MOTOR UNIT ACTIVITY IN THE VOLUNTARY CONTRACTION OF HUMAN MUSCLE

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In a muscle contracting voluntarily, the tension is proportional to the electrical activity, both under isometric (Lippold, 1952) and under isotonic conditions (Bigland & Lippold, 1954). The measure of this electrical activity was obtained by determining the area under the action potential curve recorded from surface electrodes over the belly of the muscle, and was considered to represent the 'excitation' in the muscle, i.e. to be a function of the number and the frequency of discharge of motor units. Such a composite measure, however, could not distinguish between the two means by which a voluntary contraction is graded (variation in the number of active units or their frequency), and it therefore became of interest to discover how the frequency of a unit varied with changes in tension in the muscle during a voluntary contraction. This has been investigated to a limited extent previously, but only at contraction strengths which were a small percentage of maximum levels (Gilson & Mills, 1941). This was because at high levels of activity analysis of the frequency of single units became impossible through interference from adjacent units.

The efficiency of muscle reaches its maximum level when the frequency of stimulation of its fibres is just sufficient to produce maximum tetanic tension; at frequencies above and below this, the muscle fibre is less efficient (Bronk, 1930). These facts might indicate that the fibres in a muscle would tend to operate near their tetanic frequency, and that changes in tension would, as a result, be brought about mainly by means of recruiting motor units whose frequency of discharge would rapidly rise to and remain at tetanic level.

We have studied the problem in two ways. First, by stimulating a human muscle artificially and determining the relation between frequency and tension produced as has been done already in anaesthetized animals (Adrian & Bronk, 1929; Brown & Burns, 1949). The expected results would be a proportionality between mean tension and frequency until a certain frequency is reached, above which no further increase in tension would occur, indicating that this represented full tetanic frequency in the muscle fibres.

Secondly, direct recordings of the action potentials accompanying motor unit activity and of the tension developed in the muscle were made simultaneously. In such experiments it was necessary to devise some method of reducing the interference derived from extraneous units. This was accomplished (a) by use of selective electrodes, which sampled a very small volume of muscle, so that the ratio of wanted to unwanted activity was as large as possible; (b) by partially blocking the motor nerve to reduce the total number of active fibres in the muscle.

METHODS

(1) *Stimulation experiments.* Various arm muscles were used, and it was found that the most consistent results were obtained by using the adductor pollicis and the abductor digiti minimi brevis, both supplied by the ulnar nerve. These two muscles have the advantage that when certain precautions are taken they are the only muscles concerned in the production of adduction of the thumb and abduction of the little finger, respectively.
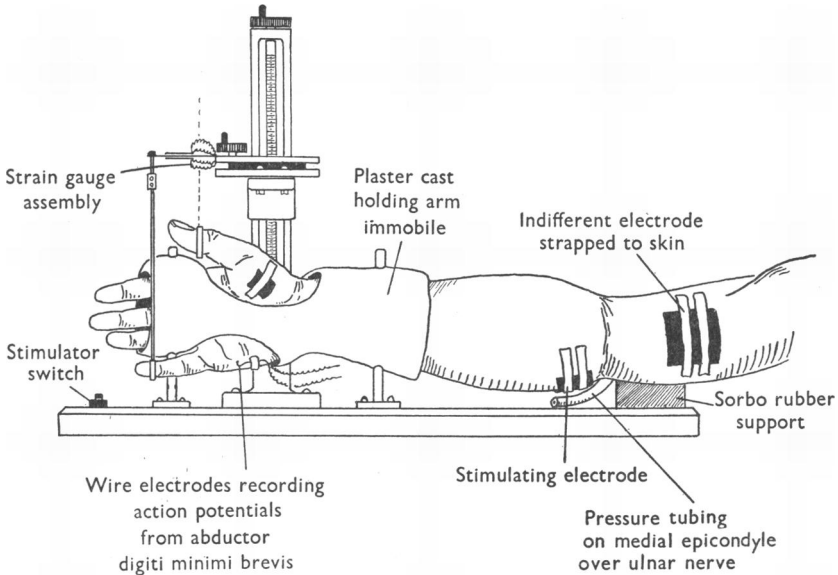

Fig. 1. Diagram of method used to immobilize arm and to record tension and action potentials in the small muscles of the hand.

In order to measure the tension exerted by these muscles with the required degree of accuracy, it was essential to fix the arm and hand rigidly. This was achieved by encasing the forearm and hand in a plaster cast (subsequently split to enable the same cast to be re-used) having openings left for the thumb or little finger (Fig. 1).

Tension was recorded with a strain gauge assembly consisting of a length of spring steel, clamped at one end and coupled to the thumb or little finger at the other. Strain gauges were mounted, one on the upper and one on the lower surface of this spring and connected to form the two arms of a Wheatstone bridge. The out of balance current was amplified and displayed on one beam of the oscilloscope.

