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CHANGES IN MOTONEURONE FIRING RATES DURING SUSTAINED MAXIMAL VOLUNTARY CONTRACTIONS

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SUMMARY

1. Tungsten micro-electrodes have been used to record the electrical activity of single motor units in the human adductor pollicis during maximal voluntary contractions. The potentials were characteristic of those from single muscle fibres.

2. In brief maximal contractions, the firing rates of over 200 motor units were obtained from five normal subjects. Four subjects had a similar range (mean 26·4 ± 6·5 Hz) while the fifth was slightly higher (35 ± 7·4 Hz).

3. When maximal voluntary force was sustained for 40–120 s, there was a progressive decline in the range and mean rate of motor-unit discharge. In the first 60 s, mean rates fell from about 27 Hz to 15 Hz. There was some evidence to suggest that those units with the highest initial frequencies changed rate most rapidly.

4. It is suggested that this decline in motor unit discharge rates is not responsible for force loss, but that it may enable effective modulation of voluntary strength by rate coding to continue during fatigue.

INTRODUCTION

Many studies have been made of changes in motor unit firing rates as voluntary effort increases (Milner-Brown, Stein & Yemm, 1973; Tanji & Kato, 1973; Monster & Chan, 1977). However, few investigors have succeeded in clearly isolating the frequencies of single motor unit potentials when the force exceeds about 75% of the maximal capacity of the muscle because of interference from surrounding active units. It is therefore unclear what the firing rates may be when maximum force is generated, or whether these rates may change if maximal force is maintained for prolonged periods.

In the present study, direct measurement of the firing rates of clearly identified individual motor units during maximal contractions of the human adductor pollicis muscle was made possible by the use of tungsten micro-electrodes. By sampling the instantaneous rates of large populations of units at different times before, during and after fatigue, their mean maximum rates, range of variability and average changes with time were measured.

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When a maximum voluntary contraction (m.v.c.) is maintained over a period of time, despite the subject making his best effort, the loss of force is accompanied by a decline in the muscle surface electromyogram (e.m.g.) (Stephens & Taylor, 1972). This is not due to increasing neuromuscular block (Merton, 1954; Bigland-Ritchie, Kukulka, Lippold & Woods, 1982). Several workers have suggested that during fatigue there is a decline in the average motoneurone discharge rate (Marsden, Meadows & Merton, 1971; Bigland-Ritchie, Jones & Woods, 1979; Bigland-Ritchie & Lippold, 1979). However, these suggestions were mainly based on indirect evidence and there have been no published reports of absolute values for maximal rates of individual motoneurones or of how these may change with fatigue when the contraction is sustained.

A preliminary account of the current work has already been published (Bigland-Ritchie, Johansson, Lippold & Woods, 1982).

METHODS

Subjects. The five subjects, male and female, ranged in age between 18–60 years. All gave their informed consent. Most had considerable previous experience of maintaining maximal voluntary contractions for the time required.

Protocol. Control values for both force and motor unit firing rates were obtained for the non-fatigued human adductor pollicis muscle during a series of five to ten brief (10 s) maximal voluntary contractions executed once every 3 min. This was followed by a maximal contraction sustained for periods ranging from 40 to 120 s. Force, surface e.m.g. and the firing rate of as many motor units as possible were recorded throughout. After a further 10 min rest, the initial pre-fatigue series was repeated. In some experiments single maximal shocks were periodically delivered to the ulnar nerve and the evoked muscle mass action potential (M wave) monitored from the surface electrodes to test the integrity of neuromuscular transmission.

Force. The force of voluntary contractions was recorded from a strain gauge as described previously by Bigland-Ritchie *et al.* (1982). In selected experiments this was also compared with the force resulting from supramaximal tetanic stimulation (50 Hz) of the ulnar nerve before, during and at the termination of the sustained maximal contraction to test for contraction maximality (Bigland-Ritchie *et al.* 1982).

