THE ORDERLY RECRUITMENT OF HUMAN MOTOR UNITS DURING VOLUNTARY ISOMETRIC CONTRACTIONS

By H. S. MILNER-BROWN, R. B. STEIN AND R. YEMM*
*From the Departments of Physiology and Oral Biology,
University of Alberta, Edmonton, Canada*

SUMMARY

1. The contractile properties of human motor units from the first dorsal interosseus muscle of the hand were studied during voluntary isometric contractions using recently developed techniques.

2. The twitch tensions produced by motor units varied widely from about 0·1–10 g. The twitch tension of a motor unit varied nearly linearly as a function of the level of voluntary force at which it was recruited over the entire range of forces studied (0–2 kg).

3. The number of additional motor units recruited during a given increment in force declined sharply at high levels of voluntary force. This suggests that even though the high threshold units generate more tension, the contribution of recruitment to increases in voluntary force declines at higher force levels.

4. Contraction times for these motor units varied from 30 to 100 msec. Over 80 % had contraction times less than 70 msec, and might be classed as fast twitch motor units. The larger motor units, which were recruited at higher threshold forces, tended to have shorter contraction times than the smaller units.

INTRODUCTION

A large number of parameters have been found to vary systematically with motoneuronal size, and this has become known as the *size principle* (Henneman, 1968). For example, the larger the cell body of a motoneurone, the higher is the conduction velocity of its axon (Kernell, 1966; Burke, 1968), and the stronger is the muscular contraction which is produced when it is stimulated (McPhedran, Wuerker & Henneman, 1965; Wuerker, McPhedran & Henneman, 1965; Burke, 1967). Larger motoneurones are also recruited at higher thresholds during reflex (Granit, Phillips, Skog-

---

* Present address: Department of Dental Medicine, University of Bristol, BS1 2LY.

lund & Steg, 1957) or intracellular electrical stimulation (Kernell, 1966). The after-potentials of larger motoneurones are shorter (Eccles, Eccles & Lundberg, 1958) and the initial rate of firing is higher (Kernell, 1965). Larger motoneurones increase their rate of firing more rapidly with increasing stimulation (Kernell, 1966) and attain higher firing rates (Granit *et al.* 1957; Kernell, 1965). Higher firing rates are necessary to produce fused contractions, because the twitches generated by larger motoneurones are briefer in time course and so the fusion frequencies are higher (McPhedran *et al.* 1965; Wuerker *et al.* 1965). Many other physiological and histo-chemical differences between fast and slow twitch motor units have been described (Burke, Levine, Zajac, Tsairis & Engel, 1971; Close, 1972).

Fast and slow twitch units have recently been demonstrated by stimu-lating single motoneurones in man (Buchthal & Schmalbruch, 1970; Sica & McComas, 1971). There is also some indirect evidence for the orderly recruitment of increasingly large motor units during human voluntary contractions (Olson, Carpenter & Henneman, 1968), based on the size of the action potentials recorded by needle electrodes in the muscle. How-ever, variations in the order of recruitment have also been found (Basma-jian, 1963; Grimby & Hannerz, 1968, 1970).

Since we have recently developed a technique for measuring the con-tractile properties of a motor unit during isometric voluntary contractions (Stein, French, Mannard & Yemm, 1972; Milner-Brown, Stein & Yemm, 1973*a*), we were anxious to determine which parameters of human motor units vary systematically with the threshold force for voluntary activa-tion. In this paper results will be described which were obtained while subjects tried to maintain a constant, low rate of firing from single motor units. The following paper (Milner-Brown, Stein & Yemm, 1973*b*) deals with the changes in firing rate which occurred when the level of voluntary force was increased or decreased linearly. We will also compare the relative importance of recruitment and changes in firing rate as mechanisms for changing the level of a voluntary contraction. Some of these results were recently demonstrated to the Physiological Society (Milner-Brown, Stein & Yemm, 1972).

