# The Number of Active Motor Units and Their Firing Rates in Voluntary Contraction of Human Brachialis Muscle

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Abstract To make clear the control mechanism of force generation in human muscle, the electrical activity of the brachialis muscle was studied at various levels of contraction force by recording single motor unit discharges as well as mass electromyograms (EMGs).

The firing rate of motor units increased with force along an S-shaped curve. At low levels of force, motor units increased their firing rates steeply with force. At intermediate levels of force, each motor unit increased its firing rate linearly with force at lower rates. As the maximum of force was approached, the firing rate increased very steeply, reaching as high as 50 Hz or more.

By applying a new method of statistical processing to mass EMGs, the number of active motor units and the size of action potential were estimated at each level of force. The number of active motor units increased monotonously with muscle force. Motor units recruited at high levels of force had larger amplitudes of action potentials than those recruited at lower levels.

Calculations were made to determine how the relative contribution to an increase in muscle force is varied between recruitment and the increase in firing rate. The contribution of recruitment gradually decreased with the increase in force. Up to about 70% of the mixmum force, recruitment is the major mechanism for increasing the force of contraction.

Voluntary contraction of the skeletal muscles is controlled by two mechanisms: One changes the number of active motor units and the other changes the firing rate of individual motor units. It has been generally believed that the former is the main factor in coarse control and the latter in fine control. Recently, MILNER-BROWN *et al.* (1973 a, b) investigated quantitatively the relation between motor unit activity and voluntary isometric force in the human first dorsal interosseus muscle and concluded that the change in the firing rate of motor units ("rate coding") plays a major part in the control of muscle force. Similar results were

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also obtained from the extensor digitorum communis muscle (MONSTER and CHAN, 1977). However, it remains unsolved whether or not the same mechanism works in larger muscles as well.

Because of technical difficulty, no work has been successfully carried out that reveals how motor units vary their firing rates when a muscle contracts with force varying from the minimum to the maximum. Therefore, a definitive conclusion has not yet been reached as to the relation between muscle force and the firing rate of motor units (See DISCUSSION; Fig. 10). To the present date, the recruitment of motor units has been generally studied by observing motor unit discharges at different levels of force (MILNER-BROWN et al., 1973 a; TANJI and KATO, 1973 a; FREUNT et al., 1975). This method, however, lacks reliability, especially when strong contraction is made, because a progressive increase of contraction force makes discrimination of individual motor unit discharges gradually more difficult due to interference of action potentials from many motor units. On the other hand, BRODY and SCOTT (1974) estimated the number of active motor units by statistically processing mass electromyograms (EMGs). In their analysis of EMGs, however, they assumed that all motor units generated action potentials of identical amplitudes and fired at a constant rate (10 Hz), regardless of the force level. Since this assumption cannot be accepted as valid, their method was inadequate to obtain reliable results.

In the present study, we first investigated the firing rate of motor units of the human brachialis muscle during voluntary isometric contraction with force varying up to the maximum (PART I). Secondly, applying a new method based on the original idea of Brody and Scott, we estimated the number of active motor units and the size of the action potential (PART II). Finally, in order to confirm the results obtained in PART II, the muscle force was calculated from the data obtained in PARTS I and II using a model for force generation, and it was compared with the force actually measured. Furthermore, it was determined in what proportion recruitment of motor units and increase in firing rate contribute to an increase in muscle force at various levels of force (PART III).

## PART I: FIRING RATE OF MOTOR UNITS

#### Methods

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Experiments were carried out on three healthy subjects. Electrical recordings were made from the brachialis muscle. A subject sat on a chair with the upper arm pressed against the body and with the elbow joint flexed at a right angle. The forearm was fixed horizontally on a stiff lever (compliance=0.25 mm/kgW) in a supine position. The isometric torque of elbow flexion was measured by a strain gauge attached to the lever. In the following, the torque will be expressed in kg measured at the wrist. The subjects were instructed not to move the shoulder and to increase the isometric force of the elbow flexion at a constant rate by tracking

a reference displayed on an oscilloscope. The rate of rise of force was set sufficiently slow (12–15 sec/maximum force). The output of the strain gauge amplifier was displayed on one channel of the oscilloscope and a target ramp (reference)