Surface e.m.g. This was recorded from two 1 cm Disa surface electrodes, one over the belly of the muscle, the other on the base of the thumb. The signals were amplified (cut-off frequencies 10 Hz–10 kHz), rectified and smoothed using a time constant of 0·1 s.

Single unit potentials. Potentials were recorded from single motor units of the adductor pollicis muscle (Fig. 1) using 0·2 mm diameter tungsten micro-electrodes. These were coated with seven layers of Voltalac varnish with a 10–15 μm length of exposed tip electrolytically sharpened to a diameter of 1–5 μm (Hagbarth & Vallbo, 1969). For successful recording of single spike trains with a high signal to noise ratio an electrode impedance greater than 100 kΩ was generally required. This was tested after electrode insertion and at intervals throughout the experiments. During each contraction the electrode was slowly advanced such that brief bursts of potentials (5–50 spikes) were recorded from each of as many units as possible, so that a large population of instantaneous rates could be sampled. Sometimes, however, it proved possible to follow the rates of a single identified unit for 10–20 s during a sustained contraction. The potentials were amplified, filtered (10 Hz–10 kHz), and monitored visually and by a loud speaker.

Data analysis. All signals were stored on FM tape together with 0·1 Hz signal pulses synchronized to a digital clock. Force and surface e.m.g. records were analysed by a TRS80 digital computer either on- or off-line. For measurement of single motor unit firing rates, spike trains of suitable amplitude were identified visually on tape replay and a digitimer was then triggered from the preceding 0·1 Hz pulse. After a variable measured delay, the first digitimer gate triggered the oscilloscope such that the chosen spike train was displayed over an appropriate period. The spike train was passed through a window discriminator and its amplified pulse output through a Bak instantaneous rate meter, the output of which was displayed on a second oscilloscope trace. The window discriminator level was adjusted until a train of uncontaminated spikes with regular intervals was obtained. Gates 2 and 3 on the digitimer were then adjusted to set the most appropriate time period for measurement, and the window discriminator pulses during this time (usually 0·2–0·5 s) were fed to a digital counter. This procedure provided not only the number of spikes per unit time, but also the precise time after the onset of each contraction during which the counts were made. It also allowed easy later retrieval of any required spike sequence. All values were also checked visually. The frequencies were then grouped into suitable time bins, and for each period mean rates and histograms of the range of motor unit frequencies were constructed. Individual spikes from each train could be displayed on a fast time base to examine their amplitude, duration and wave form. Selected trains were also transferred to a PDP 11/40 computer to measure interspike interval histograms. This analysis procedure is illustrated in Fig. 2.

For routine measurement the tape recorder was set to record spikes of up to ± 10 mV. However, since larger spikes were often seen, all potentials were simultaneously recorded on a second channel set at lower gain.