<div align="center">METHODS</div>

Methods were fully described (Milner-Brown *et al.* 1973*a*) for determining the contractile properties of a single motor unit during a voluntary, isometric contrac-tion by averaging the force, in a whole muscle, which is correlated in time to the firing of that unit. Averaging enhances the tension produced by a single unit being studied relative to that produced by all the other motor units which fire indepen-dently of the single unit. Methods were also described for measuring the extent to which these properties were affected by any tendency for other motor units to discharge close to the times at which impulses are being generated in the motor unit under study (*synchronization*). For the purposes of this and the following papers,

three subjects, whose motor units fired independently of one another, were selected for more detailed study. Two of the three subjects are authors of this paper, but the third subject was unaware of the purpose of the experiments, and his data are similar. Less complete data, collected from six other subjects, also confirm the basic findings presented here, and argue against the data being affected by the choice of subjects. It was simply more convenient to use readily available subjects since an extensive sample of motor units was required from each.

The following contractile properties of single motor units were systematically measured using these techniques: (1) twitch tension (the maximum or peak deflexion in the averaged tension record), (2) contraction time (the time from the occurrence of the impulse in the motor unit to the peak tension), (3) half-relaxation time, where possible (the time for the tension to decline from its peak value to half this value), and (4) the 'threshold' level of voluntary force for recruiting the motor unit (see below). The definition of contraction time above includes the short latent period required for excitation-contraction coupling. The duration of the latent period was unclear in some of the averaged records (see Fig. 3 in Milner-Brown *et al.* 1973*a*), whereas the occurrence of a muscle action potential was a distinct and hence preferable marker for these measurements. Some of the units are the same ones used in the previous study (Milner-Brown *et al.* 1973*a*) and the same equipment and methods were used throughout.

Sampling methods. In order to minimize sampling bias, all the units which could be recorded at one electrode position were studied. Then the electrode was moved substantially so that a completely new group could be studied. Nonetheless, the possibility that a few units were sampled more than once, or that certain types of units were sampled less often cannot be ruled out. Care was also taken in the fabrication of electrodes so as to maximize the selectivity for single units at all levels of force (Ashworth, Grimby & Kugelberg, 1967). Two 75 μm silver or platinum-iridium wires coated with teflon were inserted down the barrel of a 25-gauge needle, which was stripped of its syringe attachment to minimize weight. Epoxy was drawn up into the barrel of the needle under a vacuum and allowed to set. The epoxy was then filed down flush with the cutting edge of the needle to expose the silver wires. Recording was differential with the barrel of the needle serving as earth.

Force measurement. A force transducer was used with a stiff spring which permitted a maximum of 1 mm displacement at the maximum measurable level of force (2 kg). Brackets were mounted on the body of the transducer to accommodate the thumb, and on the lever arm to accommodate the lateral edge of the first finger, midway between the base of the finger and the proximal interphalangeal joint. This simple arrangement kept the muscle at a roughly constant and reproducible length (about 4 cm), but did not completely eliminate the contribution of other hand muscles to the measured force. The maximum voluntary force which could be maintained for short periods, and the maximum force which could be produced by stimulation of the ulnar nerve were both two to three times the highest force level studied here (2 kg). No substantial differences were noted in the maximum forces which were generated by the three subjects. The blood supply to the muscle was probably not occluded, since Stephens & Taylor (1972) indicate that occlusion only occurs at above 40 % of the maximum voluntary contraction. Stephens & Taylor were able to measure the maximal voluntary contraction of this muscle with a 2 kg transducer after more careful fixation. However, they also measured force more distally along the finger where the mechanical disadvantage would be considerably greater.

'Threshold' force for recruitment. Subjects were asked to maintain the force at a level just adequate for activating a given motor unit to discharge steadily. The force necessary to do this was read from a calibrated digital voltmeter early in the

recording period of 3–5 min. Any changes later in the recording period were also noted, but not used in the data presented here. Sometimes the threshold force declined, but particularly with high threshold units, the threshold often increased during the period of recording.

Statistical methods. Standard methods were used throughout (Draper & Smith, 1967) to compute linear regression lines on linear, semi-logarithmic and double logarithmic plots, and to test the significance of the parameters which characterize these lines. The variables were generally not normally distributed, as assumed by the standard methods. This could introduce errors in determining statistical significance.

