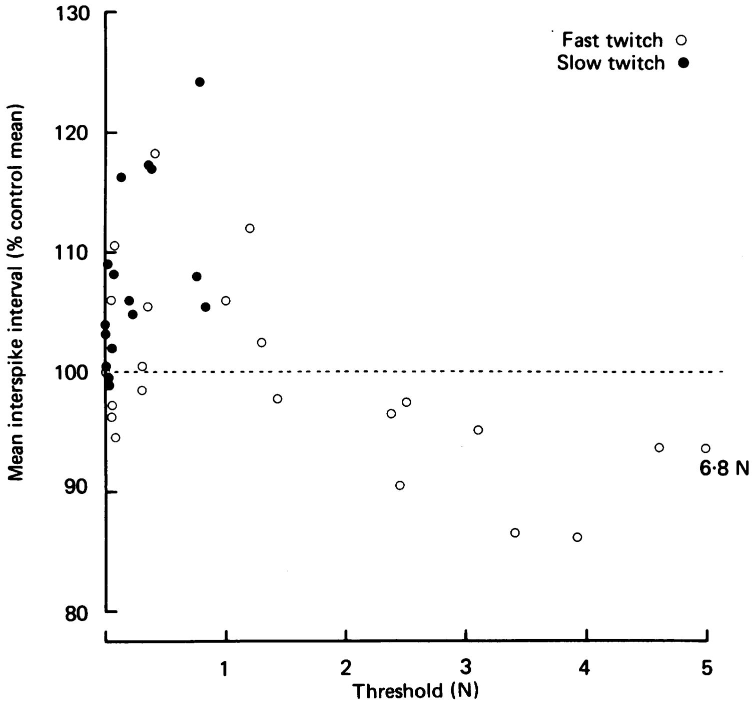

Fig. 2. The effect of 3 × threshold electrical stimulation of the digital nerves of the index finger on the firing of motor units of different recruitment threshold in human first dorsal interosseous muscle. Data for units with twitch contraction times > 75 msec shown with filled circles and those with contraction times < 75 msec shown with open circles.

Amongst those recruited at contraction strengths < 1·5 N, some were excited and some inhibited (mean test interspike interval 93·8–118·4 % control interval, $n = 21$). Those recruited at contraction strengths > 1·5 N, however, were universally excited (mean test interspike interval 86–98 % control interval, mean 93 %, $n = 7$).

The effect of changing stimulus strength has been examined in twelve motor units. Fig. 4 shows the typical behaviour of a unit recruited at low contraction strengths. As stimulus strength is increased the distribution of measured motor unit interspike intervals shifts progressively to the *right*. The stronger the stimulus the more powerful is its inhibitory effect. The behaviour of units recruited at high contraction strengths is rather different. For these units, as the stimulus strength is increased the measured interspike interval is first shortened with a progressive shift of the distribution of intervals to the left of the control. As the stimulus strength is increased further, the effect gradually reverses until at high stimulus strengths the measured interspike interval becomes longer than control, with the distribution of intervals shifting progressively to the right. An example of this effect is shown in Fig. 5. At 3 × threshold for perception the reflex effect of digital nerve stimulation is excitatory, shortening the mean interspike interval. At 4 × threshold (not shown) the effect is neutral and the mean interval not different from control. At 5 × threshold the reflex