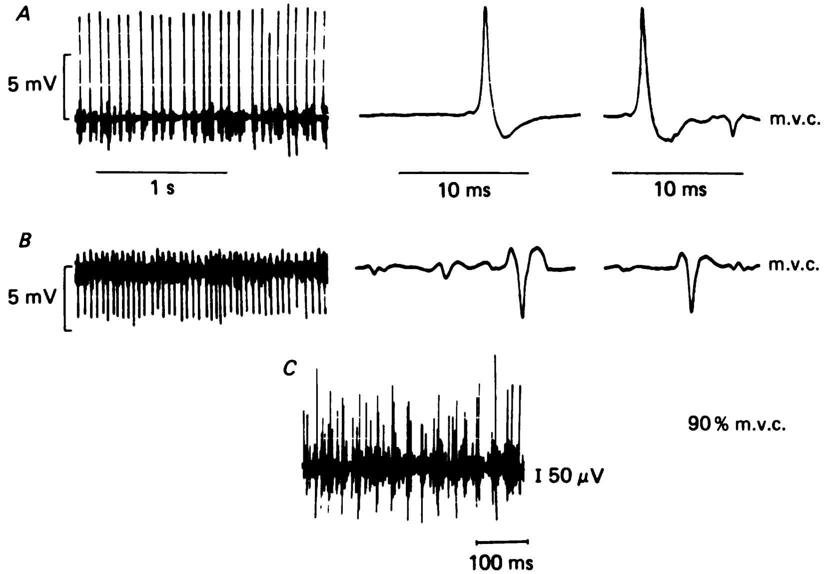

Fig. 1. *A*, *B*, motor unit potentials recorded from adductor pollicis during a maximal voluntary contraction using tungsten electrodes Single spikes from each train are shown on the right. *C* shows, for comparison, typical record of spikes obtained using fine-wire electrodes during near maximal contraction of adductor pollicis.

RESULTS

Single unit potentials

Fig. 1 *C* shows a typical record of motor unit activity obtained during a high force voluntary contraction, using conventional fine-wire electrodes (Bigland & Lippold, 1954). Potential amplitudes seldom exceed about 0·5 mV. Despite relatively high discrimination it is not possible, using their amplitude or regularity, to isolate clearly potentials originating from any one individual unit. In contrast Fig. 1 *A* and *B* shows trains of potentials recorded during a maximal contraction using tungsten micro-electrodes. Spike amplitudes varied between 2–40 mV. There is a large signal to noise ratio and the amplitude and regularity of the spikes shows them to originate from a single unit.

The methods employed for spike frequency analysis are shown in Fig. 2*A*. Generally a wide range of window discriminator settings could be used without changing the pulse rate counted. In each contraction the electrode was slowly advanced such that, under favourable conditions, bursts of activity were obtained from each of a series of different units. Typically the spike amplitudes increased and then declined as the electrode approached and passed each muscle fibre. When equidistant from two fibres, potentials from both were evident. This could be clearly detected by the irregularity and the appearance of uncharacteristically short, spike intervals. The gated period over which single unit, spike frequencies were counted was therefore adjusted to include only those portions of each spike train with the most regular intervals. These generally varied by about ±30% of the mean interval. Examples of interspike intervals for three units of different mean rates are shown in Fig. 2*B*.

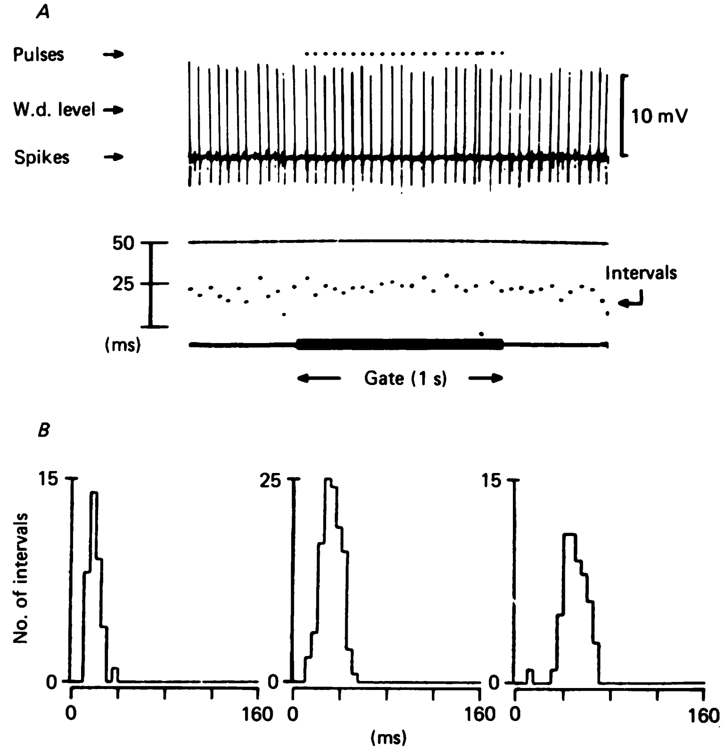

Fig. 2. *A*, spike frequency analysis (see text). *B*, three examples of spike interval histograms each from a different unit. W.d.: window discriminator.