The muscles were stimulated by square pulses from an Attree (1950) stimulator either directly through the skin over the motor point of the muscle or via the ulnar nerve. The electrodes for this

purpose were of thin stainless steel sheet, bent to the contour of the part and covered liberally with conducting paste (Unguentum Emulsificans Aquosum B.P.). The indifferent electrode was strapped to the upper arm and the stimulating electrode was similarly applied to the skin over the muscle or to the skin over the groove on the back of the medial epicondyle. The frequency of stimulation was varied in steps between 0 and 100 c/s; the stimulus strength was adjusted to be supramaximal at 50 c/s and the pulse width was maintained at 0·25 msec in order to eliminate possible repetitive firing. The stimulus was recorded on the second beam of the oscilloscope to enable a frequency check to be made if necessary.

The subject first made a series of three maximal voluntary contractions and the muscle was then stimulated at 5 min intervals with different frequencies covering the range 0–100 c/s. At the end of each experiment the strain gauge was calibrated with suspended weights: it was found to be linear over the range of tensions employed and did not vary in sensitivity from day to day.

(2) *Recording of action potentials.* The same muscles, and the same recording and fixation technique as in the stimulation experiments were employed. The second oscilloscope beam, however, recorded the action potentials derived from the muscle. These were picked up by electrodes consisting of two strands of no. 48 s.w.g. enamelled copper wire twisted together, the ends sharply cut off and introduced through a fine hypodermic needle which was subsequently withdrawn from the muscle leaving the wires *in situ*. It was found to be most important to use a sharp needle, otherwise the track of damage left in the muscle acted as a shunt, resulting in poor localization. The input from the wires was led to the two grids of a paraphase cathode follower and thence via a discriminator circuit to a conventional amplifier (time constant = 1·2 sec). The earth electrode was a metal pad strapped to the upper arm. These electrodes proved selective in use, and single motor units could be followed throughout a maximal contraction. Successful recordings were obtained about once in ten insertions of the needle, it being a matter of chance whether the electrodes were inserted into a suitable motor unit.

In order to increase further the selectivity, nerve block was performed. The ulnar nerve was compressed in the bony groove behind the medial epicondyle by means of a short length of soft rubber pressure tubing. The subject was able to control the pressure exerted upon the nerve and hence vary the degree of block. Voluntary contractions at strengths varying from 0–100 % of maximum voluntary tensions were made in the unblocked state. During block all contractions were made with the greatest force that the subject could muster. Although this proved tô be a slightly unpleasant procedure, no permanent after-effects were observed.

The oscilloscope trace was photographed in both series of experiments, the stimulation experiments on 35 mm film travelling at slow speeds and the action potentials on 70 mm bromide paper travelling at 20 cm/sec. Counting the frequency of the action potentials was performed in the following manner: ½ sec intervals (about 10 cm in length) were marked on the paper from the 50 c/s trace superimposed on the tension record. Between these limits the spikes were counted for the range of frequency of discharge. The highest frequency was found by taking the shortest interval between spikes from the same unit, recognized by the characteristics of form, size and regularity of repetition. A series of four regular action potentials which could be clearly identified was arbitrarily adopted as the minimum required for making a count. In most records the lowest frequency was easily determined, especially at tensions below 50 % of maximum and in the block experiments, because usually only one or two units were responding within the pick-up range of the electrodes.

