

## BEHAVIOUR OF HUMAN MOTOR UNITS IN DIFFERENT MUSCLES DURING LINEARLY VARYING CONTRACTIONS

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### SUMMARY

1. The electrical activity of up to eight concurrently active motor units has been recorded from the human deltoid and first dorsal interosseous (f.d.i.) muscles. The detected myoelectric signals have been decomposed into their constituent motor-unit action potential trains using a recently developed technique.

2. Concurrently active motor unit behaviour has been examined during triangular force-varying isometric contractions reaching 40 and 80% of maximal voluntary contraction (m.v.c.). Experiments were performed on four normal subjects and three groups of highly trained performers (long-distance swimmers, powerlifters and pianists).

3. Results revealed a highly ordered recruitment and decruitment scheme, based on motoneurone excitability, in both muscles and in all subject groups.

4. Differences were observed between the initial (recruitment) and final (decruitment) firing rates in each muscle. These parameters were invariant with respect to the force rates studied, although some differences were observed among subject groups.

5. In general, firing rates of f.d.i. motor units increased steadily with increasing force (up to 80% m.v.c.). The firing rates of deltoid motor units rose sharply just after recruitment and then increased only slightly thereafter.

6. Recruitment was found to be the major mechanism for generating extra force between 40 and 80% m.v.c. in the deltoid, while rate coding played the major role in the f.d.i.

7. The potential of rate coding for increasing force levels up to m.v.c. is discussed.

### INTRODUCTION

Electromyographic methods have long made it possible to distinguish accurately single motor unit activity during isometric contractions at low force levels. As the force level of the contraction is raised, however, the discharges of newly recruited motor units begin to overlap in time, producing a discouragingly complex e.m.g. signal. Various computerized and visual techniques have been employed to extract

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the activities of individual motor units during high force-level contractions (for a review see De Luca, 1979), but it is difficult to assess their accuracy. Since the statistical repercussions of even small detection errors in pulse-interval sequences (as little as 1%) can be extreme (Shiavi & Negin, 1973), a highly reliable decomposition method is essential for accurate subsequent analysis of motor-unit behaviour.

As reported previously (LeFever, 1980; LeFever & De Luca, 1982), we have recently developed a visually assisted, computerized decomposition routine which has permitted the confident separation of as many as eight concurrently active motor units during high force-level contractions (up to 80% of subject's maximal voluntary effort). In an extensive test for accuracy (LeFever, Xenakis & De Luca, 1982), a skilled operator was able to decompose successfully a mathematically synthesized myoelectric signal consisting of eight superimposed motor-unit action potential trains in Gaussian noise. Although the complexity of this synthetic signal exceeded that of experimentally obtained myoelectric signals, the operator was able to separate and classify motor-unit action potentials (m.u.a.p.s) with 99.8% accuracy. The reproducibility of the technique was demonstrated convincingly when two operators separately and consistently decomposed an empirically obtained myoelectric signal consisting of five m.u.a.p. trains. In both tests described above, the myoelectric signals were sufficiently complex to make purely visual discrimination completely impossible.

During triangular force-varying contractions, this decomposition method permits the firing rates of several concurrently active motor units to be followed from the onset of activity (recruitment), through changes associated with increasing and decreasing force output (rate coding), to the cessation of activity (decrutment). This analysis allows us to (1) compare simultaneously recruitment order with decruitment order, (2) determine the mechanisms by which an individual muscle regulates the force it develops (recruitment *vs.* rate coding) and (3) investigate the underlying motor unit control scheme which permits a muscle to achieve precise force. The first two points will be discussed in this paper, including the effects of subject training (or skill) and force-rate of contraction. The following paper (De Luca, LeFever, McCue & Xenakis, 1982) will describe an investigation of motor unit control schemes operating during triangular force-varying contractions, together with an analysis of concurrently active motor unit behaviour during constant-force isometric contractions.

#### METHODS

Between two and eight motor units were studied simultaneously during triangular force-varying isometric contractions of the human deltoid and first dorsal interosseous (f.d.i) muscles. A total of 286 individual m.u.a.p. trains were examined in the two muscles. The f.d.i. was chosen for study because the isometric tension developed in the muscle is approximately linearly proportional to the isometric force of abduction of the index finger (Stephens & Taylor, 1972). Similarly, for a specific transduction arrangement, the isometric force measured by a cuff attached to the arm is approximately linearly proportional to the isometric tension developed by the middle fibres of the deltoid (De Luca & Forrest, 1973). These relatively simple biomechanical arrangements make it feasible to correlate motor unit activity directly with the force developed by the muscles.

*Subjects.* Voluntary contractions were performed by thirteen adult males, including four normal subjects, aged 21–34, and three groups of highly trained performers: (a) three long-distance free-style swimmers, aged 17–19, including the silver medallist in the 1500 metre event at the 1976 Olympic Games, and two team-mates from the 1978 U.S. nationally ranked Harvard University

team (all were in training for international competitions); (b) three national and world champion powerlifters, aged 20–35, including a 1978 world record holder (all were in training for the powerlifting World Championships in 1978); (c) three U.S. nationally known concert pianists, aged 24–52, with a combined total of 88 years experience.