Fig. 1. Representative results of an experiment in which the subject slowly increased the voluntary isometric force of elbow flexion. A, B and C: records at different levels of contraction force. Force was increased from A to C. Upper trace: action potential of brachialis motor units. Action potentials of one and the same motor unit are marked with dots. Lower trace, output from strain gauge for measuring contraction force. Increase in force is indicated as an increase in the number of pips. D: firing rate of the unit marked with dots in A, B and C (open circles) and force (dots) are plotted against time. The firing rate is defined as the inverse of the mean value of consecutive five inter-spike intervals. The times at which records A, B and C were taken are indicated with arrows. A large open circle shows the point at which the motor unit was first recruited.

was on the second channel. The contraction was repeated five times a day at the most. A resting period of more than 15 min was interposed between separate trials.

Action potentials of motor units were recorded by means of bipolar fine wire electrodes made from polyurethane-insulated copper wires 50  $\mu$ m in diameter. Electrodes were guided into the brachialis through the lumen of a hypodermic needle (27 gauge). The signal was amplified by a low noise differential amplifier with 20 M $\Omega$  input impedance. An indifferent electrode of Ag-AgCl plate (diameter, 1 cm) was placed on the skin of the shoulder. Electrodes were also inserted in the m. triceps brachii and used to verify that there was no activity in the antagonistic muscle.

Signals from the electrodes and the strain gauge were recorded on magnetic tape, and later they were rewritten on recording paper moved at a speed of 320 cm/sec. Individual motor unit discharges could be identified by examining wave forms, amplitudes and intervals of appearance. The upper trace in records A, B and C of Fig. 1 shows discharges of motor units of the brachialis muscle at different force levels. The discharges of one and the same motor unit are marked with dots. In record C, which was taken while the brachialis was contracting maximally, this same unit could still be identified. Figure 1 D shows time courses of the firing rate of this motor unit (open circles) and the muscle force (dots).

## Results

In each subject, about 35 motor units were recorded with contraction force varying in a sufficiently wide range. Figure 2 shows three typical examples of the relation between the isometric force of elbow flexion and the firing rate of motor units. For a given period of sampling, the firing rate is defined as the inverse of the mean of five consecutive inter-spike intervals and the force is defined as the



Fig. 2. Firing rates of three motor units (A, B and C) plotted against force. Large open circles represent the point at which each motor unit was recruited.

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Fig. 3. Force-firing rate curves of many motor units obtained from three subjects (K.K., K.A. and M.S.). The maximum force of voluntary contraction was 26 kg for K.K., 21 kg for K.A. and 22 kg for M.S. Broken lines were drawn by eye with data points such as shown in Fig. 2. Solid lines are the best fitting lines determined by the least square method for the data of the intermediate force range in which the firing rate varies linearly with force (correlation coefficients were all higher than 0.6). Open circles indicate the point at which each motor unit was recruited. For Roman numerals I, II and III on the abscissas, see text.

mean of forces during that period. Large open circles represent the points at which each motor unit was recruited. Figure 3 shows force-firing rate curves of motor units for each of the subjects. It is seen that there is a close similarity among the three groups of data with regard to distribution and configuration of the force-firing rate curve of motor units. For the sake of simplifying the description, the force-firing rate curves are regarded as consisting of three sections by dividing the abscissa into three regions, I, II and III. In region I the force increased from 0 to about 35% of the maximum. Here the motor units increase their firing rates steeply with force just after recruitment, though the rate of increase progressively decreases. In region II, which covers the force from about 35 to 80% of the maximum, the firing rates of motor units increase approximately in a linear way with lower rates of increase than in regions I and III. Finally, in region III where the force is above 80% of the maximum, the rate of increase of the firing rate becomes steep again; the firing rate often reaches values as high as 50 to 60 Hz at the maximum.



