

CONTROL SCHEME GOVERNING CONCURRENTLY ACTIVE HUMAN MOTOR UNITS DURING VOLUNTARY 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 muscles. The resulting composite myoelectric signals have been decomposed into their constituent motor-unit action potential trains using a recently developed technique.

2. A computer cross-correlation analysis has been performed on motor-unit firing rate and muscle-force output records obtained from both constant-force and triangular force-varying isometric contractions performed by normal subjects, and three groups of highly trained performers (long-distance swimmers, powerlifters and pianists).

3. The temporal relationships between firing rate activity and force output have provided evidence that the deltoid of long-distance swimmers has a significantly higher percentage of slowly fatiguing fibres than that of normal subjects.

4. Results showed that both muscles are incapable of producing a purely isotonic contraction under isometric conditions. Small, possibly compensatory force variations at 1–2 Hz result from a common drive to all active motoneurons in a single muscle pool.

5. Rapid force reversals during triangular, force-varying isometric contractions appear to be accomplished through a size-related motor-unit control scheme. All firing rates decline prior to the force peak, but small motor units with slow-twitch responses tend to decrease their firing rates before large, fast-twitch motor units. This mechanism is not visually controlled, and does not depend on force rate in non-ballistic contractions.

INTRODUCTION

The force developed by a single muscle is a complex function of the recruitment level and firing-rate distribution of its active motor-unit population. While size-related, orderly recruitment behaviour is well documented for linearly force-varying contractions (Henneman, Somjen & Carpenter, 1965; Milner-Brown, Stein & Yemm, 1973*b*; and others), current descriptions of motor-unit firing-rate properties are less detailed (Person & Kudina, 1972; Milner-Brown, Stein & Yemm, 1973*c*). Only recently has it been possible to identify the discharges of concurrently active motor units with

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a degree of accuracy necessary to reveal subtle interplay between firing rate and force adjustments (LeFever, 1980; LeFever & De Luca, 1982; LeFever, Xenakis & De Luca, 1982; De Luca, LeFever, McCue & Xenakis, 1982).

In this paper an extensive cross-correlation analysis is described which elucidates the temporal relationships between force output and firing-rate behaviour during both constant-force and triangular force-varying isometric contractions. The apparent effects of muscle composition on these relationships will be pointed out, but the main thrust of this work is to demonstrate how the varied responses of individual motor units are controlled to produce precise mechanical effects.

METHODS

Between two and eight motor units were studied simultaneously in each of thirty-seven separate constant force and forty separate force-varying isometric contractions of the human deltoid and first dorsal interosseous (f.d.i.) muscles. A total of 214 individual motor-unit action potential (m.u.a.p.) trains were examined in the two muscles. Methods for obtaining myoelectric signal and force recordings have been fully described (LeFever & De Luca, 1982; De Luca *et al.* 1982).

The same highly trained (long-distance swimmers, powerlifters and pianists) and control subjects were used for both this and the previous study. Levels of required contractions were assigned as a percentage of the subject's maximal voluntary contraction (m.v.c.). Two types of isometric contractions were studied in each muscle: constant force (30 and 60% m.v.c.), and triangular force-varying (to 40% m.v.c.) at three different force rates (10, 20 and 40% m.v.c./sec). It is important to note that subjects were unable to track the fastest of these contractions (40% m.v.c./sec) visually, but could perform them easily after a short practice period.

Correlation methods

As before, an impulse train representation of the firings of each m.u.a.p. train was passed through a Hanning averaging filter, producing an unbiased estimate of the time-varying mean firing rate of each motor unit.

Constant-force isometric contractions. To examine small firing rate fluctuations during constant-force contractions, a narrow (400 msec wide) Hanning filter was used. The temporal relationships between motor unit activity and tension developed during constant-force contractions were extracted using a computer-implemented cross-correlation routine. A 5 sec interval of relatively stable force output was examined in each contraction; the interval was chosen to include a maximal number of consistently active motor units, while avoiding large, transient deviations from the assigned force level. The firing-rate record of each motor unit active during this period was cross-correlated with (1) the force output during the same interval and (2) the firing-rate record of another concurrently active motor unit. When comparing firing rates, the activity of the earliest recruited motor unit was cross-correlated with that of each later recruited unit. The exact choice of interval location in long contractions was found to be relatively unimportant; similar results were obtained when different intervals of the same contraction were cross-correlated. In order to reveal any underlying common variation, the force and firing-rate records were digitally high-pass filtered prior to cross-correlation; a simple zero-phase filter, $H(f) = 1 - (\sin \pi f) / \pi f$ with a low frequency 3 dB point of 0.75 Hz, was used to completely eliminate d.c. bias. A sample constant-force isometric contraction record and the resulting cross-correlation functions are shown in Fig. 1.