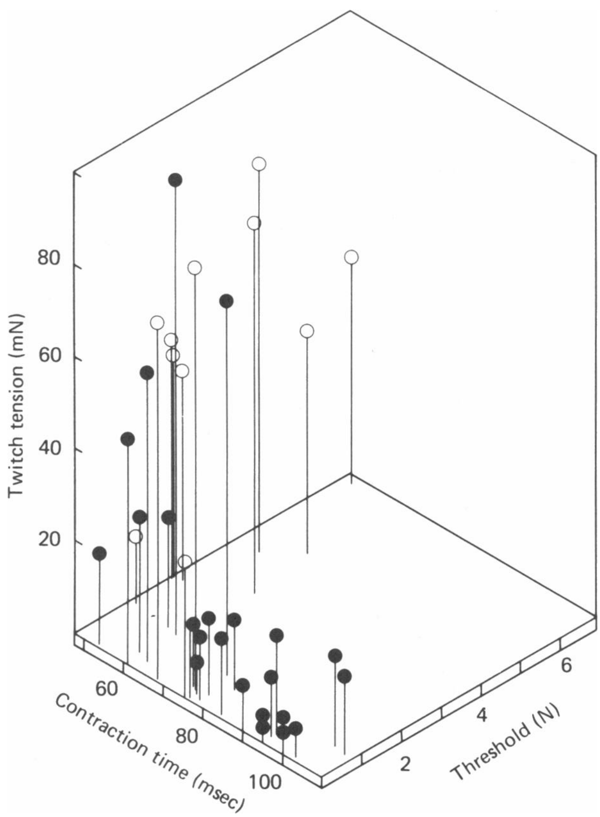

Fig. 3. A three-dimensional histogram of the relationship between motor unit recruitment threshold, twitch tension and twitch contraction time in human first dorsal interosseous muscle. Units identified by filled circles had their mean interspike interval lengthened and those identified by open circles had their interspike intervals shortened by 3 × threshold electrical stimulation of the digital nerves of the index finger.

effect of the stimulus has reversed. The distribution of motor unit interspike intervals has now been shifted to the right of control. At high stimulus strengths the net reflex effect of the stimulus is inhibitory rather than excitatory.

DISCUSSION

The present results show that electrical stimulation of the index finger at modest stimulus strengths has an over-all inhibitory effect on slow twitch motor units recruited at low levels of voluntary contraction strength in first dorsal interosseous muscle and an over-all excitatory effect on fast twitch units recruited at higher contraction strengths.

This difference in the behaviour of different motor unit types is consistent with earlier reports in cat (Burke, Jankowska & Bruggencate, 1970; Burke, Rymer & Walsh, 1976; Burke, 1978) and with the results of a previous study in our laboratory