Fig. 4. Slopes (A) and intercepts (B) of the solid lines in Fig. 3. Inset shows that the slope is determined as  $\Delta Y/\Delta X$  and the intercept as  $F_{int}$ . Open circles represent the data obtained from subject K.K., crosses from K.A. and triangles from M.S.

mum force. As a whole, motor units increase their firing rates with force along an S-shaped curve.

For the middle part of the force-firing rate curves (most of them are in region II) regression lines (solid lines in Fig. 3) are drawn with correlation coefficients of more than 0.6 (p < 0.05). The regression lines are distributed in such a way that the lower the threshold force for recruitment, the higher the firing rate. It is noted, however, that the rate of increase of the firing rate is about the same irrespective of the threshold force for recruitment. This is shown in Fig. 4. As shown in the inset figure in the right, for each of the regression lines, slopes ( $\Delta Y/\Delta X$ ) and intercepts with the ordinate axis ( $F_{int}$ ) were calculated. They are plotted in the left and the middle of Fig. 4 as functions of the threshold force. Although the slope has no significant dependence on the threshold force (C.C.=0.260; p < 0.05) (Fig. 4 A), the intercept is found to decrease with increasing force (C.C.=0.609; p < 0.05) (Fig. 4 B).

## PART II: THE NUMBER OF ACTIVE MOTOR UNITS AND SIZE OF ACTION POTENTIAL

In the present study, a new method of processing mass EMGs was used to estimate the number of active motor units and the size of action potential. For this purpose, a model for generation of mass EMGs is proposed (Fig. 5). When a nerve impulse of an  $\alpha$ -motoneurone reaches a muscle, an action potential is generated in a group of muscle fibers innervated by that  $\alpha$ -motoneurone. It is observed as a part of mass EMGs, after being filtered through the muscle tissue.



Fig. 5. Model for generation of mass EMG. For details, see text.

The filtered action potential is an electrical output of the motor unit corresponding to the nerve impulse, and is defined as  $Kh(\tau)$ , where

$$\int_{-\infty}^{\infty} h^2(\tau) d\tau = 1 \tag{1}$$

and

$$\int_{-\infty}^{\infty} h(\tau) d\tau = 0.$$
 (2)

In this paper superscripts refer to exponents. The gain K means the size of motor unit action potential. Then the total electrical activity of the motor unit can be represented by

$$E(t) = \sum_{\zeta = -\infty}^{\infty} Kh(t - t_{\zeta})$$
(3)

where  $t_{\zeta}$  is the time of arrival of the nerve impulse.

For convenience, let us divide the range of force into a number of segments and consider the *j*th segment (j=1, 2, 3, ...), which extends from force level  $P_{j-1}$ to  $P_j$  ( $P_0=0$ ). Suppose  $N_j$  is the number of active motor units recruited in this segment, and  $K_j$  the mean size of their action potentials.  $S_j(t)$  means the arithmetic sum of the myoelectric signals generated by all motor units recruited in segment *j*. The mean firing rate of the motor unit recruited in the *j*th segment is expressed by  $f_j(P_i)$ , which is a function of force  $P_i$ . In the present work, two assumptions are introduced:

(1) All motor units show action potentials with identical wave form (h(t)), and

(2) all motor units discharge independently in the statistical sense. The first assumption has already proved valid (MILNER-BROWN and STEIN, 1975). The second assumption was also confirmed experimentally in the present study (See *Results*).

On the basis of this model,  $N_j$  and  $K_j$  are estimated successively from j=1. (1) j=1. At this level of force  $(P_1)$ ,  $N_1$  motor units are already active. Their mean firing rate is  $f_1(P_1)$  and the mean size of their action potentials is  $K_1$ . According to the first assumption, the mass EMG  $X_1(t)$  can be considered as the output of a filter with impulse response  $K_1h(t)$  resulting from the input of an impulse train of the average frequency  $N_1f_1(P_1)$ . Note that according to the second assumption the input can be regarded as a Poisson impulse train (Cox and SMITH, 1954). By applying the characteristics of the Poisson impulse train such as Campbell's theorem (PAPOULIS, 1965), the second moment  $m_2(P_1)$  and the fourth moment  $m_4(P_1)$  of the mass EMG  $X_1(t)$  (= $S_1(t)$ ) are given by (BRODY and Scorr, 1974)