Fig. 1 *A*, *B*, shows typical single spikes recorded on a fast time scale. The smaller ones, typically 2–5 mV, were either initially positive or negative going in sign and usually had a polyphasic wave form typical of extracellular recordings. Those of larger amplitude, 10–40 mV, generally had a biphasic wave form. They always had a positive initial spike of 1–2 ms duration followed by a slower negative phase. The potential shape, its duration and smooth profile suggested that each was recorded from a single muscle fibre.

Motor unit firing rates during brief maximal contractions

The firing rates of 20–100 motor units were recorded from the adductor pollicis muscle of each of five subjects during a series of brief maximal voluntary contractions. To minimize any effects of fatigue, each 10 s contraction was followed by 3 min rest. The maximality of the contractions was checked by (a) constant monitoring of force; (b) periodically comparing it to the force generated by supramaximal tetanic nerve stimulation and (c) superimposing a single maximal shock. If no additional force resulted in the latter case the voluntary contraction was deemed to be maximal (Merton, 1954).

For all subjects a wide range of firing rates was observed (10–50 Hz). The mean values (±S.D.) for each subject were 24·5±5·1 Hz; 22·5±7·2 Hz; 24·1±8·9 Hz; 27·4±6·6 Hz and 35·4±7·4 Hz respectively. Fig. 3 shows pooled data from the four subjects with mean rates of 22–28 Hz. This is compared with that from the fifth subject who consistently showed higher values.

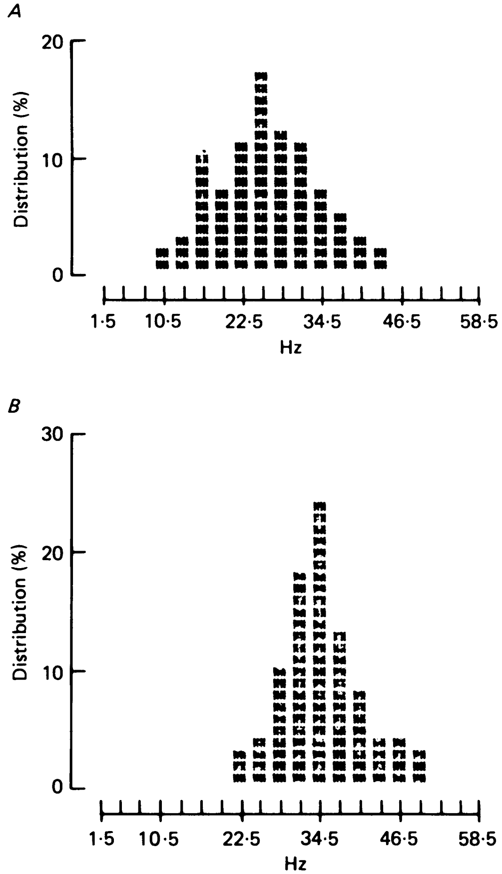

Fig. 3. Distribution of firing rates during brief (10 s) maximal contractions of non-fatigued adductor pollicis (bin width 3 Hz). *A*, pooled data from four subjects with similar mean rates. Group mean 26·9±8·7 Hz; $n = 202$ units. *B*, data for one subject with higher mean rate of 35·4±7·4 Hz; $n = 104$ units.