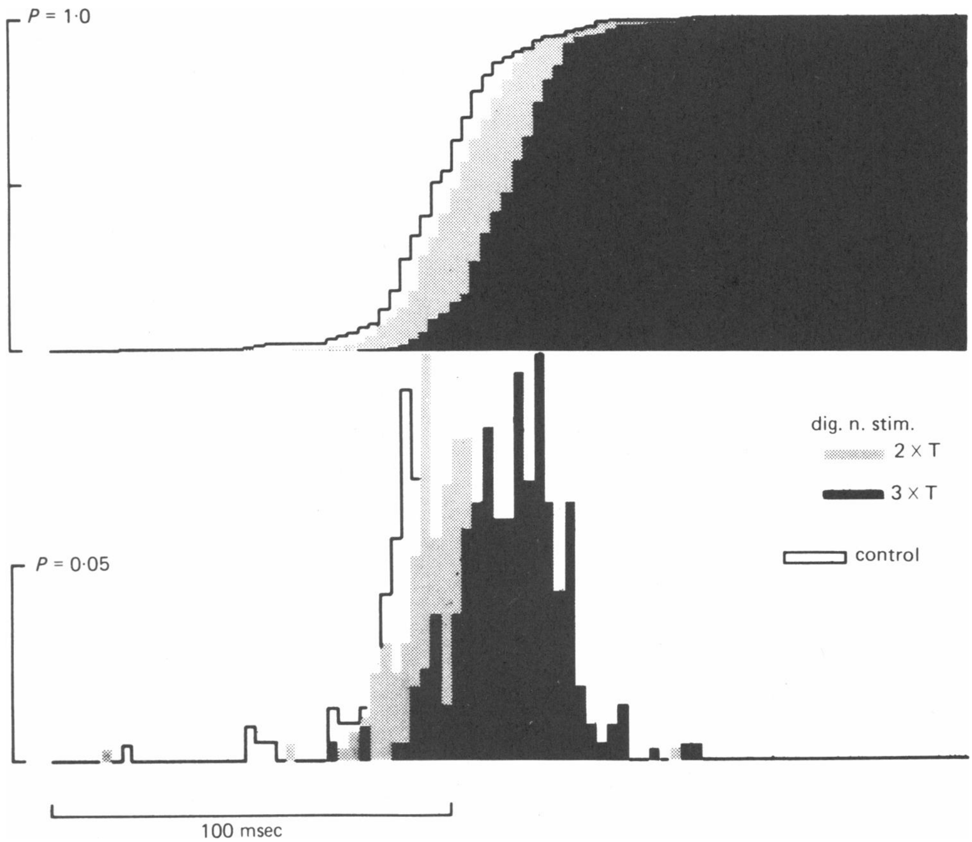

Fig. 4. Comparison of the effects of different strengths of stimulation of the digital nerves of the index finger on the firing of a low threshold slow twitch motor unit in human first dorsal interosseous muscle (motor unit recruitment threshold 0·38 N, twitch contraction time 80 msec, twitch tension 15 mN).

in man (Garnett & Stephens, 1980). Electrical stimulation of the index finger produces a triphasic reflex response in first dorsal interosseous muscle. Recording from single motor units, post-stimulus histograms of the times of occurrence of unit spikes following each stimulus show three corresponding changes in probability of firing. The first component of the reflex is excitatory raising the probability of unit firing at a latency similar to the tendon jerk for this muscle. After some 10 msec this is followed by inhibition and a reduction in unit firing probability, again lasting about 10 msec and terminated by a second period of excitation and increased probability of firing. Comparing the size of the short latency excitatory and inhibitory components expressed in terms of the relative amplitude of the corresponding fluctuations in firing probability, units recruited at low levels of voluntary contraction strength and with slow twitch contraction times were found to have predominantly inhibitory responses while those in which the short latency excitatory response predominated were found to have fast twitch contraction times and were recruited at high levels of contraction strength. On this basis it was concluded that the over-all effect of digital nerve stimulation, at least for the short latency components of the reflex, was inhibitory for slow twitch, low threshold units and excitatory for high threshold fast twitch units.