$$m_2(P_1) \stackrel{\triangle}{=} E\{S_1^2(t)\} = N_1 K_1^2 f_1(P_1)$$
(4)

and

$$m_4(P_1) \stackrel{\triangle}{=} E\{S_1^4(t)\} = N_1 K_1^4 f_1(P_1) \alpha + 3N_1^2 K_1^4 f_1^2(P_1),$$
(5)

where  $E\{\cdot\}$  means the expectation and

$$\alpha = \int_{-\infty}^{\infty} h^4(\tau) \mathrm{d}\tau. \tag{6}$$

From Eqs. (4) and (5), one obtains the values of  $N_1$  and  $K_1$  normalized with the constant  $\alpha$  as

$$\tilde{N}_{1} \stackrel{\triangle}{=} \frac{N_{1}}{\alpha} = \frac{\{m_{2}(P_{1})\}^{2}}{\{m_{4}(P_{1}) - 3m_{2}^{2}(P_{1})\}f_{1}(P_{1})}$$
(7)

and

$$\tilde{K}_1 \stackrel{\triangle}{=} \sqrt{\alpha} K_1 = \sqrt{\frac{m_4(P_1) - 3m_2^2(P_1)}{m_2(P_1)}}.$$
(8)

(2) j=2. In the second segment,  $N_2$  motor units which generate action potentials of  $K_2$  in mean size are recruited. Therefore, at force  $P_2$ ,  $N_1$  plus  $N_2$ motor units are active in all. In this case, the second moment  $m_2(P_2)$  and the fourth moment  $m_4(P_2)$  of mass EMG  $X_2(t)$  can be written as

$$m_{2}(P_{2}) \stackrel{\bigtriangleup}{=} E\{X_{2}^{2}(t)\} = E\{(S_{1}(t) + S_{2}(t))^{2}\} = E\{S_{1}^{2}(t)\} + E\{S_{2}^{2}(t)\}$$
$$= \tilde{N}_{1}\tilde{K}_{1}^{2}f_{1}(P_{2}) + \tilde{N}_{2}\tilde{K}_{2}^{2}f_{2}(P_{2})$$
(9)

and

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$$m_{4}(P_{2}) \stackrel{\triangle}{=} E\{X_{2}^{4}(t)\} = E\{(S_{1}(t) + S_{2}(t))^{4}\}$$

$$= E\{S_{1}^{4}(t)\} + E\{S_{2}^{4}(t)\} + 6E\{S_{1}^{2}(t)\}E\{S_{2}^{2}(t)\}$$

$$= \tilde{N}_{1}\tilde{K}_{1}^{4}f_{1}(P_{2}) + 3\tilde{N}_{1}^{2}\tilde{K}_{1}^{4}f_{1}^{2}(P_{2}) + \tilde{N}_{2}\tilde{K}_{2}^{4}f_{2}(P_{2})$$

$$+ 3\tilde{N}_{2}^{2}\tilde{K}_{2}^{4}f_{2}^{2}(P_{2}) + 6\{\tilde{N}_{1}\tilde{K}_{1}^{2}f_{1}(P_{2})\}\{\tilde{N}_{2}\tilde{K}_{2}^{2}f_{2}(P_{2})\}.$$
(10)

Hence,  $N_2$  and  $K_2$  are given by

$$\tilde{N}_{2} \stackrel{\Delta}{=} \frac{N_{2}}{\alpha} = \frac{\{m_{2}(P_{2}) - R_{2}\}^{2}}{\{m_{4}(P_{2}) - 3m_{2}^{2}(P_{2}) - Q_{2}\}f_{2}(P_{2})}$$
(11)

and

$$\tilde{K}_{2} \stackrel{\triangle}{=} \sqrt{\alpha} K_{2} = \sqrt{\frac{m_{4}(P_{2}) - 3m_{2}^{2}(P_{2}) - Q_{2}}{m_{2}(P_{2}) - R_{2}}}, \qquad (12)$$