Firing rates during sustained maximal effort

For each subject motor unit firing rates were recorded from as many units as possible during a series of maximal contractions sustained for 40–120 s. Despite maintained maximum effort both the force developed and the mean firing-rate of motor units declined with time. Fig. 4 *A* shows the force and e.m.g.; *B*, the discharge rates recorded during a single maximal contraction lasting to 40 s; *C*, the combined results of nine contractions from one subject (lasting for up to 110 s) and *D*, the changes with time of mean rates (±S.D.) for the pooled data from all subjects. The latter are expressed as a percentage of their pre-fatigue control values. All show a decline of some 50 % in the mean discharge rate when the contraction was sustained for 60 s. When the pooled data was divided into time bins the corresponding histograms showed little change in the minimum rate (8–10 Hz) but a marked decline in the higher frequencies, suggesting that the units with the highest initial firing rates tend to change most rapidly.

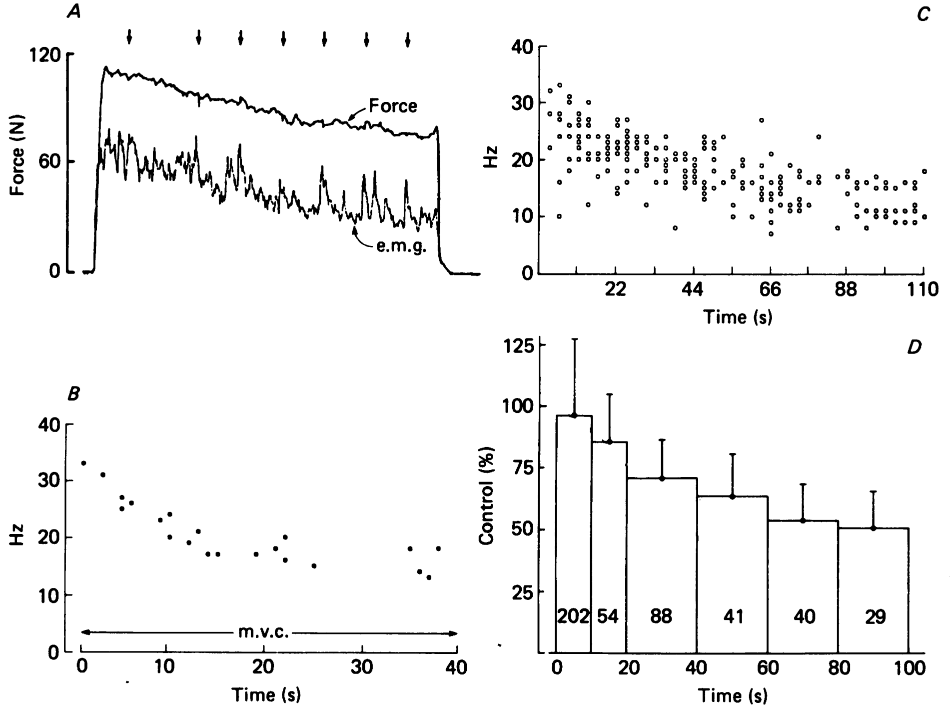

Fig. 4. Effect of fatigue: *A*, typical force and surface e.m.g. of the adductor pollicis muscle during a sustained maximal voluntary contraction. Arrows show times when single maximal shocks were delivered to test for contraction maximality and neuromuscular transmission (see text); *B*, discharge rates recorded from twenty-one single motor units during one experiment. Each point is the mean rate of a spike train recorded at the times shown; *C*, pooled data from nine experiments on one subject (219 units) and *D*, pooled data: mean firing rates (±S.D.) recorded from all five subjects during sustained maximal contractions. The mean rates for each time bin are expressed as a percentage of the pre-fatigue control values, with the number of units shown in each bin.

In several experiments the integrity of neuromuscular transmission was tested throughout by the methods described by Bigland-Ritchie *et al.* (1982). Since no decline was seen in the muscle mass action potential evoked by single maximal shocks to the ulnar nerve, the reduction in motor unit potential frequencies was attributed to a corresponding change in motoneurone discharge rate, rather than to progressively increasing neuromuscular block.