**Force recording.** To record the force output of the f.d.i., a device was constructed to immobilize the subject's right hand with the index finger isolated between a rigid support and a pad attached to a force transducer of negligible compliance ( $2.7 \mu\text{m}/\text{kg}$ ). The pad made contact with the index finger at the proximal interphalangeal joint. This arrangement only measured force produced in the plane of the hand. To record from the deltoid, the subject was strapped to a padded table in the supine position, with right arm extended and pronated. A bracket secured to the table restricted the shoulder from shrugging, and a cuff around the forearm permitted vertical support by a cable lateral to the table. A second cuff was placed around the subject's arm just proximal to the elbow, connected by a cable to a force transducer, and positioned perpendicularly to the arm in the coronal plane. The transducer again had compliance of  $2.7 \mu\text{m}/\text{kg}$  and was secured to the table, oriented perpendicularly to both the arm and the supporting cable. As such, only isometric abduction in the horizontal plane was measured. Transducer outputs were recorded on FM tape and later transferred to digital storage with the myoelectric signal.

To provide a means for comparing the performance of the different skilled subject groups, the level of a subject's maximal voluntary contraction (m.v.c.) was averaged after three brief, non-fatiguing contractions. Every effort was made to maintain consistency in the measurement of the m.v.c. The level of subsequent required contractions was then assigned as a percentage of this force (% m.v.c.). Maximal forces (100% m.v.c.) ranged in the deltoid from 13 kg by a pianist to as much as 39 kg by a powerlifter. In the f.d.i., maximal forces ranged from 3 to 8 kg.

Triangular force-varying isometric contractions were studied in each muscle under the following conditions. Peak forces of 40% m.v.c. and 80% m.v.c. were achieved during contractions with durations producing three different force rates (10, 20, and 40% m.v.c./sec). The subjects were provided with visual feed-back of their force output during all contractions.

**Myoelectric signal recording.** A single bipolar needle electrode was inserted into the muscle and positioned to record the discharges of between two and eight individual motor units during each of the above contractions. A commercially marketed Disa (13K 80) electrode was modified to reduce external force on the needle; the heavy cable was replaced with three 15 cm long 0.078 mm diameter polyurethane insulated copper wires. As detailed by LeFever (1980) and LeFever & De Luca (1982), three myoelectric signal channels were recorded from the three available electrode pairs (between the two platinum-wire surfaces and additionally between each surface and the needle cannula) to facilitate subsequent m.u.a.p. identification. To minimize shunt capacitance and permit wide band recording, the electrode was connected to unity-gain Field Effect Transistor buffer pre-amplifiers, located adjacent to the recording site. A ground reference electrode was attached to the wrist. The electrical activity was then (1) filtered with a low frequency cut-off of 1 kHz and a high frequency cut-off of 10 kHz, (2) displayed on an oscilloscope, (3) recorded on an FM tape recorder, (4) compressed and transferred to digital storage, using a PDP 11/34 computer with an analogue-to-digital converter at a sampling rate of 50 kHz. The digitized e.m.g. signals were decomposed into constituent m.u.a.p. trains using an elaborate visually assisted, computerized system based upon maximum *a posteriori* probability receiver techniques (LeFever, 1980; LeFever & De Luca, 1982; LeFever *et al.* 1982). Fig. 1 provides a simple schematic representation of this procedure operating on a myoelectric signal consisting of five m.u.a.p. trains.

The time-varying mean firing rate of each motor unit was estimated by passing an impulse train corresponding to the motor unit firing times through a unit-area, symmetric, Hanning-window digital filter (Oppenheim & Schaffer, 1975). This method was chosen since the degree of smoothing is independent of the firing rate, and the calculated firing rate estimate is unbiased and free of time delay distortion (LeFever, 1980; LeFever & De Luca, 1982). The width of the filter could be altered to average over a variable amount of time, thus affecting the smoothness of firing rate fluctuations. A 400 msec wide filter was used to examine firing rate variations during the triangular force-varying contractions studied here. As shown in Fig. 2, firing rates of concurrently active motor units could be displayed simultaneously with the force output of the muscle during a single contraction.

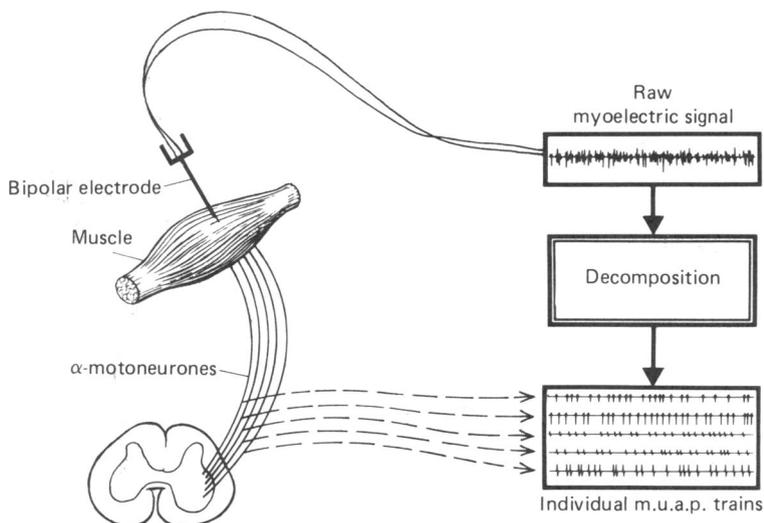


Fig. 1. Schematic illustration of the origination, myoelectric recording and subsequent decomposition of five superimposed motor-unit action potential (m.u.a.p.) trains. Overlap of individual m.u.a.p.s prevents accurate visual identification, necessitating a computer-aided decomposition algorithm (LeFever & De Luca, 1982).