RESULTS

(1) *Tension-frequency experiments.* Electrical stimulation of the ulnar nerve and direct stimulation of the muscle proved to be painful at supramaximal strengths of excitation. It was found much easier to bear this if the stimulator was controlled by the subject. Nearly always, on stimulating the ulnar nerve, it was possible to produce a tension as great as that attained during a maximal voluntary contraction (Fig. 2).
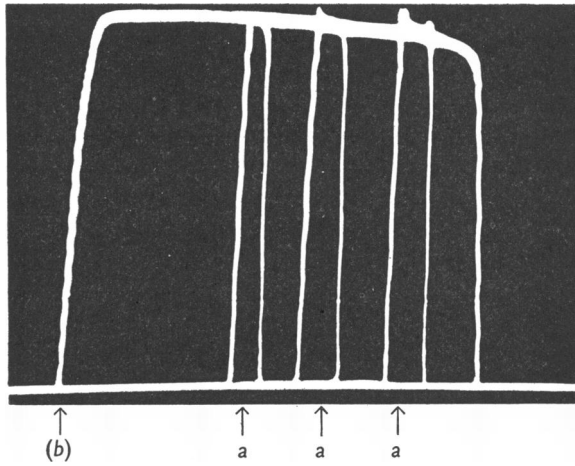
Fig. 2. Comparison of tension produced by a maximal voluntary contraction (*a*)
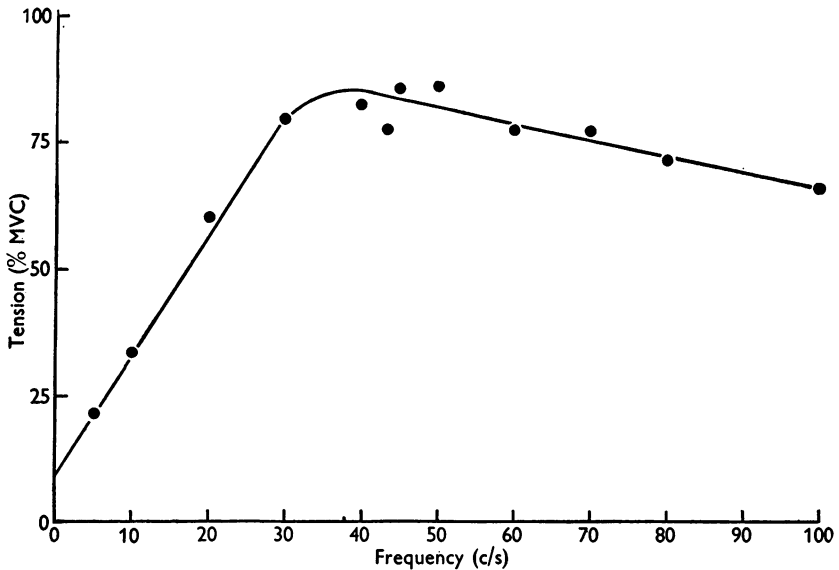and maximal stimulation of the motor nerve (*b*).

Fig. 3. The relation between the frequency of maximal stimulation of the ulnar nerve
and the tension produced in the human adductor pollicis.

In all experiments the tension exerted by the muscle increased with the
frequency of stimulation; the tension was directly proportional to frequency
until this reached a value between 35 and 45 c/s. At this frequency the tension
increased no further and the plotted curve reached a plateau (Fig. 3).

On increasing the frequency of stimulation still further, the usual result was a slight decrease in tension, although in a few cases the plateau remained flat or fell steeply.

The same relation was found whether the muscle was stimulated through the motor nerve or directly through the skin over the muscle. It also held for the submaximally excited muscle, although in this case, as would be expected, the scatter of the experimental points about the straight line was greater (Fig. 4).
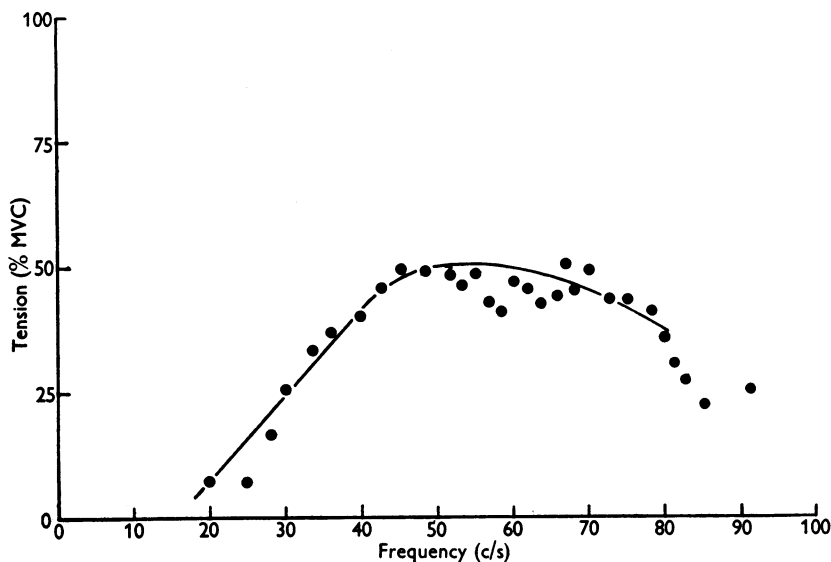

Fig. 4. The relation between the frequency of submaximal stimulation of the ulnar nerve and the tension produced in the human adductor pollicis.

(2) *Action potential recording experiments.* In most experiments it was possible during voluntary contractions to identify clearly four or five separate motor units responding regularly, even when the muscle was contracting maximally. Such recordings are shown in Fig. 5. Frequencies above 50/sec were never observed and frequencies between 40 and 50/sec only occurred when the tension was above 75% of the maximum voluntary contraction strength (MVC). Over the greater range of tensions (25–75% MVC) the majority of the fastest units responded at frequencies between 25 and 35/sec (Fig. 6).