RESULTS

Table 1 summarizes the measured values for the contractile properties of 145 motor units from the first dorsal interosseus muscles in the hands of three adult, male subjects. These values are typical of the nine subjects studied to date.

TABLE 1. Contractile properties of motor units for three subjects

Subject	Twitch tension (g)	Contraction time (msec)	Half-relaxation time (msec)	Recruitment threshold (g)
R.B.S.	$1·36 \pm 1·56$ (64)	$51·5 \pm 12·6$ (43)	$42·8 \pm 10·3$ (22)	269 ± 309 (68)
R.Y.	$1·31 \pm 1·44$ (45)	$55·6 \pm 11·4$ (42)	$44·9 \pm 14·6$ (16)	493 ± 460 (46)
A.M.	$2·26 \pm 2·8$ (29)	$59·1 \pm 16·9$ (29)	$40·5 \pm 7·7$ (6)	352 ± 346 (31)

In each case the mean $\pm$ S.D. of an observation is listed with the number of observations (n) in brackets.

Twitch tensions. The mean values for twitch tension are somewhat smaller than those found for extensor hallucis brevis of the foot (5·5 g; Sica & McComas, 1971), the only other human muscle which, to our knowledge, has been investigated in detail. However, the actual forces generated by the motor units will depend to an unknown extent on the series elasticity, the angle and the point of insertion of the fibres relative to the point of recording. Anatomical details were obviously not available for the subjects studied, but Feinstein, Lindegard, Nyman & Wohlfart (1955) report that all the muscle fibres appear to run the entire length of this muscle.

More important than the absolute values is the histogram shown in Fig. 1A which gives the relative number of motor units with various twitch tensions. A wide range of twitch tensions was found, but small units were much more common than large units. Since the standard deviations

(S.D.) of the observations in Table 1 are comparable to the mean twitch tensions, a nearly exponential distribution might be anticipated. This is a good approximation to the data, as shown in Fig. 1 *B*. Because of the small numbers of large motor units, the data were grouped into increasingly large bins in Fig. 1 *B* at high twitch tensions (for the purposes of curve-fitting the S.D.s of all points should be comparable). The fitted line indicates that the probability of finding motor units of a particular size
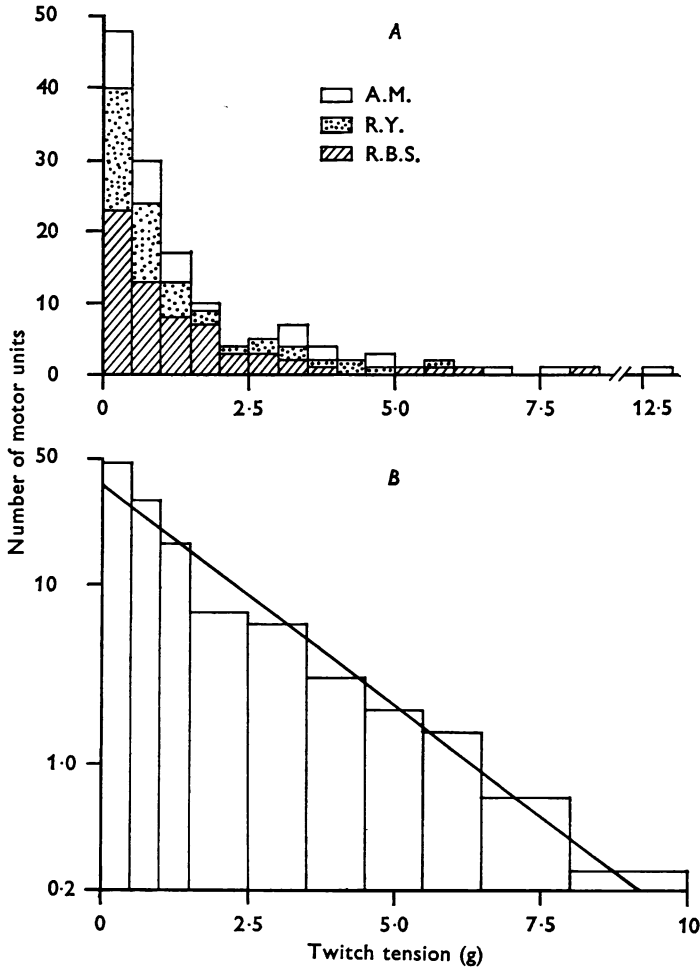