## RESULTS

An attempt is made to present here a vast amount of data concerning motor unit behaviour during triangular force-varying isometric contractions of the human deltoid and f.d.i. muscles. The effects of the following experimental variables on this behaviour have been examined: (a) subject skill (powerlifters, long-distance swimmers and pianists); (b) force rate of contraction (10, 20 and 40 % m.v.c./sec); and (c) peak force of contraction (40 and 80 % m.v.c.). Despite the apparent complexity introduced by these variables, certain generalizations can be drawn regarding motor unit activity in each of the muscles under study.

### *General motor-unit behaviour*

Force output records from isometric contractions of both the deltoid and f.d.i. are shown in Fig. 2, together with firing-rate records of several concurrently active motor units. Firing-rate patterns exhibited by these motor units were typical for their respective muscles at all force rates, and are characterized by the following properties.

(1) Motor units began firing at lower rates in the f.d.i. than in the deltoid (Table 1). These recruitment firing rates did not differ at the three force rates examined in the f.d.i. In the deltoid, slightly higher initial firing rates were observed at 40 % m.v.c./sec ( $13.8 \pm 2.1$  pulses/sec; mean  $\pm$  s.d. of an observation;  $n = 42$ ) than at the two slower rates ( $12.7 \pm 2.3$  pulses/sec;  $n = 82$ ), but this difference was not significant at the 1 % level (two-tailed *t* test). Recruitment firing rates did not depend on threshold force in the deltoid, but increased slightly with increasing threshold in the f.d.i. (approximately 0.5 pulses/sec for every 10 % m.v.c.).

(2) During 40 % m.v.c. contractions, firing rates of f.d.i. motor units increased steadily with increasing force (Fig. 2). Firing rates of deltoid motor units, on the other

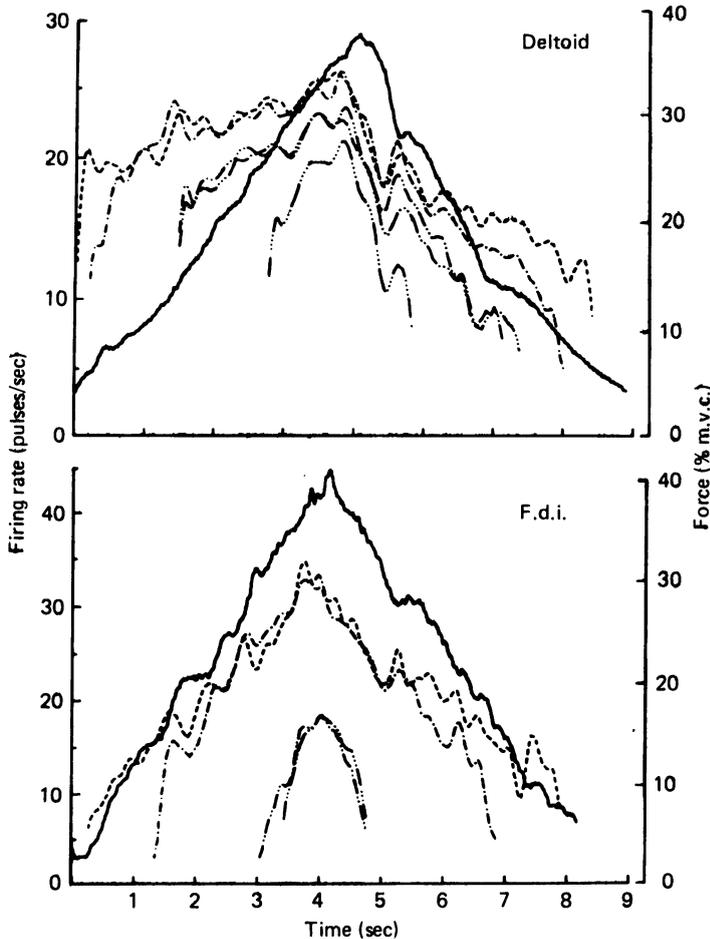


Fig. 2. Firing-rate records of concurrently active motor units (dashed lines) are shown superimposed on the force output (continuous line) recorded during triangular force-varying contractions of the deltoid and first dorsal interosseous (f.d.i.). Force levels are given in percent of maximal voluntary contraction (m.v.c.) at right. These firing rate patterns are characteristic of those obtained for each muscle at all force rates examined and both peak forces (40 and 80% m.v.c.). Note the presence of separate vertical scales for each of the displayed parameters. Firing rate and force values were related through the time axis.

hand, rose sharply just after recruitment and then showed little further increase with increasing force. Deltoid motor units behaved similarly during 80% contractions, while a few high threshold f.d.i. motor units displayed drastically different firing rate patterns (see *Rate coding near maximal voluntary contraction*). The distribution of peak firing rates attained during 40 and 80% m.v.c. contractions are listed in Table 1, together with the number of motor units studied in each muscle.

(3) Prior to cessation of activity (decruitment), motor units in both muscles tended to reach lower firing rates than their initial firing rates at recruitment; this effect was more pronounced in the deltoid than in the f.d.i. Table 1 shows the distribution of decruitment firing rates found in both muscles; no differences were observed at the

three force rates examined. At all force rates studied in the two muscles, low threshold motor units tended to reach slightly lower decruitment firing rates than higher threshold units (approximately 0.4 pulses/sec for every 10% m.v.c. change in recruitment threshold).