The slowest motor units behaved in a similar way, but the plateau was more evident. Thus over the tension range 5–60% MVC the frequency increased. The curves illustrating these findings were obtained from 200–300 measurements of frequency in each experiment, each point on the graph being the mean of all the determinations within a 5% tension range.
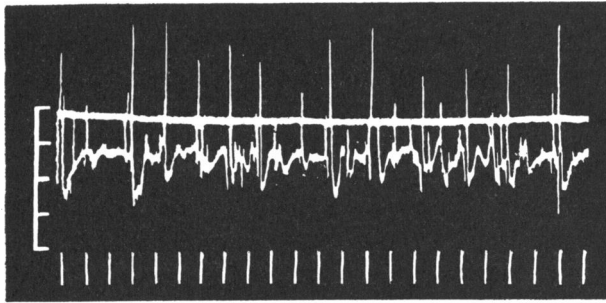
(a)
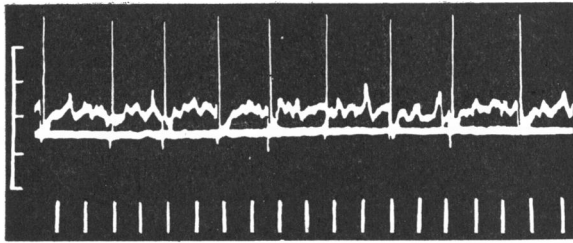
(b)

Fig. 5. Recording from a maximal voluntary contraction in the abductor digiti minimi brevis. (a) Tension (vertical bar) 0–100% MVC (maximal voluntary contraction). Time tracing at 50/sec. (b) Same recording but at submaximal strength.
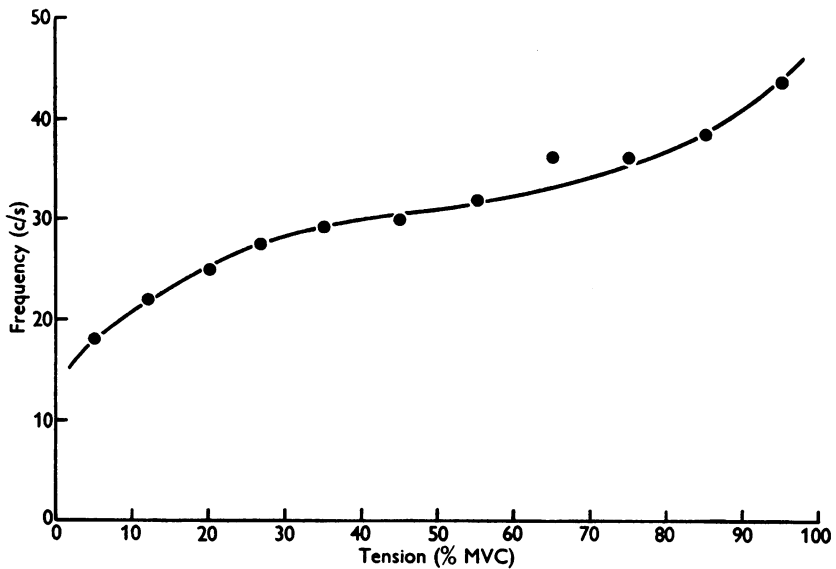

Fig. 6. Composite curve showing relation between tension in a voluntary contraction of abductor digiti minimi brevis and maximum frequency of motor unit discharge (see text).

On several occasions it was possible to obtain records of one clearly identi-
fiable unit during the whole of a voluntary contraction, in one case throughout
the course of a complete experiment of 2 hr. Fig. 7 shows how the frequency
of such a unit varied with the tension in the muscle during a near-maximal
contraction. This particular unit commenced firing when the tension rose to
15% of the maximum, at a frequency about 20/sec. During the contraction
it can be seen that the frequency increased with the tension, but only from
20 to 30/sec. Other units were observed which commenced firing at different
tensions, the one shown in Fig. 8 doing so at 48% MVC, as the tension rose,
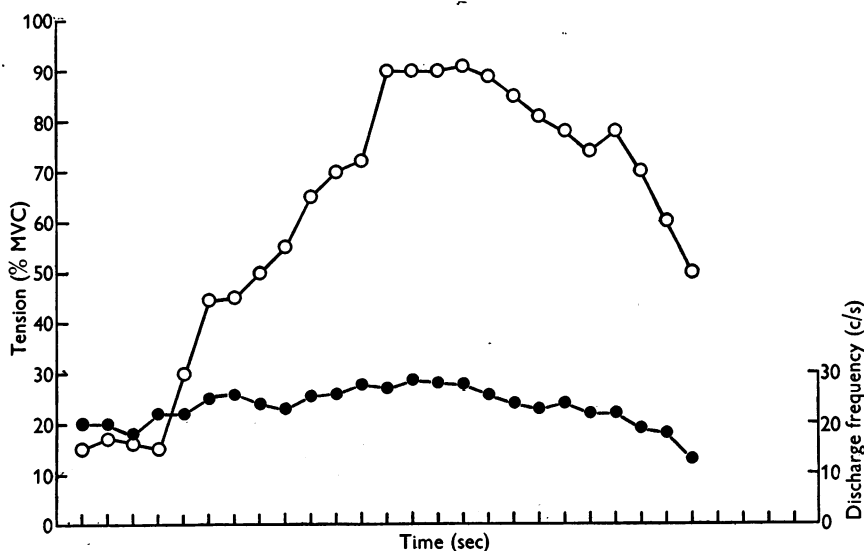falling out again when it was reduced to 60% MVC.