Changes in single motoneurone firing rates

The object of the current experiments was to determine changes in the mean firing rate of a large population of motoneurones as fatigue developed. Thus in most experiments, the electrode was advanced relatively rapidly such that only short bursts of potentials were recorded from many different fibres. No deliberate attempt was made to follow changes in the firing rates of individual units. Occasionally, however, uninterrupted spike trains of 10–20 s duration were obtained, each appearing to originate continuously from a single muscle fibre. Changes in the discharge rates of three such units are shown in Fig. 5. Recording from one unit started within the first 2 s after the onset of contraction and continued until the 15th second, after which the unit was lost. During this time the frequency declined rapidly and smoothly from

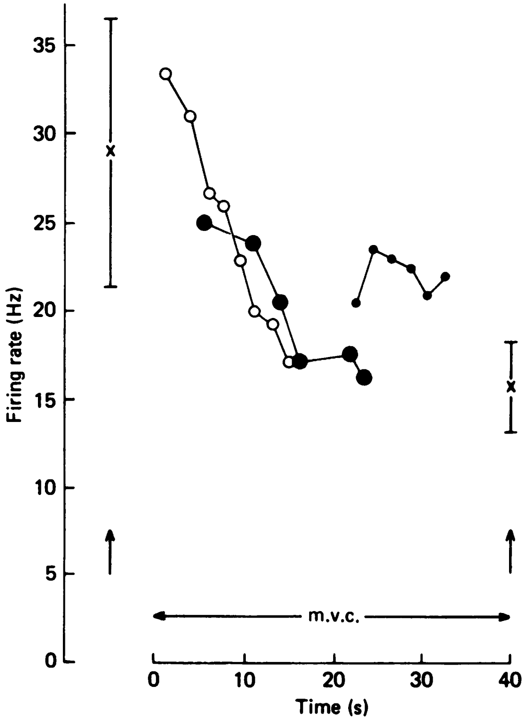

Fig. 5. Changes with time in the firing rates of three single identified units during a sustained maximal contraction. Recording from the unit with open circles (○) was commenced within 2 s of onset of contraction and continued for 15 s. Decline in frequency was smooth and no evidence of irregular firing or dropping-out of individual discharges was seen. The rates for the two other units (●) and (•) are also shown. Mean discharge rates (±S.D.) for all units measured at the onset and termination of contractions are shown (×).

34 Hz to 17 Hz. There was no sudden discontinuity of rate such as would be expected if, while recording from a single muscle fibre, neuromuscular block had occurred. Although the number of units recorded in this way was small they suggest a wide variety in the behaviour of different motor units, or motor unit types.

DISCUSSION

Motoneurone firing rates during maximal voluntary contractions. The use of tungsten micro-electrodes has now made it possible to measure accurately the firing rates of large populations of motoneurones during maximal voluntary contractions. This technique also allows examination of the wave form of potentials from individual muscle fibres.

During brief m.v.c.s, the firing rates of over 200 muscle fibres were recorded from the adductor pollicis muscles of five subjects. From four of them a similar range of discharge rates was recorded (mean 26·4 ± 6·5 Hz). A somewhat higher rate (35·4 ± 7·4 Hz) was found for the fifth subject. These values are of considerable interest for they are the maximum rates that can be sustained by voluntary effort. They may provide an estimate of the upper limit of the range of motoneurone firing rates employed for force modulation in most voluntary activities. Higher instantaneous rates have been observed during the ballistic onset of contractions (Desmedt & Godeaux, 1977), but are not sustained for more than a few spikes. They increase the rate of initial force generation, but would not be functionally useful thereafter if maximum force can be maintained at lower discharge rates. The rates reported here apply to the adductor pollicis muscle and may differ from other muscles of different function, fibre composition, and/or contractile properties (Bellemare, Bigland-Ritchie, Johansson, Smith & Woods, 1982).