Fig. 1. Number of motor units, plotted on a linear scale (*A*) and on a logarithmic scale (*B*), having the twitch tensions indicated. The numbers from each of the three subjects are indicated on Figs. 1 and 2. The distributions are similar for all three subjects. The computed best-fitting line on the semi-log plot of (*B*) indicates an approximately exponential relation between number of motor units and twitch tension.

is halved for every 1·2 g increase in twitch tension. A similar, highly skewed histogram was found by McPhedran *et al.* (1965) for medial gastrocnemius muscle of the cat. More symmetrical histograms were obtained by stimulating motor axons to soleus muscle in the cat (Wuerker *et al.* 1965) and extensor hallucis brevis in man (Sica & McComas, 1971).
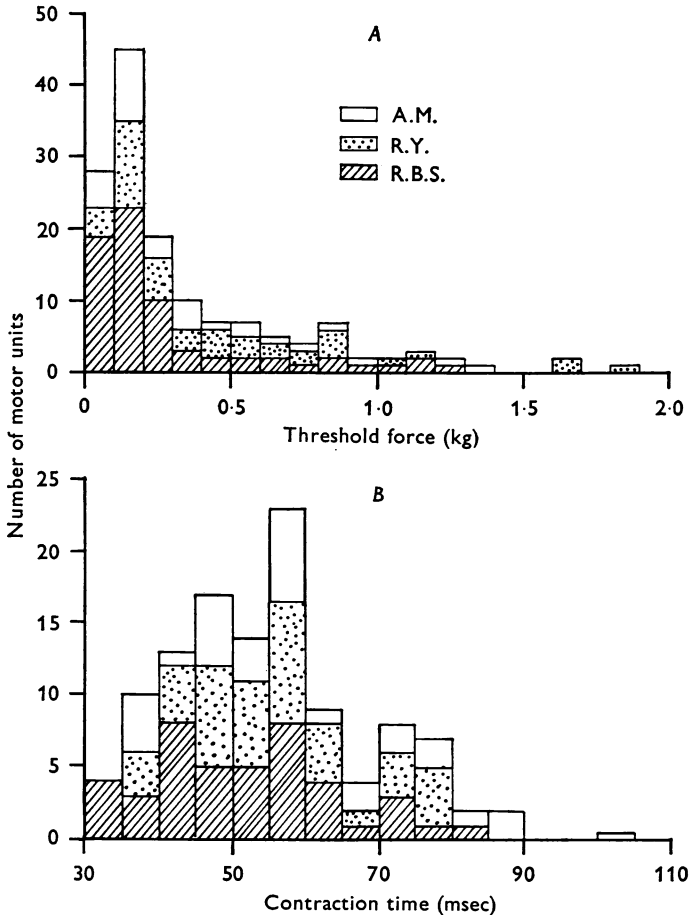

Fig. 2. Histograms of the numbers of motor units which were recruited at different levels of force (*A*) and which had the contraction times shown (*B*).

Fig. 2*A* shows a histogram of the number of additional motor units which were recruited within a range of 100 g at different levels of voluntary contraction. A wide range is again observed, but the largest number were recruited at low force levels. Over half of the units were recruited at below 200 g, even though with the fixation used (see Methods), the subjects

could exert well over 2 kg (the maximum force measurable with the transducer). The significance of this distribution, which is similar to that found during reflex stimulation in cats (Henneman, Somjen & Carpenter, 1965) will be discussed later.