Fig. 7. The frequency response of a single unit measured at 1 sec intervals during a voluntary
contraction of abductor digiti minimi brevis. Open circles O show changes in tension between
15 and 92% MVC, while filled circles ● are the corresponding discharge frequencies, varying
between 10 and 30/sec.

Single units could be identified easily by their characteristic sound when the
amplified spikes were reproduced on a loudspeaker and they could be followed
at different tensions through most of the contraction range. It was clear that
during a voluntary contraction when the tension reached a certain value,
a particular motor unit would come in and remain firing until the tension
dropped again to nearly the same value. The same unit always started firing at
about the same tension level. It was also apparent from examination of the
records and from the loudspeaker sounds that most units started and stopped
abruptly and varied in their discharge rates relatively little, in the course of
a contraction. This held for units coming in at the higher tensions (about

25% MVC). Units active at low tensions (below 5% MVC), on the other hand, usually had a lower starting frequency and showed a greater frequency range than those active only at higher tensions (Fig. 9).

Discharge rates were seldom regular and showed fluctuations sometimes corresponding with slight changes in tension. Often units would miss one discharge and then continue at the same rate. At high tensions activity often appeared to be in the form of five to ten fairly regular responses then a pause of variable length, followed by further activity. This type of activity in 'bursts' was most common when the muscle was fatigued.
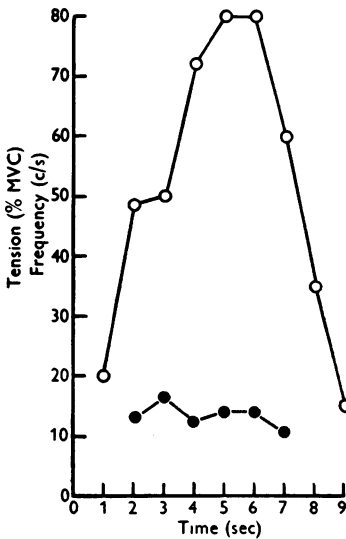

Fig. 8

Fig. 9

Fig. 8. Frequency response of single unit, commencing at 48% MVC
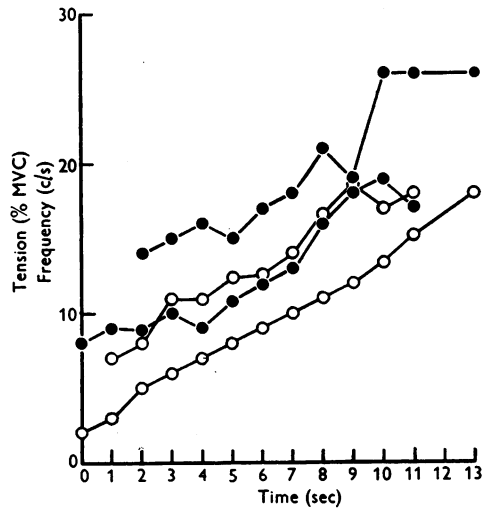with a discharge rate of 13/sec and ceasing at 60% MVC.

Fig. 9. Behaviour of two units at low tensions showing increase of frequency with tension.

No electrical activity could be detected when the muscle was relaxed. When it was fatigued, as at the end of a series of maximum contractions, it was found that the amplitude of single unit spikes tended to decrease gradually, although there was no alteration that could be observed in the frequency of discharge. We have no evidence to show whether this was a true reduction in muscle potentials or was an artifact due to the recording apparatus, although the latter seems unlikely. Apart from this effect, the amplitude of single units did not vary in any one experiment.

Although the usual response of the muscle was an asynchronous discharge, under certain circumstances synchronization of the potentials occurred. If the muscle was fatigued, this was particularly evident; during the phase of relaxa-

tion the action potentials were often grouped at about 14/sec (Fig. 10). This could possibly have been due to clonic reflex activity, because it can be shown that the repetition rate of clonus in a part, is dependent upon the twitch time which, in the case of the little finger, would give a tremor approximately of this frequency. The synchronization was not observed in the partial nerve block experiments.