Full tetanic force cannot be generated in most human muscles by motor nerve stimulation at rates less than 50–80 Hz (Edwards, Young, Hosking & Jones, 1977). For the adductor pollicis and quadriceps muscles these forces can be matched by maximum voluntary effort (Merton, 1954; Bigland & Lippold, 1954; Bigland-Ritchie, Jones, Hosking & Edwards, 1978). Belanger & McComas (1981) have shown that many other muscles are also fully activated during m.v.c.s. The results reported here therefore serve to emphasize the functional importance of Rack & Westbury's (1969) original observation (see also Lind & Petrofsky, 1978) that when motoneurones are stimulated asynchronously, as in voluntary activation, the same force can be generated at substantially lower rates than are required during synchronous nerve stimulation. However, even with synchronous nerve stimulation, only a relatively few of the faster (and larger) motor units may require high excitation rates for full force production.

Numerous workers have attempted to record single motor unit activity during m.v.c.s. However, it has previously only been possible to make these measurements from units with aberrant innervation patterns (Marsden *et al.* 1971; Grimby & Hannerz, 1970), or from giant units resulting from partial denervation (Grimby, Hannerz & Hedman, 1981), neither of which may behave normally during voluntary contractions. Most other studies have failed to provide accurate frequency measurements at the highest forces because the spikes from individual units could not be clearly discriminated (see Fig. 1*A*). However, the maximum rates observed are generally compatible with those reported here. For example, in ramp contractions Monster & Chan (1977) followed the firing rates of sixty-four units of the extensor digitorum communis and found maximum rates of 25–28 Hz; but most units were 'lost' at forces above about 75 % of the maximum. For the adductor pollicis, Bigland & Lippold (1954) were unable to distinguish rates above 35 Hz. More recently Kukulka & Clamann (1981) succeeded in following two units in that muscle to near maximum force levels. They fired at 25 and 30 Hz respectively, rates well within the range reported here.

The distribution of firing rates described in the present experiments are those recorded from individual muscle fibres. While the *range* of frequencies must correspond with those originating in the motoneurone pool, the mean rates may not. If neurones that innervate larger numbers of muscle fibres have discharge rates which are uncharacteristic of the pool generally, these will be sampled more frequently and distort the over-all distribution. Additional bias may also result from more frequent sampling of larger diameter fibres.

Changes in motor unit firing rates during fatigue. When maximal voluntary contractions were sustained for 40–120 s there was a progressive decline in both the range and mean rate of motor unit potentials. During the first 60 s, mean rates fell from about 27 to 15 Hz (i.e. by nearly 50 %). Not all units appeared to behave in a similar manner. As shown in Figs. 4 and 5 some evidence suggests that those with the highest initial frequencies changed rates most rapidly.

Several authors have noted that sustained maximal contractions are accompanied by a decline in the muscle surface integrated e.m.g. Stevens & Taylor (1972) attributed this to increasing degrees of neuromuscular block, which they suggested was responsible for the concomitant loss of force. However, with the demonstration that the intramuscular muscle mass action potential evoked by motor nerve stimulation does not decline during a 1 min m.v.c. (Bigland-Ritchie *et al.* 1982) it is unlikely that this is responsible for the reduction in either the surface e.m.g. or the mean motor unit potential frequencies. Both must result from a reduced mean discharge rate from the spinal motoneurone pool. Indeed, the progressive decline in motoneurone discharge rate may be the reason why neuromuscular block does not occur, since the rate of onset of block is critically dependent on excitation frequency (Krnjevic & Miledi, 1958; Thesleff, 1959).

Loss of force during fatigue has often been attributed to a decline in motor drive; i.e. to 'central fatigue' (Mosso, 1915; Reid, 1928; Asmussen, 1979; Ikai, Yabe & Ishii, 1967). We have recently shown that this can be overcome in sustained maximal contractions of the adductor pollicis when performed by adequately motivated and practised subjects; for the lost force cannot be restored by supramaximal tetanic nerve stimulation (Bigland-Ritchie, 1982). Throughout fatigue, the force from both voluntary and brief periods of supramaximal tetanic nerve stimulation declined in parallel. Moreover, in the current experiment single shocks administered throughout the contractions failed to elicit additional force. Thus all motor units can remain fully activated throughout a sustained maximal voluntary contraction despite the reduced motoneurone discharge rates.