Individual values of twitch tensions for motor units from one subject are plotted in Fig. 3 as a function of the threshold force for recruiting each motor unit. Both variables cover roughly a hundredfold range, and logarithmic co-ordinates have therefore been used for both ordinate and
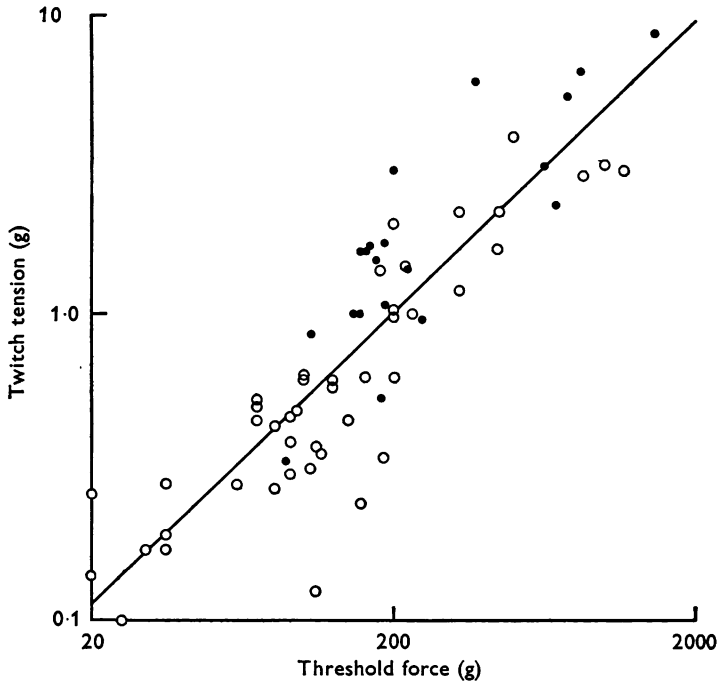

Fig. 3. Twitch tensions produced by single motor units in one subject (R.B.S.) as a function of the force at which the motor units were recruited. The filled circles in Fig. 3 and Fig. 4 are measurements from single experiments, while the open circles are measurements in other experiments with the same subject. The computed best-fitting straight line shown on this log-log plot had a slope close to unity, indicating a nearly linear relation between these two variables.

abscissa. The best-fitting slopes for these plots (in the sense of least mean square deviation) were close to unity for all three subjects (mean slopes ± s.e. of the mean were 0·945 ± 0·065, 0·922 ± 0·086 and 1·04 ± 0·12). This indicates a nearly linear relationship between twitch tension and threshold force over this entire range. The linear correlation coefficients were all

greater than 0·8 which is highly significant. Thus, there appears to be an orderly recruitment of successively larger motor units during increasing human voluntary contractions, as has been found during reflex studies in animals (Henneman, 1968). This orderly recruitment has been observed in all nine subjects examined to date.
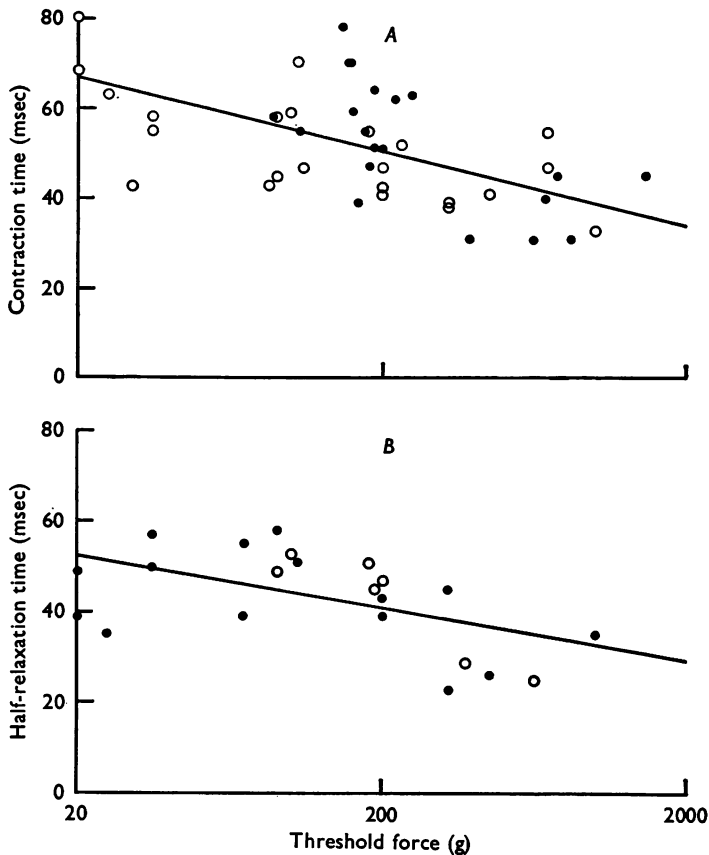