where

$$Q_2 = \tilde{N}_1 \tilde{K}_1^4 f_1(P_2) \tag{13}$$

and

$$R_2 = \tilde{N}_1 \tilde{K}_1^2 f_1(P_2). \tag{14}$$

(3) j=i. Repeating similar calculations, one can obtain

$$\tilde{N}_{i} \stackrel{\triangle}{=} \frac{N_{i}}{\alpha} = \frac{\{m_{2}(P_{i}) - R_{i}\}^{2}}{\{m_{4}(P_{i}) - 3m_{2}^{2}(P_{i}) - Q_{i}\}f_{1}(P_{i})}$$
(15)

and

$$\tilde{K}_i \stackrel{\Delta}{=} \sqrt{\alpha} K_i = \sqrt{\frac{m_4(P_i) - 3m_2^2(P_i) - Q_i}{m_2(P_i) - R_i}}, \qquad (16)$$

where

$$Q_{i} = \sum_{j=1}^{i-1} \tilde{N}_{j} \tilde{K}_{j}^{4} f_{j}(P_{j})$$
(17)

and

$$R_{i} = \sum_{j=1}^{i-1} \tilde{N}_{j} \tilde{K}_{j}^{2} f_{j}(P_{i}).$$
(18)

Hence, the number of motor units recruited in each segment and the mean size of their action potentials can be calculated from mass EMGs and the firing rate of individual motor units. Practically,  $m_2(P_i)$  and  $m_4(P_i)$  are calculated as

$$m_2(P_i) = \frac{1}{T} \int_0^T \{X_i(t)\}^2 dt$$
(19)

and

$$m_4(P_i) = \frac{1}{T} \int_0^T \{X_i(t)\}^4 dt,$$
(20)

where T is an integration time which is sufficiently long. Evidently, the number of active motor units at force  $P_i$  is given by

$$N(P_i) = \sum_{j=1}^{i} N_j.$$
<sup>(21)</sup>

### Methods

The experimental system was the same as described in PART I. Since the brachialis muscle is located beneath the biceps brachii, its mass EMGs were picked up by means of wire electrodes. The electrodes were made from polyurethaneinsulated copper wires (diameter,  $50 \ \mu m$ ) whose tips were exposed to the extent of 1 cm by stripping the insulating coat off. A pair of these electrodes were inserted into the muscle 2 cm apart along muscle fibers; potential differences between them were amplified by a differential amplifier. To observe motor unit activities and to examine their statistical independence (the second assumption), the same wire electrodes as described in PART I were inserted into the muscle.

The subjects were asked to maintain a constant force. The experiment was repeated at different levels of force with a sufficiently long resting period between each session. The data obtained under steady contractions were fed into a minicomputer (HITAC-10) through an A-D converter with a sampling rate of 2 kHz, and then the number of active motor units and the size of action potentials were calculated.

### Results

(a) Estimations. For the estimation of the number of active motor units and the size of their action potentials, it is necessary to determine the following parameters: (1) the relation between muscle force and firing rate of motor units, and (2) the second and fourth moments of mass EMGs. The former were already obtained, as noted in PART I. On the basis of the experimental data in Figs. 3 and 4,  $f_i(P_i)$  was approximated with the equations

$$f_{j}(P_{i}) = \begin{cases} c_{1}(P_{i} - P_{j_{0}}) + d_{1}[1 - \exp\{-\tau_{1}(P_{i} - P_{j_{0}})\}] + e_{1} \\ (P_{j_{0}} < 6.6 \text{ kg}) \\ c_{2}(P_{i} - P_{j_{0}}) + d_{2}[1 - \exp\{-\tau_{2}(P_{i} - P_{j_{0}})\}] + e_{2} \\ (P_{j_{0}} \ge 6.6 \text{ kg}), \end{cases}$$

$$(22)$$

where  $P_{j0}$  is the threshold force of the motor unit recruited in the *j*th segment  $(P_{j0}=(P_{j-1}+P_j)/2)$  and  $c_n$ ,  $d_n$ ,  $e_n$  and  $\tau_n$  (n=1, 2) are constants. These constants for two subjects are given in Table 1 A. The second and fourth moments of mass EMGs were computed by Eqs. (19) and (20). They are plotted against force in Fig. 6 and regression curves are expressed by the equations