This apparent paradox has been explained by the parallel slowing of muscle contractile speed (relaxation rate) (Bigland-Ritchie, 1981; Bigland-Ritchie, Johansson, Lippold & Woods, 1983). The slower the muscle the lower is the excitation rate required to maintain maximal tetanic force. Thus the decline in motoneurone discharge rate during prolonged activity at high force levels appears to result in no functional disadvantage with respect to force generation. On the contrary it may assure its optimal output by safe-guarding against peripheral conduction failure.

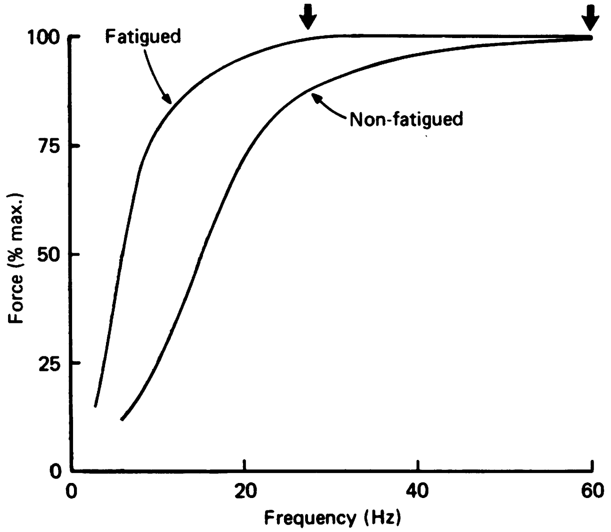

Fig. 6. Theoretical force–frequency curves for muscle. For effective rate coding of contraction strength, the range of motoneurone firing rates must be upon the steep part of the curve. In the fatigued state the latter is displaced to the left and it would be predicted that after 1 min maximal contraction, firing rates would be lowered as indicated by the two arrows (for detailed explanation, see text).

The discharge rates recorded during maximal voluntary efforts, either at the contraction onset or during the development of fatigue, may be maximum rates each motoneurone can achieve depending solely on its excitability, after-hyperpolarization, etc. This seems unlikely since for most subjects many units fired at only 10–15 Hz even in the first 10 s of contraction (Fig. 3*A*). Rates of 60–120 Hz have also been recorded from other human muscles during the ballistic onset of contractions (Desmedt & Godeaux, 1977). Both motor and sensory neurones elsewhere in the nervous system can sustain high firing rates for extended periods. It seems more likely, therefore, that once the required force has been generated firing rates are somehow limited to include, but not exceed, those required for maximum force production. As contractile speed slows during fatigue the excitation frequency required for full tetanic tension declines. If there were no parallel decline in the upper range of neural firing rates these would become markedly supratetanic (Fig. 6), and rate coding as a means of force modulation would be ineffective. When a reduction of force is desired a large reduction in neural rates would be necessary before any loss of force occurred. Sensitive force regulation requires that the range of motoneurone firing rates be mainly limited to the steeper parts of the force/frequency curve (Fig. 6). This is particularly important if the high degree of co-ordination required from small, hand muscles is to be maintained since, in these muscles, all motor units are thought to be recruited at relatively low forces (Milner-Brown *et al.* 1973). If this is so, then rate coding is the only means of force modulation at the higher force levels (Bigland-Ritchie, 1982). The concurrent slowing of motoneurone firing rates with reduced contractile speed during fatigue, may be a functionally useful coincidence or may result as a response to some as yet undescribed regulatory mechanism.

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