In the experiments in which the recording was well localized, the action potentials were clearly identifiable and discharged regularly enough to leave no doubt as to their true frequency. In other experiments, however, there may have been more than one unit of similar appearance, and confusion between them was possible. This would always have led to an over-estimation of frequency. Since this was more likely to have happened at high tensions, the actual variation in frequency may well have been even less than we have shown.
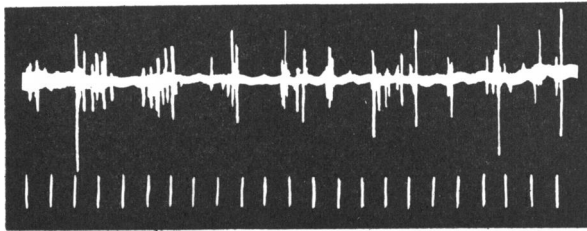

Fig. 10. Synchronization of motor units during an isometric, submaximal contraction.

(3) *Motor nerve block experiments.* It was decided to attempt partial block of the motor nerve, first because if the blocked fibres were randomly distributed within the muscle, the number of responding units in the vicinity of the recording wires would be reduced, thus making the identification of units easier, especially at near-maximum strengths. Secondly, it was possible that, as increasing numbers of units were blocked and the tension in a maximum voluntary effort fell, remaining units would be forced to respond at their maximum rate. Thus a tension range of say 5% of the unblocked MVC might permit recording the whole of the frequency range of one unit, uninterrupted by interference from nearby fibres.

The first supposition proved correct; when units fell out as a result of the block a clearer record was obtained, commonly only one unit firing at tensions up to 25 or 30% of the maximum. Pressure on the ulnar nerve gave rise to proprioceptive and sensory loss over the typical distribution within 15–20 min without measurable loss of motor power. After 40–50 min diminution of motor activity occurred and in the space of the next 5–10 min the tension in response to maximum voluntary effort fell from 100% to nil. This was the result of reduced motor unit activity as could be demonstrated in the records and was

apparent from the loudspeaker. The procedure was unpleasant only at the beginning of the period of block, when pain was experienced at the site of pressure, especially if the same nerve had been blocked previously. With a certain amount of practice the subject could control the degree of block by varying the pressure on the nerve.

Maximum effort was not rewarded by maximum response of the motor units. When recordings of maximum efforts at different degrees of block, and hence different maximum tensions, were analysed in the same way as before, the resulting curves followed those obtained from normal muscle (Fig. 11). This result was also quite obvious from the loudspeaker, because falling tension during the progress of the block was accompanied by progressively lower discharge rates of the remaining units. When, however, the degree of block was considerable and kept constant, changes in voluntary effort resulted in little or no effect on discharge rate, other than starting or stopping it. This contrasted with the normal unblocked state at the same tension, in which considerable control over discharge rate could be exercised.
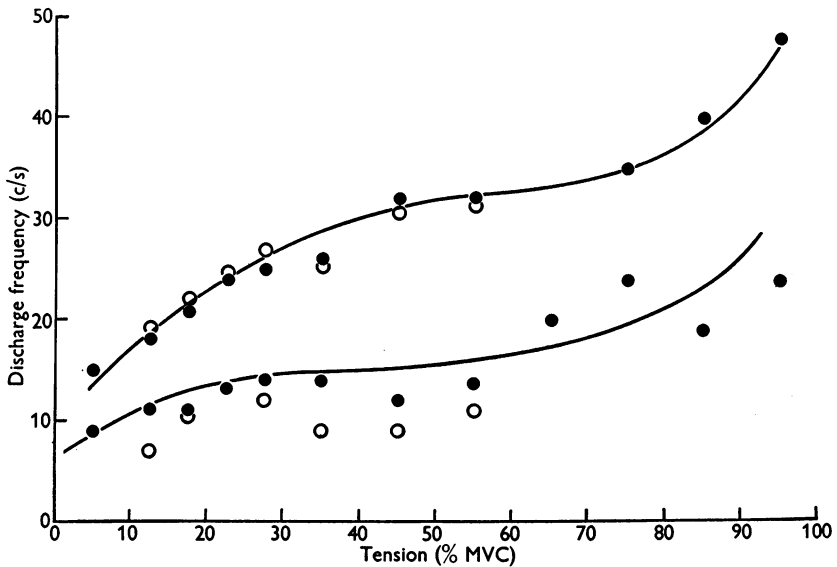

Fig. 11. Comparison of relation between tension and discharge frequency during voluntary contractions in the normal muscle ● and in the same muscle having nearly complete pressure block of its motor nerve, ○. Upper curve is of maximum and lower of minimum frequencies observed. Abductor digiti minimi brevis; ulnar nerve block at the elbow.