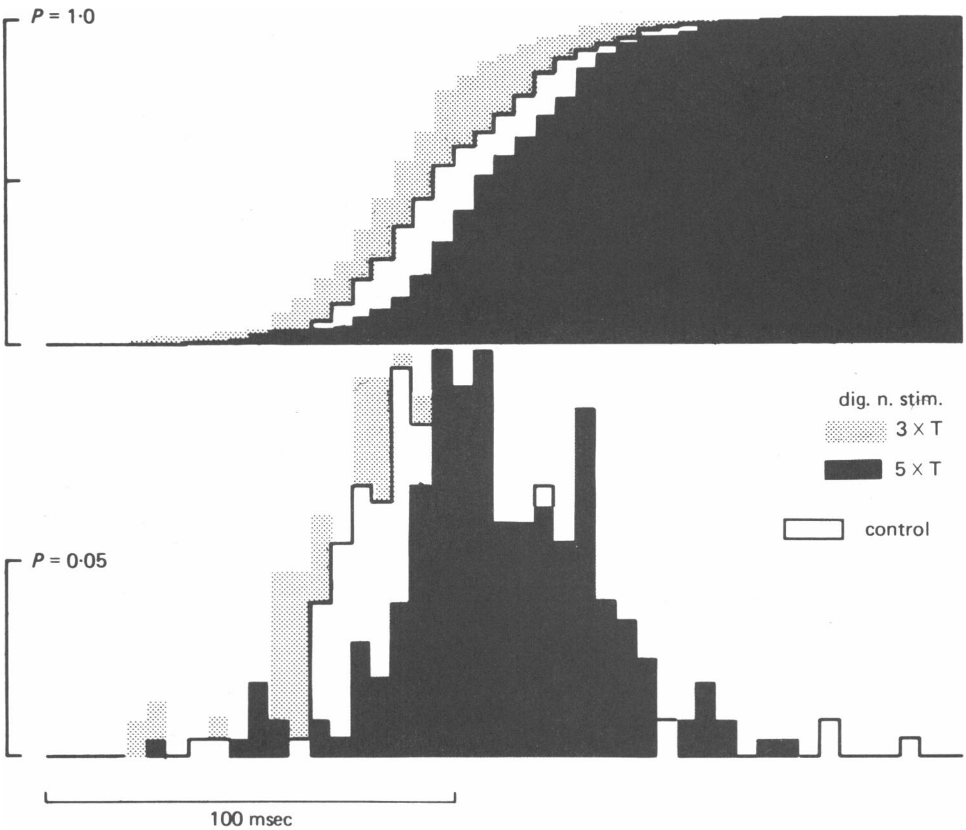

Fig. 5. Comparison of the effects of different strengths of stimulation of the digital nerves of the index finger on the firing of a high threshold fast twitch motor unit in human first dorsal interosseous muscle (motor unit recruitment threshold 2·40 N, twitch contraction time 44 msec, twitch tension 60 mN).

In the present study we have confirmed this result directly by exploiting the integrative properties of the motoneurone to sum physiologically the synaptic effects of the different components of the cutaneous reflex.

Subject to constant current stimulation motoneurones maintain a steady firing frequency, equal increments of injected current producing equal increments of firing frequency (Granit, Kernell & Shortess, 1963; Kernell, 1965*a*, *b*). Stated in another way, changes in the interval between spikes are inversely proportional to the change in the average current injected during that interval. In the present study, stimuli were timed such that the reflex effects took place during the first 50–60 msec following the previous motoneurone discharge. This timing ensured that none of the individual components of the cutaneous reflex response would cause sufficient depolarization to cause the motoneurone to fire directly. If as a result of stimulation the next firing of a motoneurone is delayed, then the effect of the stimulus has been to reduce the effective average excitatory synaptic current driving the motoneurone. If, on the other hand, the next firing of a cell is brought forward, then the effect of the stimulus has been to increase the effective driving current. In the present study the changes in firing interval we have observed (85–125 % control) correspond to changes in instantaneous firing frequency of ± 2 per second. Assuming the frequency–current relationship for human first dorsal interosseous motoneurones to be the same as that reported for cat medial gastrocnemius motoneurones (1·5 pulses per second/nA; Kernell, 1979), a change in a motoneurone's instantaneous firing frequency of 2 per second can be expected to have resulted from a change in the mean synaptic current driving that cell during that interspike interval of about 1 nA.

Both the order of recruitment and pattern of firing of motoneurones are determined by and indicative of the relative weighting of depolarization amongst those motoneurones. During a gradually increasing voluntary muscle contraction, motoneurones innervating slow twitch muscle fibres are generally recruited before those innervating fast twitch muscle fibres (Milner-Brown *et al.* 1973*b*; Stephens & Usherwood, 1977), and we can therefore assume that motoneurone depolarization is weighted in favour of the earlier recruited motoneurones. In the present experiment, single cutaneous stimuli have been shown to reduce the mean synaptic current driving motoneurones innervating slow twitch muscle fibres during steady voluntary contraction and to increase the mean synaptic current driving motoneurones innervating fast twitch muscle fibres. On this basis, continuous cutaneous stimulation during certain steady voluntary contractions can be expected to reduce the synaptic current driving some motoneurones below that required for firing and to increase the synaptic current of other, silent motoneurones above that required for firing. Cutaneous stimulation thus alters the weighting of synaptic drive during voluntary contraction in favour of the more powerful fast twitch units. It is presumably this mechanism that underlies the experimental result that continuous cutaneous stimulation changes the population of motor units active during steady voluntary contraction in first dorsal interosseous muscle (Stephens *et al.* 1978), and alters the order and threshold of motor unit recruitment during gradually increasing voluntary contraction (Garnett & Stephens, 1978, 1981).

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