*Subject dependence.* The behaviour described above was generally consistent during all contractions within each subject group. However, significant differences in recruitment and decruitment firing rates were observed among the subject groups. Fig. 3 illustrates these differences, as well as pointing out the relationships between recruitment and decruitment firing rates in general for both muscles. A level of significance ( $P$  value) is only reported when the difference between two subject groups was significant at the 1% level. In the deltoid, the highest level of significant difference ( $P < 0.004$ ) was found between long-distance swimmers and powerlifters, with the latter having lower recruitment and higher decruitment firing rates. In the f.d.i. long-distance swimmers had significantly higher mean recruitment firing rates than all other groups ( $P < 0.001$ ). All trained performers had higher mean decruitment firing rates than normal subjects ( $P < 0.01$ ).

TABLE 1. Motor-unit firing rates in two different muscles

Muscle	Recruitment rate (pulses/sec)	Decruitment rate (pulses/sec)	Peak rate at 40% m.v.c. (pulses/sec)	Peak rate at 80% m.v.c. (pulses/sec)
F.d.i.	8.9 ± 2.2 (119)	7.3 ± 2.2 (119)	25.3 ± 8.2 (81)	41.4 ± 9.6 (38)
Deltoid	12.9 ± 2.5 (158)	9.1 ± 2.5 (158)	26.3 ± 4.8 (124)	29.4 ± 3.4 (34)

In each case the mean ± s.d. of an observation is listed, with the number of observations ( $n$ ) in parentheses.

#### *Orderly recruitment of motor units*

In an effort to describe recruitment and decruitment order for all triangular force-varying contractions, force levels associated with initiation and cessation of continuous motor-unit activity were plotted in Fig. 4. Positive linear correlations were observed in both muscles, with linear regression co-efficients ( $r$ ) of 0.94 for the deltoid and 0.83 for the f.d.i. (all data grouped). Little deviation from this relationship was seen (Fig. 4A and C) among the four subject groups (deltoid:  $0.61 < r < 0.99$ ) and f.d.i.:  $0.69 < r < 0.98$ ). Furthermore, Fig. 4C and D illustrates invariant behaviour across the force rates of 10, 20, and 40% m.v.c./sec respectively (f.d.i.:  $r = 0.73, 0.86$  and  $0.86$ ; deltoid:  $r = 0.91, 0.95$  and  $0.96$ ). This relationship points to a highly ordered recruitment and decruitment scheme: low threshold motor units tend to be decruited at subsequent low force levels, while higher threshold motor units have a corresponding tendency to be decruited at higher force levels (see Henneman, Somjen & Carpenter, 1965). In most cases, concurrently active motor units were decruited in the opposite order in which they were recruited. Order reversals were seen rarely (3–5%); however, the possibility of these observations being induced by relative movement of the electrode with respect to the active motor units during high force levels could not be completely excluded. Small, upward shifts observed in the regression lines of Fig. 4 indicate that motor units in general had a tendency to cease firing at relatively

higher force levels than those at which they began. This effect was also reported for single units in the f.d.i. by Milner-Brown, Stein & Yemm (1973*b*) and may result simply because the force developed by a motor unit inevitably lags its discharge.

Fig. 4 also demonstrates a clear difference in the recruitment force ranges of the two muscles. Despite a careful and rigorous search, no newly recruited motor units were observed at force levels above 52% m.v.c. in the f.d.i., while recruitment was seen up to 80% m.v.c. in the deltoid.

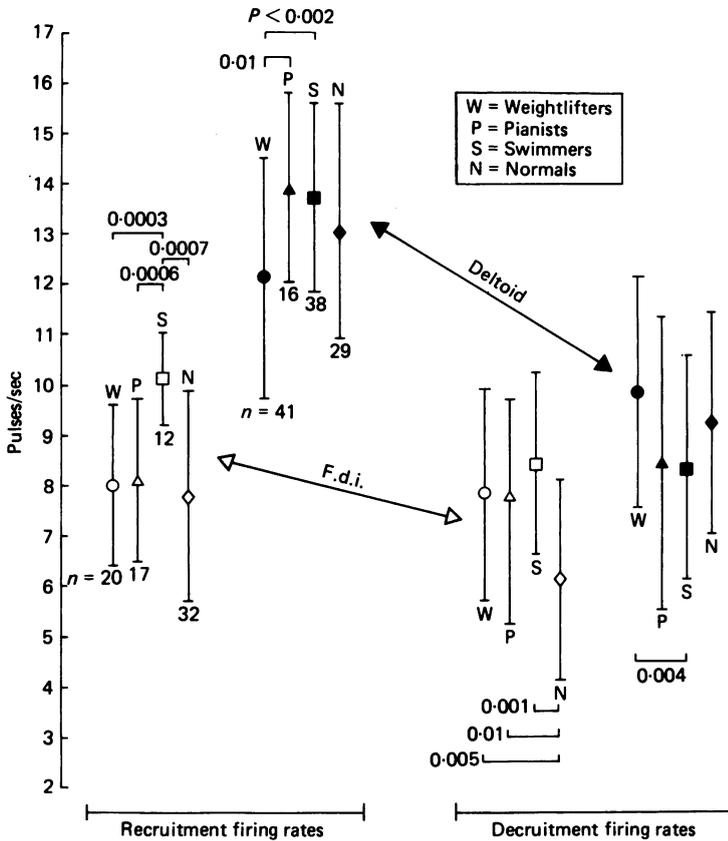


Fig. 3. The distribution of motor-unit firing rates at initiation (recruitment) and cessation (de-recruitment) of continuous activity during triangular force-varying contractions reaching 40% m.v.c. In general, de-recruitment firing rates are lower than recruitment firing rates, but both of these parameters are greater in the deltoid than in the f.d.i. Significant differences between subject groups are indicated by bars showing the upper limits of the P values.