DISCUSSION

The interesting feature of the relation between unit discharge frequency and tension in the whole muscle during voluntary contraction, is the comparatively small range through which the firing rate varies. It appears that in the muscles

used for these experiments the starting rate of most units is quite high, in the region of 20/sec and that this frequency changes little until the contraction of the muscle is almost maximal. It may be that the behaviour of the units which were studied in these experiments was not typical of the whole muscle. That this contention is unlikely, is evident from the composite curves drawn from the multiple counts of motor unit frequencies (Figs. 6 and 11) which show a clear plateau in the region of 25–75 % MVC. These curves do not typify the response of particular units to tension in the muscle; from them, however, can be found the average maximum rate at which a unit responds at any tension. It is quite probable that most units do not fire at rates much above 35/sec, the frequencies above this being accounted for by units recruited only at near-maximal strengths.

This is also supported by the form of the frequency-tension curve (Fig. 3) resulting from artificial stimulation of the muscle. Here, although maximum tension is not reached until a frequency of 40/sec is applied, there is a distinct decrease in slope in the region of 35/sec indicating that different fibres may have slightly different tetanic frequencies. At frequencies above 45/sec no further increase in tension occurred.

In these experiments the tension measured represents the mean level attained during a series of stimulations: it is impossible with simple apparatus to record either the maximum or the minimum peak level, because of the distortion due to the inertia of the muscle.

The proportionality found between the mean tension and frequency depends on the time course of the active state (Hill, 1949) and on the properties of the elastic elements, and suggests that each contraction after a shock contributes a certain amount of tension-time ($\int T \mathrm{d}t$, where T is the tension and t the time) which summates simply with the next. If the summation process is assumed to depend solely upon the addition of tension during each response and not to involve the factor of time, it becomes necessary to presuppose that the rate of relaxation of the contractile element in the muscle is linear. When the stimuli are so closely spaced that a contraction occurs at the time of development of peak tension due to the previous one, the muscle will exert its maximum tetanic tension.

Bronk (1930) showed that as the rate of stimulation of a muscle is increased, the economy or amount of tension-time maintained per unit of energy expended increases. He suggested that this was mainly due to a greater degree of fusion of the muscle twitches, there being no further increase in economy with frequencies above that needed to produce complete tetanus. This may be interpreted in terms of Hill's active-state theory: the shorter the interval between stimuli, the less the active state declines between each successive contraction and therefore the less the energy required to maintain a given amount of tension-time. Thus a grading of activity more by recruitment than

by changes of frequency over the major range of tensions exerted would lead to greater economy within the muscle. This would result in individual fibres starting to fire abruptly at relatively high frequencies, as we have found in these experiments. On the other hand, the results of the recording experiments confirm previous work that changes in frequency of discharge do play a part in the contraction of voluntary muscle, particularly at low tensions (Adrian & Bronk, 1929; Lindsley, 1935; Hoefer & Putnam, 1939). The lack of activity at rest confirms the work of Smith (1934) and Gilson & Mills (1941).

A scheme of the pattern of activity which might agree with this experimental evidence is given in Fig. 12.
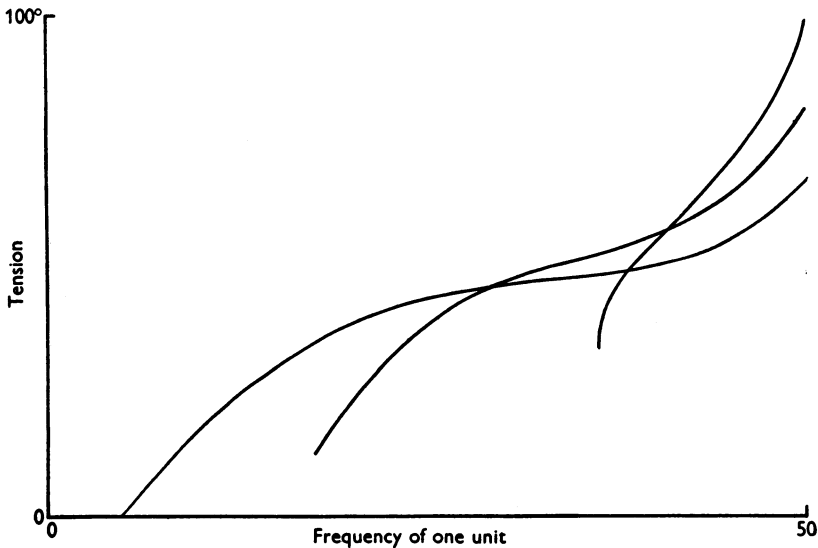

Fig. 12. Scheme illustrating possible mode of behaviour of individual motor units during the voluntary contraction of a muscle. A particular unit starts firing when the tension in the muscle reaches a certain level, its frequency increasing with tension over a comparatively small range except at low and high tensions.

When the ulnar nerve was partly blocked, maximum voluntary efforts did not result in maximum rates of firing of individual units, but showed a similar relation between frequency and tension to that observed in submaximal contractions in the unblocked state. This could mean that tension, rather than the degree of voluntary effort made, in some way determines the frequency of motor unit firing. This connexion between frequency and tension may depend entirely upon the conditions of the experiment or it may be a physiological mechanism operating in the intact muscle. The former possibility can be accounted for by supposing that the block of motor nerve fibres by pressure is preferential, so that as the block proceeds, those fibres subserving the higher frequencies succumb first.