$$\log m_2 = a_0 + a_1 P_i + a_2 P_i^2 + a_3 P_i^3 \tag{23}$$

and

(A)						
Sub.	K.K.	K.A.	Sub.	K.K.	K.A.	
<i>c</i> <sub>1</sub>	0.652	0.632	<i>C</i> <sub>2</sub>	0.790	0.632	(Hz/kg)
$d_1$	15.0	7.0	$d_2$	6.5	7.0	(Hz)
$\tau_1$	0.988	1.98	$ au_2$	1.98	1.98	(1/kg)
<i>e</i> <sub>1</sub>	15.0	15.0	e <sub>2</sub>	15.0	15.0	(Hz)
<b>(B)</b>						
Sub.	K.K.	K.A.	Sub.	K.K.	K.A.	
$a_0$	1.85	0.611	$b_0$	4.86	2.73	
<i>a</i> <sub>1</sub>	0.396	0.504	$b_1$	0.603	0.757	(1/kg)
$a_2$	-0.0256	-0.0354	$b_2$	-0.0297	-0.0478	(1/kg <sup>2</sup> )
<i>a</i> <sub>3</sub>	0.627×10 <sup>-3</sup>	0.937×10 <sup>-3</sup>	$b_3$	$0.617 \times 10^{-3}$	$0.122 \times 10^{-2}$	(1/kg <sup>3</sup> )
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Table 1. Constants for the relations of force vs. firing rate of motor units (A) and force vs. the second and fourth moments (B).



Fig. 6. Second and fourth moments of mass EMGs of the brachialis muscle computed by Eqs. (19) and (20). Each point was obtained with the integration time T=4 sec. Regression curves are drawn according to Eqs. (23) and (24) with the parameters in Table 1B.

$$\log m_4 = b_0 + b_1 P_i + b_2 P_i^2 + b_3 P_i^3. \tag{24}$$

Constants  $a_n$  and  $b_n$  (n=1, 2, 3, 4) are given in Table 1 B.

Substituting these relations into Eqs. (4)–(18), we obtained  $N_j$  and  $K_j$  at various force levels. Figure 7 shows that the results obtained from two subjects (K.K. and K.A.) are similar to each other. The total number of active motor units N increases approximately linearly with force at low levels of force; motor units are recruited in succession as the force increases. However, after the force exceeded some intermediate value, say 10 kg, the number of recruited motor units ceased to increase steeply.



Fig. 7. Estimated total number of active motor units N (crosses) and mean amplitude  $K_j$  of action potentials of motor units recruited in each segment, j=1, 2, ..., 12 (open circles).

The mean size of motor unit action potentials,  $K_j$ , becomes large as their threshold force for recruitment is higher. The larger the potentials of a motor unit, the greater the force it exerts (MILNER-BROWN and STEIN, 1975; MONSTER and CHAN, 1977). It can be thus concluded that the "size principle" (HENNEMAN *et al.*, 1965) holds good in voluntary contraction of the human brachialis muscle.

(b) Validity of the assumption. The estimation method proposed in this paper is based on the assumption that in the statistical sense single motor units discharge independently of each other. It is well known that this holds good at low levels of force but needs to be verified at higher levels of force. This was done by compiling cross-correlation histograms between many pairs of motor unit discharges; the cross-correlation histogram indicates the frequency of discharge of a motor unit as a function of time before and after the discharge of another motor unit.

Figure 8 shows typical cross-correlation histograms. Periodic peaks are seen in Fig. 8 A; that is, the discharges of these two motor units are not independent in this case. On the contrary, the histogram in Fig. 8 B has no apparent peaks. This means that the two motor units fire independently in the statistical sense. Thirty-four histograms were compiled at various levels of force in three subjects and three of them showed periodic peaks. It should be noted that among nine

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Fig. 8. Cross-correlation histograms for two pairs of motor units. A: periodic peaks indicate that two motor units fire synchronously. B: absence of peak shows the independence of the discharges of two motor units.

histograms obtained at high levels of force (21 kg), only one showed obvious peaks. Consequently, it can be concluded that most of the motor units fire independently in the statistical sense even when the contraction force is fairly strong.