Force-varying contractions. During triangular force-varying isometric contractions, the mean firing rate of each motor unit was found to peak prior to the peak of the force output (Fig. 5A). The time between corresponding peaks in the force and firing rate was termed *firing-rate reversal lead*, and was estimated by cross-correlating between the force and firing-rate records. Since the duration of the fastest contractions was only 2 sec, a 1 sec interval surrounding the peaks of the two records was chosen for analysis in all triangular contractions studied. In order to smooth out transient firing-rate changes occasionally found in the vicinity of the firing-rate peak, a wide averaging filter (1000 msec) was used on the inter-pulse intervals of each motor unit prior to this cross-correlation. A sample triangular force-varying contraction and associated motor-unit cross-correlation functions are shown in Fig. 5.

RESULTS

Constant-force contractions. As Fig. 1A shows, the firing rates of motor units active during constant-force isometric contractions exhibited small fluctuations at a frequency of 1–2 Hz. Similar firing-rate fluctuations were found in all of the ninety-nine motor units examined in this segment of the study; furthermore, these fluctuations occurred almost simultaneously in all recorded motor units. It is important to realize that these motor units were not firing synchronously, but were being similarly modulated about different mean (bias) firing rates. Motor-unit firing-rate fluctuations were also echoed in the force output record with time delays (*firing-rate lead*) presumably characteristic of each motor unit's mechanical properties.

The firing-rate records of concurrently active motor units during each contraction were cross-correlated to determine the extent of observed simultaneous behaviour (Fig. 1B). Results from all subjects at both levels of contraction are assembled in histogram form in Fig. 2; mean and standard deviation information is provided at the base of each histogram. High correlations (mean > 0.6) were found in both muscles at 30 and 60% m.v.c.

As shown by *t* tests, no significant differences were found in either muscle between the mean cross-correlation levels of motor units belonging to (1) different subject groups at the same level of contraction or (2) the same subject groups at different levels of contraction. However, it is clear from this analysis that all motor units active during constant-force isometric contractions receive strong common excitation, probably from several sources.

The force and firing-rate records were then cross-correlated over the same period to (1) determine the extent of electro-mechanical coupling and (2) obtain an estimate of the firing-rate lead. Fig. 1C shows such a cross-correlation function for each of the motor units of Fig. 1A.

Resulting cross-correlation levels for all motor units in each type of contraction were plotted as histograms in Fig. 3. The mean correlation is greater in the f.d.i. than in the deltoid, and is greatest during high level (60% m.v.c.) contractions of the f.d.i. In the deltoid, athletes (long-distance swimmers and powerlifters) had a significantly ($P < 0.001$) lower mean cross-correlation than the normal subjects at 30% m.v.c., but not at the higher force level. While no significant difference was seen in the mean cross-correlation levels between 30 and 60% m.v.c. (subjects grouped) in the deltoid, a highly significant difference ($P < 0.0002$) was seen between the two force levels in the f.d.i. Consistently high cross-correlation values between firing-rate activity and force output (mean > 0.4) show that small force fluctuations at 1–2 Hz observed during these constant-force isometric contractions are inherent, due to simultaneous modulation of motor-unit firing rates.

Firing-rate lead times were obtained from individual cross-correlation functions (Fig. 1C) for all subject groups. Although such estimated firing-rate leads have durations (80–340 msec) slightly larger than motor-unit contraction times (30–150 msec), the two parameters are unquestionably related. While no significant difference between long-distance swimmers, powerlifters and normal subjects was found in the f.d.i., a remarkable shift in the firing-rate lead was observed in the deltoid (Fig. 4). Long-distance swimmers with muscles trained for endurance were found to have a significantly ($P < 0.002$) longer mean firing-rate lead than normal subjects.