*Recruitment vs. rate coding*

In an attempt to discern fundamental differences between the force-generating mechanisms of the deltoid and f.d.i., data from all subjects were grouped to compare recruitment-force threshold and peak firing rate (Fig. 5). In both muscles, motor units recruited at low force thresholds generally reached higher peak firing rates than those recruited at higher force levels. This relationship is extremely clear in the f.d.i. (Fig. 5), due to the broad range of peak firing rates observed during single

contractions (Fig. 2). Linear regression co-efficients were high for both 40% m.v.c. ( $r = -0.73$ ) and 80% m.v.c. ( $r = -0.56$ ) contractions. While the scatter of peak firing rates observed here is primarily due to the grouping of data from all subjects, some discrepancies may have resulted from the widely varied firing-rate properties recently attributed to distinct types of motoneurons (Harris & Henneman, 1977, 1979).

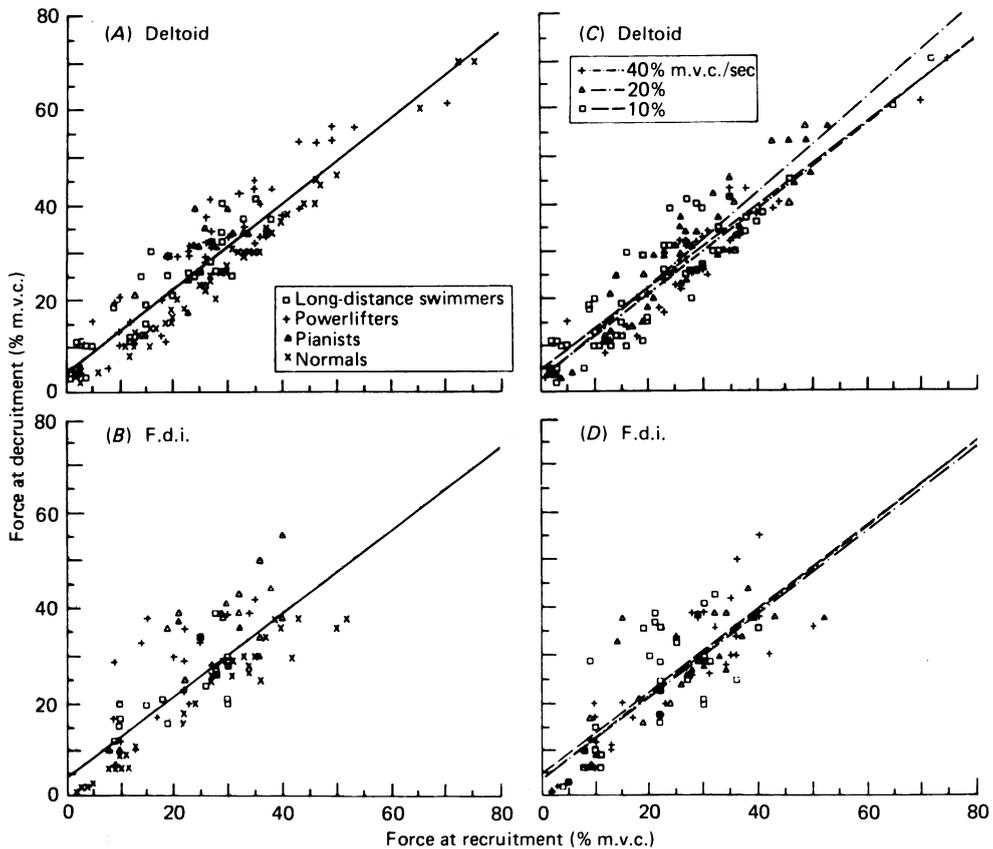


Fig. 4. Force levels, given as % m.v.c., associated with motor-unit recruitment and de-recruitment. The linear relationship observed for both muscles (regression co-efficients  $> 0.8$ ; all data grouped) was consistent across all subject groups (A and B) and was invariant at the three force rates examined (C and D). Recruitment was only observed up to 52% m.v.c. in the f.d.i., but was seen as high as 80% m.v.c. in the deltoid.

In contrast to the f.d.i., low threshold deltoid motor units achieved only slightly higher peak rates than did concurrently active higher threshold units, resulting in a much smaller distribution of peak firing rates (Table 1). Despite this problem, a highly significant negative correlation ( $P < 0.008$ ) was seen between peak firing rate and threshold force during 40% m.v.c. of the deltoid. This relationship was less significant ( $P < 0.08$ ) during 80% m.v.c.; however, records of concurrently active motor units from individual contractions reveal a consistent trend which has been somewhat obscured by grouping data in this manner. The linear regressions plotted in Fig. 5 are therefore indicative of a solid negative correlation between peak firing rate and threshold force in the deltoid.

Fig. 5 also shows that the firing rates of deltoid motor units do not increase greatly as force output increases from 40 to 80 % m.v.c. (see also Table 1). As a result, rate coding can have only a minor effect on extra force developed and recruitment must play the major role in increasing force output above 40 % m.v.c. in the deltoid. In contrast, f.d.i. motor units discharging during 80 % m.v.c. reached much higher peak firing rates than those active during 40 % m.v.c. (Fig. 5 and Table 1). This fact, coupled with the previous observation that few f.d.i. motor units were recruited above 40 % m.v.c. (none above 52 % m.v.c.), indicates that rate coding is primarily responsible for increasing force output at high force levels in the f.d.i. (see also Milner-Brown *et al.* 1973b).