## PART III: MECHANISM OF MUSCLE FORCE CONTROL

To lend further support to the validity of the estimation method proposed in this paper, muscle force was calcualted by using  $N_i$  and  $K_i$  estimated in PART II and it was compared with the force experimentally measured. Simultaneously, we calculated relative contributions of firing rate increase and recruitment of new motor units to the total force. The theoretical basis for this treatment is as follows.

The force range is divided into segments of equal size in the same way as in PART II. Consider a motor unit whose action potential size is K. The twitch force of motor units is approximately proportional to the action potential size (MONSTER and CHAN, 1977). Thus, the force generated by the motor unit can be given by

$$\hat{p} = CKx(f), \tag{25}$$

where C is a constant and x(f) is the normalized force which is a function of the firing rate, f. It is known that as the frequency of motor nerve stimulation increases, the force increases along a nonlinear, sigmoid curve. Here, referring to data obtained from human muscles (BIGLAND and LIPPOLD, 1954; MONSTER and CHAN, 1977), we express x(f) in a simple form;

$$x(f) = \begin{cases} 0.16 & (f < 10) \\ 0.042f - 0.26 & (10 \le f < 30) \\ 1 & (30 \le f). \end{cases}$$
(26)

As shown in PART I, the firing rate of individual motor units increases with the total

force of the muscle. Consider that in the *i*th segment, a motor unit recruited in the *j*th segment fires with frequency  $f_j(i)$ . Then, the force exerted by it at the *i*th segment can be represented by

$$\hat{p}_j(i) = CK_j x(f_j(i)), \qquad (27)$$

where  $K_j$  is the size of its action potential. The total force at the end of the *i*th segment is given by

$$\hat{P}(i) = \sum_{j=1}^{i} N_j \hat{p}_j(i) = \sum_{j=1}^{i} N_j C K_j x(f_j(i)),$$
(28)

where  $N_j$  is the number of motor units recruited in the *j*th segment.

It follows that the total force increment in segment *i*,  $\hat{P}(i)-\hat{P}(i-1)$ , can be divided into two parts: One is the increment due to recruitment of new motor units,

$$\Delta \hat{P}_{\text{rec}} \stackrel{\triangle}{=} N_i \hat{p}_i(i) = N_i C K_i x(f_i(i))$$
<sup>(29)</sup>

and the other is the increment due to an increase in the firing rate of already recruited, active motor units,

$$\varDelta \hat{P}_{\mathrm{fr}} \stackrel{\triangle}{=} \sum_{j=1}^{i-1} N_j C K_j \{ x(f_j(i)) - x(f_j(i-1)) \}.$$

$$(30)$$

Consequently,  $\hat{P}(i)$ ,  $\Delta \hat{P}_{ree}$  and  $\Delta \hat{P}_{fr}$  can be calculated by using  $N_j$ ,  $K_j$  (in Fig. 7) and  $f_j(i)$  (= $f_j(P_i)$  in Table 1 A). The results thus obtained are shown in Fig. 9. Calculated force  $\hat{P}(i)$  is proportional to the force measured in the experiment (C.C.=0.987 and 0.988 for two subjects, Fig. 9 A). Evidently, this implies that  $N_j$  and  $K_j$  estimated in PART II are most reliable.



Fig. 9. A: force calculated by using the number of active motor units  $(N_j)$  and their size  $(K_j)$  estimated in PART II (Fig. 7). The calculated force (ordinate) is proportional to the force experimentally measured (abscissa), indicating that the estimated values of  $N_j$  and  $K_j$  are reliable. B: relative contribution of recruitment and increase in firing rate to the increment of force.

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Figure 9 B shows how the relative contribution to an increase of muscle force is varied between recruitment of motor units and increase in the firing rate of already recruited motor units. The ordinates are the percentage of the force increment due to each mechanism and the abscissa is the muscle force experimentally measured. The contribution of recruitment gradually decreases with the increase in force. It should be noted that more than 50% of the force increment is due to recruitment of new motor units, even at high levels of force (60% of the maximum force for subject K.K. and 70% for subject K.A.).