Fig. 4. Contraction times (*A*) and half-relaxation times (*B*) for single motor units in one subject (R.B.S.) as a function of the force at which the motor units were recruited. The computed best-fitting straight lines on these semi-log plots had slopes significantly different from zero at the 1 % (*A*) and 5 % (*B*) levels of confidence.

Time course of the twitch. Fig. 2*B* shows a histogram of the number of motor units with different contraction times. The range of contraction times was from 30 to 100 msec in these subjects, and the mean contraction times in Table 1 were close to the values obtained by single maximal stimuli applied to the muscle (between 55 and 60 msec). No clear division

between fast and slow twitch motor units was found, but over 80 % of the units had contraction times less than 70 msec, and might be classified as fast twitch motor units (Sica & McComas, 1971).

There was a definite tendency for the first units recruited (Fig. 4A) to contract more slowly than those recruited at higher levels of force. The values for threshold force have again been plotted on logarithmic co-ordinates because of the wide range of observed values. The fitted straight line for this subject had a linear correlation coefficient of 0·6 which was highly significant. Similar results, although with a somewhat weaker correlation, were obtained when contraction time was plotted as a function of the twitch tension developed by individual motor units. Some correlation would be expected from the observed relation (Fig. 3) between twitch tension and the threshold force for recruitment. The same trends were observed for the other two subjects, although the decline in contraction time with increasing threshold was only significant at the 5 % level in one subject and was not significant in the other subject.

Values for the half-relaxation times of motor units could only be measured for about 30 % of the units studied using our techniques, and the values could have been influenced by several factors (details in Milner-Brown *et al.* 1973*a*). Some tendency was observed for the units recruited at higher thresholds to have shorter half-relaxation times (Fig. 4B), but the best-fitting straight line had a slope which was only significantly different from zero at the 5 % level.

DISCUSSION

Our results provide the first direct evidence that motor units are recruited during increasing voluntary contraction in an orderly fashion according to the size of contraction they produce. This evidence strongly confirms the 'size principle' expounded by Henneman (1968) and his colleagues, based on animal experiments and on recording the size of motor unit potentials in man (Olsen *et al.* 1968). Indeed, the degree of ordering (Fig. 3) is remarkably high (linear correlation coefficients > 0·8 for all three subjects), when one considers that the recordings were made in experiments over a period of several months, and that there are inevitably many uncontrolled variables in human experiments. Since the size of unit recruited (ΔF) is proportional to the mean force level (F) over such a wide range, the fractional increments in force ($\Delta F/F$) produced by recruiting each unit will be constant (see also Merton, 1951). This result is reminiscent of the constant Weber functions ($\Delta S/S$) sometimes obtained when just-noticeable differences (ΔS) are measured at various stimulus intensities (S) in sensory experiments (Werner, 1968).

Considerable flexibility in the order that motor units are recruited in different tasks has been reported (Basmajian, 1963; Grimby & Hannerz, 1968, 1970; R. Wyman, 1972, personal communication). Typically, in these studies, a wide range of movements has been possible, while the very orderly pattern found here may only apply to simple movements where there is a strong synaptic input which is rather homogeneously distributed among the component motor units. In the following paper (Milner-Brown *et al.* 1973*b*), experiments will be described in which subjects generated nearly linearly rising and falling forces. The threshold for a motor unit could be measured under these dynamic conditions as well as under static conditions. Although the two measurements were highly correlated (linear correlation coefficient = 0·88), individual motor units were found which had thresholds differing by a factor of two or more. This is consistent with the finding of Grimby & Hannerz (1970) that the order of recruitment could be quite different in tonic and phasic reflexes.