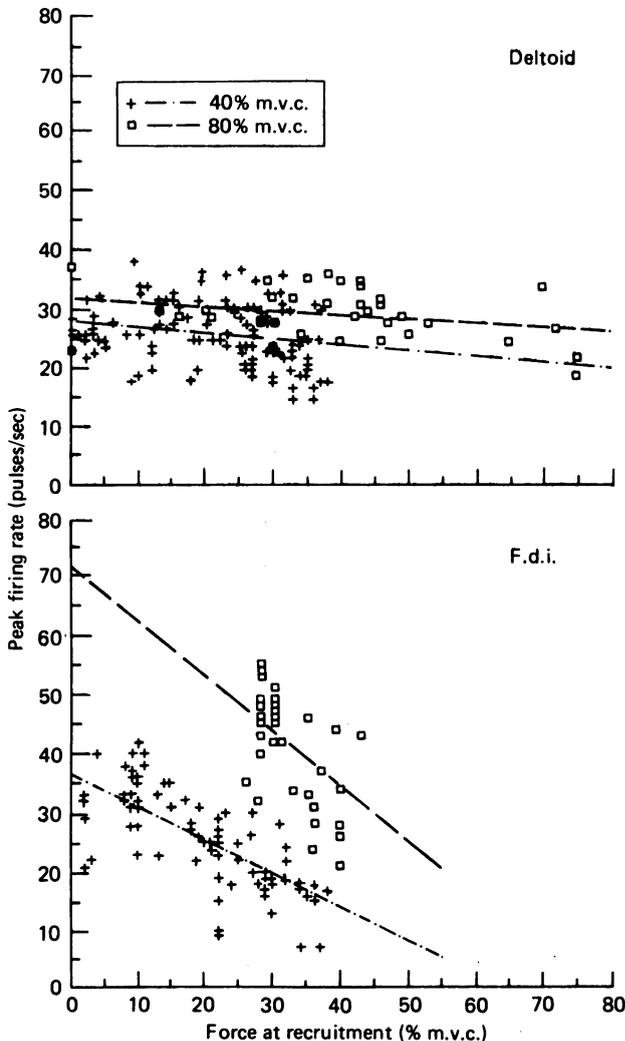


Fig. 5. Peak firing rates achieved during triangular contractions reaching 40% and 80% m.v.c. as a function of recruitment-force threshold. The computed least-squares linear regressions in the f.d.i. show strong negative correlations (linear regression co-efficients  $> 0.56$ ). In the deltoid, the linear regressions had slopes significantly different from zero at 40% m.v.c. ( $P < 0.008$ ), but not at 80% m.v.c. ( $P < 0.08$ ).

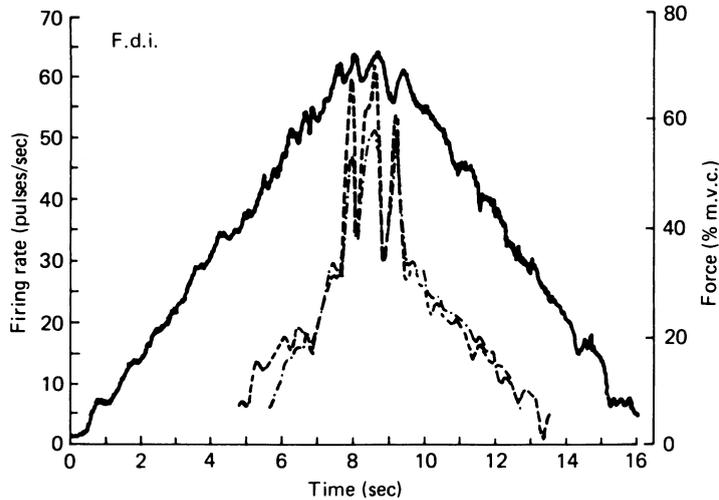


Fig. 6. Firing-rate activity of two high force-threshold motor units (dashed lines) superimposed on the force output (continuous line) during a triangular force-varying contraction of the f.d.i. The highest rate is achieved by the lower threshold motor unit (recruitment-force thresholds for the two units were 31 and 42 % m.v.c.). Note the presence of separate vertical scales for each of the displayed parameters. Firing rate and force values were related through the time axis.

#### *Rate coding near maximal voluntary contraction*

Firing-rate changes associated with force development (at high force levels) in the f.d.i. fell into two categories. The first pattern was similar to that shown in Fig. 2. Such behaviour was typical of low force threshold (less than 30 % m.v.c.) motor units during 80 % m.v.c., with firing rates increasing steadily to as high as 50 pulses/sec. Strikingly different behaviour was seen in several high threshold (greater than 30 % m.v.c.) motor units (Fig. 6). As force levels approached 80 % m.v.c. these motor units displayed sharp bursts of activity, with firing rates rapidly increasing from 30 to 60 pulses/sec. This phenomenon appears to reveal a mechanism of force generation at extremely high force levels (see Discussion). It was only observed during slowly increasing (10 % m.v.c./sec) contractions of 16 sec duration, indicating that both fatigue and the level of exertion may play important roles.

#### DISCUSSION

This study presents a substantially comprehensive characterization of human motor-unit behaviour during high force-level isometric contractions. Until now, it has been impossible to follow simultaneously and accurately the activity of several individual motor units from recruitment, through large force variations, to subsequent decruitment. An effort has been made here to present only the most reliably separated m.u.a.p. trains (greater than 99 % accuracy). Highly accurate examination of the individual properties of motor units, as well as their interaction, has permitted us to uncover several of the underlying mechanisms which control motor unit behaviour in two different muscles.