It might also be explained by pressure on the nerve producing an intermittent block, although if this were the case it would be unlikely that the composite curve would be of the same form under both normal and blocked conditions. Moreover, it should have been possible to discern periods of 2/1, 3/1, 4/1 etc. block in single fibres as the tension fell, but this type of discontinuity was never seen.

Leksell (1945) has shown that a selective pressure block can be set up in a motor nerve such that conduction in the large fibres can be eliminated, while the small motor fibres remain functionally intact. Thus in our experiments the muscle spindle afferents were probably the first to be blocked (Seddon, 1944), a supposition supported by the rapid loss of proprioceptive function during the early stages of each experiment. Like Matthews (1933) Leksell also found that on stimulation of the remaining small motor fibres there was no contraction of the muscle but the afferent discharge from the muscle proprioceptors was augmented.

Our results may indicate the existence in man of a physiological mechanism controlling unit discharge frequency either in the manner suggested by Holmgren & Merton (1954) or which might be linked with the control of muscle spindles in some way. Such a system might well result if the cortex is able to control muscle spindle activity without directly altering tension, as has been shown by Granit & Kaada (1952).

SUMMARY

1. Human muscles were stimulated with square pulses applied locally and via the motor nerve at different frequencies: the tensions were recorded with a strain gauge. The maximum tension produced by tetanic stimulation equalled that developed in a maximum voluntary contraction. This maximum occurred at frequencies between 35 and 40/sec.

2. Recordings were made from single motor units with fine wire electrodes during voluntary contractions of various strengths, and the frequency of firing was measured.

3. The relation between strength of contraction and rate of firing is an S-shaped curve.

4. The ulnar nerve was partially blocked by pressure at the elbow, and motor unit frequencies were measured during maximum efforts as the tension declined. The frequencies of discharge were not higher than those occurring when the nerve was normal and the relation between strength of contraction and rate of firing was the same as in the unblocked state.

5. These results indicate that gradation of contraction in the muscles investigated is brought about mainly by motor unit recruitment, except at very low and high contraction strengths.

REFERENCES

ADRIAN, E. D. & BRONK, D. W. (1929). Discharge of impulses in motor nerve fibres, part II. *J. Physiol.* **67**, 119–151.

ATTREE, V. H. (1950). An electronic stimulator for biological research. *J. sci. Instrum.* **27**, 43–47.

BIGLAND, B. & LIPPOLD, O. C. J. (1954). The relation between force, velocity and integrated electrical activity in human muscle. *J. Physiol.* **123**, 214–224.

BRONK, D. W. (1930). The energy expended in maintaining a muscular contraction. *J. Physiol.* **69**, 306–315.

BROWN, G. L. & BURNS, B. D. (1949). Fatigue and neuromuscular block in mammalian skeletal muscle. *Proc. Roy. Soc.* B, **136**, 182–195.

GILSON, A. S. JR. & MILLS, W. B. (1941). Activities of single motor units in man during slight voluntary efforts. *Amer. J. Physiol.* **133**, 658–669.

GRANIT, R. & KAADA, B. R. (1952). The influence of stimulation of central nervous structures on muscle spindles in the cat. *Acta physiol. scand.* **27**, 130–160.

HILL, A. V. (1949). The abrupt transition from rest to activity in muscle. *Proc. Roy. Soc.* B, **136**, 399–420.

HOEFER, P. F. A. & PUTNAM, J. J. (1939). Action potentials of muscles in normal subjects. *Arch. Neurol. Psychiat., Chicago*, **42**, 201–218.

HOLMGREN, B. & MERTON, P. A. (1954). Local feedback control of motoneurones. *J. Physiol.* **123**, 47–48 *P*.

LEKSELL, L. (1945). The action potential and excitatory effects of the small ventral root fibres to skeletal muscle. *Acta physiol. scand.* **10**, suppl. 31, 1–84.

LINDSLEY, D. (1935). Electrical activity of human motor units during voluntary contraction. *Amer. J. Physiol.* **114**, 90–99.

LIPPOLD, O. C. J. (1952). The relation between integrated action potentials in a human muscle and its isometric tension. *J. Physiol.* **117**, 492–499.

MATTHEWS, B. H. C. (1933). Nerve endings in mammalian muscle. *J. Physiol.* **78**, 1–53.

SEDDON, H. J. (1944). Three types of nerve injury. *Brain*, **66**, 237–288.

SMITH, O. C. (1934). Action potentials from single motor units in voluntary contraction. *Amer. J. Physiol.* **108**, 629–638.