There was a tendency for the larger motor units, which were recruited at higher levels of voluntary force, to have a briefer time course (Fig. 4), as is commonly found in animal studies (McPhedran *et al.* 1965; Wuerker *et al.* 1965; Burke, 1967). However, the correlations we measured between contraction time and threshold were lower than those between twitch tension and threshold, and the trend was not statistically significant in one of the three subjects. However, the twitch tensions generated by this subject at a given level of force were only about half of those recorded from the other two subjects, so the signal-to-noise ratios in the averages were smaller. The range of contraction times (30 to 100 msec) is also considerably smaller than the range of twitch tensions (0·1–10 g) which would tend to make it more difficult to detect any relationship. In the only other human study to our knowledge on this question, Sica & McComas (1971) were unable to demonstrate a relationship between twitch tension and contraction time.

Another interesting result of the present study is the rapid, nearly exponential decline in the number of additional motor units recruited with the larger twitch tensions or the higher thresholds. If the additional number of motor units recruited declines exponentially as the level of a voluntary contraction is increased, while the twitch tensions of the extra units recruited increases linearly, then it follows immediately that recruitment will account for less and less of the increases in force at high force levels. However, we only recorded from a fraction of the motor units in any individual so sampling biases are possible. Our methods required that the steady discharge of a unit be recorded for several minutes, and it is notoriously difficult to resolve single units at the limit of voluntary contraction. Thus, our sample is biased in that we probably did not record

from the highest threshold units. It would be interesting to repeat the experiments using stimulation techniques (Buchthal & Schmalbruch, 1970; Sica & McComas, 1971), where the tendency should be to excite the largest motor units preferentially. However, care was taken (see Methods) to minimize sources of bias as much as possible, and we restricted ourselves to a range of forces (up to 2 kg) where we could consistently record single units. Yet, the trend of the histograms was obvious throughout most of this range. Very similar histograms for the number of motor units with various twitch tensions (McPhedran et al. 1965) and thresholds for recruitment (Henneman et al. 1965) have been found in animal experiments. Moreover, Grillner & Udo (1971) found that 90 % of the motor units in soleus muscle of the cat had been recruited by the time the active tension in a stretch reflex had reached 50 % of its final value. Finally, we will show in the next paper (Milner-Brown et al. 1973b) that the increased rate of firing from active motor units accounts for an increasing percentage of force at higher levels of voluntary contraction. This can only be true if recruitment becomes less important during increasingly strong voluntary contractions.

Results from a single muscle should obviously not be extrapolated too far. Nonetheless, the striking similarity of our results (during voluntary contraction of a small human muscle, which is used in manipulation) to those of Henneman (1968) and his collaborators (during reflex contraction of large, postural muscles in the cat) certainly suggests the presence of rather general principles.

REFERENCES

ASHWORTH, B., GRIMBY, L. & KUGELBERG, E. (1967). Comparison of voluntary and reflex activation of motor units. J. Neurol. Psychiat. Lond. **30**, 91–98.

BASMAJIAN, J. V. (1963). Control and training of individual motor units. Science, N.Y. **141**, 440–441.

BUCHTHAL, F. & SCHMALBRUCH, H. (1970). Contraction times and fibre types in intact human muscle. Acta physiol. scand. **79**, 435–452.

BURKE, R. E. (1967). Motor unit types of cat triceps surae muscle. J. Physiol. **193**, 141–160.

BURKE, R. E. (1968). Firing patterns of gastrocnemius motor units in the decerebrate cat. J. Physiol. **196**, 631–654.

BURKE, R. E., LEVINE, D. N., ZAJAC, F. E., TSAIRIS, P. & ENGEL, W. K. (1971). Mammalian motor units: physiological-histochemical correlation in three types in cat gastrocnemius. Science, N.Y. **174**, 709–712.

CLOSE, R. I. (1972). Dynamic properties of mammalian skeletal muscles. Physiol. Rev. **52**, 129–197.

DRAPER, N. R. & SMITH, H. (1967). Applied Regression Analysis. New York: John Wiley and Sons, Inc.

ECCLES, J. C., ECCLES, R. M. & LUNDBERG, A. (1958). The action potentials of the alpha motoneurones supplying fast and slow muscle. J. Physiol. **142**, 275–291.