*Recruitment and decruitment properties*

Differences in the recruitment and decruitment firing rates of the two muscles are summarized in Fig. 3. The decline in firing rate from recruitment to decruitment has been seen previously by recording single motor units (Milner-Brown *et al.* 1973*b*; Clamann, 1970) and is evidence of motoneuronal adaptation. The fact that motor units examined here were decruited at slightly higher forces than their recruitment thresholds reveals a seeming contradiction: lower firing rates producing higher force levels. Since decruitment order was orderly and the opposite of recruitment order (see below), this effect cannot be explained by differences in the number of active motor units. Rather, it points to mechanical as well as motoneuronal adaptation. The potentiation of motor-unit twitch tension after repetitive stimulation has been well documented (for a review, see De Luca, 1979) and seems a likely mechanism to explain this phenomenon. Olson & Swett (1971) have localized twitch potentiation to fatigue-resistant muscle fibres having slow-twitch characteristics. Since the deltoid of long-distance swimmers has been shown to have a significantly higher percentage of these fibres than that of powerlifters (Gollnick, Armstrong, Saltin, Saubert, Sembrowich & Shepherd, 1973), the probability of detecting potentiation is greater and one could expect a more pronounced decline in firing rate from recruitment to decruitment (to produce an equivalent force output). This was actually the case for the deltoid (Fig. 3), adding support to this conjecture. Furthermore, the difference between recruitment and decruitment firing rates in the deltoid was greater for low threshold motor units than for higher threshold units (see points (1) and (3) of *General motor-unit behaviour*), indicating a greater tendency toward twitch potentiation in low threshold units. As an interesting contrast, this decline in the f.d.i. was less noticeable in the pianists and powerlifters than in the other two groups, indicating less of a tendency toward twitch potentiation. These specialities are known to exert explosive training influences on the f.d.i., although little evidence of fibre type conversion (slow-twitch to fast-twitch) with training has been reported (Salmons & Henriksson, 1981).

Highly significant differences in the absolute firing rates among different subjects (both at recruitment and decruitment) provide circumstantial evidence for variation in motoneuronal properties (e.g. the time course of after-hyperpolarization), either as the result of training or due to genetic factors. However, these results await further investigation by more direct methods and cannot be discussed meaningfully here.

*Mechanisms of force generation*

It is well known that mechanical properties of a particular muscle are highly dependent on its fibre composition; in particular, the ratio of fast-twitch to slow-twitch fibres can determine whether a muscle is primarily postural or dynamic. Since these differences must exert a considerable effect on force-generation mechanisms, for this study two muscles were chosen with similar composition (approximately 55% slow-twitch; for exact values see Johnson, Polgar, Weightman & Appleton, 1973). Results showed that these muscles use different mechanisms to increase force output above 40% m.v.c.: the deltoid relies primarily on recruitment, the f.d.i. on rate coding (Figs. 2 and 5). This behaviour was invariant at the three different force

rates studied here (10, 20 and 40 % m.v.c./sec). It seems reasonable to relate these contrasting force generation mechanisms to the anatomy and function of the two muscles.

The f.d.i. is an anatomically confined, small muscle composed of approximately 120 motor units (Feinstein, Lindegard, Nyman & Wohlfart, 1955). Once they have become active, even the smallest of these must contribute noticeably to the total force output of the muscle. If recruitment were the only (or even principal) means by which additional force was developed, the muscle would be incapable of producing a smoothly increasing contraction. As force increased, the orderly addition of large motor units would produce a 'staircase' effect in the force output record. Yet, the function of the f.d.i. is to produce small, accurate movements of the index finger, requiring fine force gradation. To compensate for its sparsity of motor units, the f.d.i. relies on highly dynamic rate coding to produce smooth, linearly varying isometric contractions. This conclusion, first reached by Milner-Brown *et al.* (1973*b*), is supported both qualitatively (Fig. 2) and numerically (Table 1) over the much wider range of forces studied here.

In contrast, the deltoid is a large muscle with as many as 1000 motor units (compare with approximately 770 motor units in the biceps; Christensen, 1959), each contributing a relatively small percentage to the total force output. Since the deltoid is used primarily for generating large, powerful contractions, finely controlled firing-rate activity is unnecessary during normal voluntary effort. Each newly recruited motor unit can provide a sufficiently small force increment to produce functionally smooth contractions.

Although other factors certainly help to determine the firing-rate pattern most beneficial for individual muscles, our analysis may reconcile some of the disparity in motor-unit behaviour separately reported for 'phasic' muscles (Kosarov & Gydikov, 1976; Hannerz, 1974; Milner-Brown *et al.* 1973*b*) and for 'tonic' muscles (Kanosue, Yoshida, Akazawa, & Fujii, 1979; De Luca & Forrest, 1973; Clamann, 1970; Leifer, 1969). Due to the complex firing-rate behaviour observed in concurrently active motor units during force variations (Fig. 2), we resisted classifying individual units as either 'tonic' or 'phasic' (Kosarov & Gydikov, 1976). Rather, a general firing-rate behaviour was ascribed to each muscle, based on accurate examination of a large number of motor units in thirteen different subjects. Whether distinct 'tonic' and 'phasic' motoneurons actually exist (Granit, Phillips, Skoglund & Steg, 1957) is the subject of some debate. However, the wealth of evidence presented here indicates that the distribution of 'tonic' and 'phasic' behaviour in different muscles can be related to their structure and function.