#### DISCUSSION

In the present study, the firing rate of individual motor units, the number of active motor units and the size of action potentials were examined at various force levels in the human brachialis muscle.

From an anatomical study of the elbow joint, WILKIE (1950) disclosed that the major portion (about 50%) of elbow flexion torque is generated by the brachialis muscle. We also confirmed that integrated EMGs of three flexor muscles (m. biceps brachii, m. brachialis, m. brachioradialis), recorded under isometric contraction, increase in amplitude with the increasing torque of elbow flexion. From these facts, it is reasonably assumed that the force measured in the present experiment should be proportional to the force exerted by the brachialis muscle alone.

We found that the firing rate of motor units increases essentially in an S-shaped manner with the increase in the force (Fig. 10 A). Our results are compared with those reported previously on other muscles. BIGLAND and LIPPOLD (1954) also observed an S-shaped force-firing rate relation in many motor units

	А	В	С	D
	Present study	B.Bigland et al. (1954)	J.Tanji et al. (1973b)	A.Gydikov et al. (1974,1976)
muscle	Brachialis	Adductor pollicis ,abductor digiti minimi	Abductor digiti minimi	Many muscles
force – frequency	Ledneuch 0 Force max	0 max	0 max	0 max

Fig. 10. Schematic diagrams showing relations between muscle force and firing rate of motor units as established in the present study (A) and reported by three groups of previous workers (B, C and D).

of the adductor policis muscle and the abductor digiti minimi muscle (Fig. 10 B). Those authors did not succeed in observing single motor unit activities along the whole extent of the force from the threshold for recruitment to the maximum. TANJI and KATO (1973 b) investigated motor units in the abductor digiti minimi muscle by using tungsten electrodes with  $1-2 \mu m$  tip diameters and concluded that each motor unit increases the firing rate with force and the lower the threshold force of a motor unit is, the higher firing rate it reaches (Fig. 10 C). Their findings are in good accord with those in regions I and II of our force-firing rate curves. By using small surface electrodes of 2 mm diameter, GYDIKOV and KOSAROV (1974) and KOSAROV and GYDIKOV (1976) succeeded in observing action potentials of motor units in various muscles with high selectivity even when the contraction force increased up to the maximum. They concluded that motor units can be classified into two groups: phasic and tonic types (Fig. 10 D). The phasic motor units increase their firing rates linearly with force, while the firing rates of the tonic motor units rise at lower levels of force and cease to increase at higher levels. Our results differ from theirs in the following points. First, we could not identify the two types of motor units clearly on the basis of the force-firing rate relation. Secondly, all motor units observed here increased firing rates steeply with force at high levels of force (in region III). No units were found whose forcefiring rate relations were like those of the tonic units described by previous workers.

Our results obtained from the brachialis muscle showed that recruitment of new motor units is the major mechanism for increment of muscle force even at 60 to 70% of the maximum force (Fig. 9 B). As indicated in Fig. 7 few motor units are recruited when the force becomes strong, but their sizes are far larger than those recruited at low levels of force. Therefore, the force arising from them could significantly contribute to increment of the total force. The importance of recruitment at high levels of force was also observed in the biceps brachii by KUKULKA and CLAMANN (1978) and in the soleus muscle by MONSTER and CHAN (1977).

On the contrary, MILNER-BROWN *et al.* (1973 b) found in the first dorsal interosseus muscle that the contribution of recruitment to generation of muscle force rapidly decreases with increasing force levels; there was no recruitment at force levels more than 1,500 g for two subjects out of three (maximum force, 4 to 6 kg). Further, MONSTER and CHAN (1977) reported similar characteristics in the human extensor digitorum communis muscle.

From these facts, it is suggested that in small muscles such as those of the fingers whose tension must be adjusted delicately rate coding may be the major mechanism for controlling force, whereas in large muscles of extremities which generate strong force recruitment would be more important.

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