FEINSTEIN, B., LINDEGÅRD, B., NYMAN, E. & WOHLFART, G. (1955). Morphologic studies of motor units in normal human muscles. *Acta anat.* **23**, 127–142.

GRANIT, R., PHILLIPS, C. G., SKOGLUND, S. & STEG, G. (1957). Differentiation of tonic from phasic ventral horn cells by stretch, pinna and crossed extensor reflexes. *J. Neurophysiol.* **20**, 470–481.

GRILLNER, S. & UDO, M. (1971). Recruitment in the tonic stretch reflex. *Acta physiol. scand.* **81**, 571–573.

GRIMBY, L. & HANNERZ, J. (1968). Recruitment order of motor units on voluntary contraction: changes induced by proprioceptive afferent activity. *J. Neurol. Psychiat. Lond.* **31**, 565–573.

GRIMBY, L. & HANNERZ, J. (1970). Differences in recruitment order of motor units in phasic and tonic flexion reflex in 'spinal man'. *J. Neurol. Psychiat. Lond.* **33**, 562–570.

HENNEMAN, E. (1968). Peripheral mechanisms involved in the control of muscle. In *Medical Physiology*, 12th edn., ed. MOUNTCASTLE, V. B., pp. 1697–1716. St Louis: C. V. Mosby Co.

HENNEMAN, E., SOMJEN, G. & CARPENTER, D. O. (1965). Functional significance of cell size in spinal motoneurons. *J. Neurophysiol.* **28**, 560–580.

KERNELL, D. (1965). The limits of firing frequency in cat lumbosacral motoneurones possessing different time course of after-hyperpolarization. *Acta physiol. scand.* **65**, 87–100.

KERNELL, D. (1966). Input resistance, electrical excitability and size of ventral horn cells in cat spinal cord. *Science, N.Y.* **152**, 1637–1640.

McPHEDRAN, A. M., WUERKER, R. B. & HENNEMAN, E. (1965). Properties of motor units in a homogeneous red muscle (soleus) of the cat. *J. Neurophysiol.* **28**, 71–84.

MERTON, P. A. (1951). The silent period in a muscle of the human hand. *J. Physiol.* **114**, 183–198.

MILNER-BROWN, H. S., STEIN, R. B. & YEMM, R. (1972). Mechanisms for increased force during voluntary contractions. *J. Physiol.* **226**, 18–19*P*.

MILNER-BROWN, H. S., STEIN, R. B. & YEMM, R. (1973*a*). The contractile properties of human motor units during voluntary isometric contractions. *J. Physiol.* **228**, 285–306.

MILNER-BROWN, H. S., STEIN, R. B. & YEMM, R. (1973*b*). Changes in firing rate of human motor units during linearly changing voluntary contractions. *J. Physiol.* **230**, 371–390.

OLSON, C. B., CARPENTER, D. O. & HENNEMAN, E. (1968). Orderly recruitment of muscle action potentials. *Archs Neurol. Psychiat. Lond.* **19**, 591–597.

SICA, R. E. P. & McCOMAS, A. J. (1971). Fast and slow twitch units in a human muscle. *J. Neurol. Psychiat. Lond.* **34**, 113–120.

STEIN, R. B., FRENCH, A. S., MANNARD, A. & YEMM, R. (1972). New methods for analysing motor function in man and animals. *Brain Res.* **40**, 187–192.

STEPHENS, J. A. & TAYLOR, A. (1972). Fatigue of maintained voluntary muscle contraction in man. *J. Physiol.* **220**, 1–18.

WERNER, G. (1968). The study of sensation in physiology: psychophysical and neurophysiologic correlation. In *Medical Physiology*, 12th edn., ed. MOUNTCASTLE, V. B., pp. 1643–1671. St Louis: C. V. Mosby Co.

WUERKER, R. B., McPHEDRAN, A. M. & HENNEMAN, E. (1965). Properties of motor units in a heterogeneous pale muscle (*m. gastrocnemius*) of the cat. *J. Neurophysiol.* **28**, 85–99.