#### *Orderly recruitment and firing-rate properties*

Since the 'size principle' of Henneman *et al.* (1965) was first proposed (based on work with cat motoneurons), much effort has been devoted to verifying its existence in human muscles. Some of the most solid evidence has been presented by Milner-Brown, Stein & Yemm (1973*a*), who examined single f.d.i. motor units with highly selective electrodes, correlating threshold force with twitch tension and contraction time. More recently, Freund, Budingen & Dietz (1975) have shown that motor-unit threshold force increases with axonal conduction velocity in the f.d.i. In this paper

we have demonstrated a basic precept of the 'size principle' in humans: both the recruitment and decruitment order of motor units is related to their susceptibility to discharge. Lower threshold motor units respond to a homogeneously distributed synaptic input with higher firing rates (see also Freund *et al.* 1975; Tanji & Kato, 1973; Person & Kudina, 1972) and are subsequently decruited at lower force levels. Evidence presented here supports the general existence of this relationship during isometric contractions in both the f.d.i. and deltoid muscles (Figs. 3 and 4).

While this result is quite sensible on a superficial level, it points to a seeming contradiction. Higher threshold motor units tend to have shorter twitch durations and thus require higher stimulus frequencies to produce fused contractions (Wuerker, McPhedran & Henneman, 1965). In the motor units studied by Milner-Brown *et al.* (1973*a*), twitch contraction times in the f.d.i. ranged from 30 to 100 msec. If this is indeed the case, the slowest-twitch units are completely fused at 20 pulses/sec, while the fastest-twitch motor units must reach at least 25–30 pulses/sec before substantial fusion begins. Yet, we have seen the lowest threshold motor units steadily increasing their firing rates to as high as 50 pulses/sec, well beyond the rates required for complete fusion. These apparently unnecessary firing-rate increases add further support to the existence of a passive, size-related response to a homogeneously distributed synaptic drive. Furthermore, the highest threshold and presumably fastest twitch motor units generally reach lower firing rates than those required for even partial fusion to occur (Fig. 5), pointing to the idea that (in man) large, fast-twitch motor units may never be completely fused during normal voluntary effort. While the twitch responses of unfused or partially fused motor units still contribute substantially to the total force output, their presence suggests a large, seldom used potential for force generation.

A means of tapping this force reserve may be seen in Fig. 6, where evidence of a firing-rate burst phenomenon in some of the highest threshold f.d.i. motor units is presented. The type of contraction in which this phenomenon is clearly seen (10% m.v.c./sec) is important, since these strenuous contractions were the only type in which the subject reported definite effects of fatigue on performance. As force output slowly increases toward 80% m.v.c., muscular fatigue causes the actual level of maximal voluntary effort to fall below that possible in a non-fatigued state. During the contraction shown in Fig. 6, the individual (a normal subject) actually reported the sensation of reaching maximal voluntary contraction at the time of the firing-rate bursts.

Brief firing-rate bursts of 50 pulses/sec have been reported in single units during maximal voluntary contractions of the human quadriceps muscles (Warmolts & Engels, 1972), but only in patients with chronic low-grade motor neuropathies. Muscle biopsy revealed that this behaviour was only seen in homogeneous fields of fast-twitch fibres (greater than 96%), apparently arising as the result of collateral reinnervation. Because of the difficulties inherent in separating the activities of several rapidly firing motor units, we were unable to determine whether all units displayed this bursting activity or whether large units were activated preferentially. The mechanical contribution of smaller units would presumably be small, however, since most are probably fused at the relatively high firing rates observed prior to the bursts (approximately 30 pulses/sec).

Although intermittent firing-rate bursts have been observed using single-unit recording, Fig. 6 to our knowledge is the first evidence of a bursting phenomenon in continuously active motoneurons during non-ballistic contractions. Whether these rapidly increasing firing rates result from a sudden increase in synaptic excitation is difficult to determine. However, evidence of this type of non-linearity is well documented in cat spinal motoneurons subject to increased levels of current injection (Kernell, 1965). Baldissera, Gustafsson & Parmiggiani (1978) have accounted for this effect (the so-called secondary range of motoneurone firing) by a model based on the time course of motoneuronal after-hyperpolarization, indicating that it may well be a passive response to high levels of synaptic current injection. This effect may also account for the extremely rapid firing-rate bursts (60–120/sec) seen by Desmedt & Godaux (1977) during ballistic contractions of the tibialis anterior, where high levels of synaptic current are necessary.

In contrast, no evidence of a firing-rate burst response was seen during voluntary contractions of the deltoid up to 80% m.v.c. Because of the 'tonic' behaviour observed in the deltoid, motor-unit firing rates remained much lower than those reached in the f.d.i. (Table 1). If twitch contraction times are comparable for motor units in the two muscles, most fast-twitch deltoid units are probably unfused even at 80% m.v.c. Interestingly, a recent study of single motor units in the neighbouring human brachialis muscle (Kanosue *et al.* 1979) has demonstrated behaviour similar to that seen here in the deltoid, but with an increased reliance on rate coding above 70% m.v.c. Our study did not investigate the force range between 80 and 100% m.v.c.; however, the presence of unfused motor units indicates that rate coding has a tremendous potential for increasing force output up to (and even beyond) maximal voluntary levels in muscles like the deltoid. If the central nervous system were to increase firing rates or generate firing-rate bursts in the large fast-twitch motor units of the deltoid (such as those seen in the f.d.i.), extraordinary force levels could be achieved for short periods of time. This mechanism may indeed be the explanation for many of the incredible feats performed by humans under high stress conditions and during hypnotic states.

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