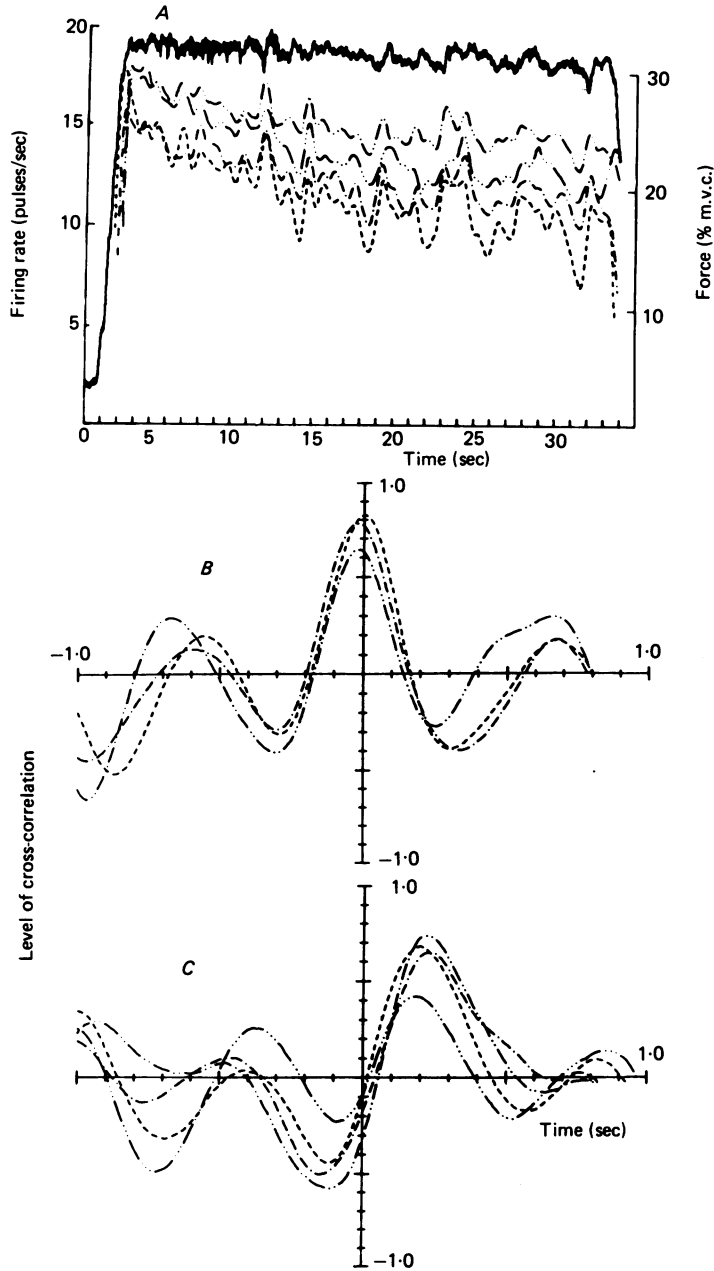


Fig. 1. *A*, firing-rate records of four concurrently active motor units (dashed lines) are shown superimposed on the force output (continuous line) recorded during a constant-force isometric abduction of the deltoid. The force level is given in percent of maximal voluntary contraction (m.v.c.) at right. *B*, functions obtained by cross-correlating between firing rates, and *C*, between firing rates and force output. Positive shift of peaks in *C* indicates that firing-rate activity leads force output.

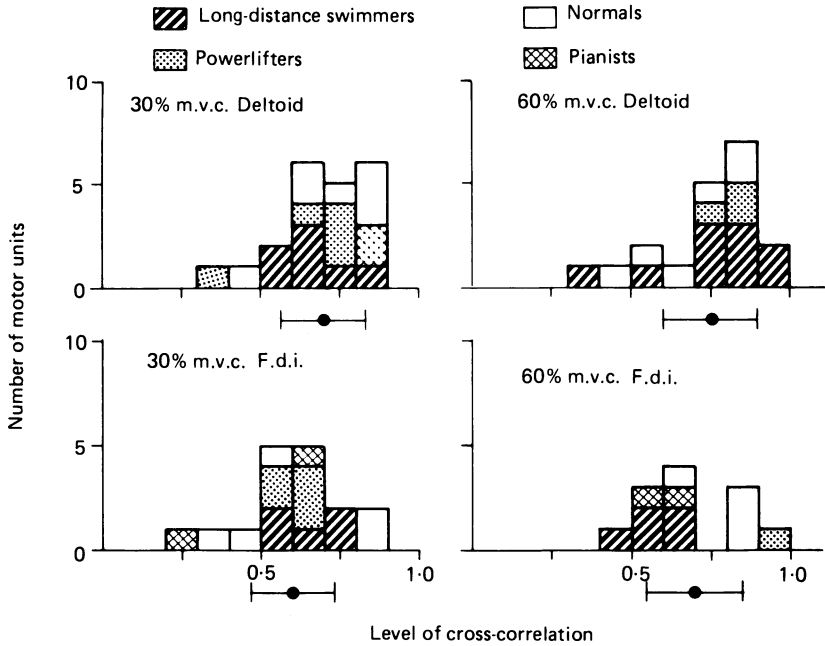


Fig. 2. Maximal cross-correlation levels obtained between firing rates of all concurrently active motor units during a 5 sec interval (as shown in Fig. 1 B). Means and standard deviations for all contraction levels are provided at the base of each histogram. High cross-correlation levels (means > 0.6) indicate that all motor units receive common excitation. No differences are observed between subject groups.

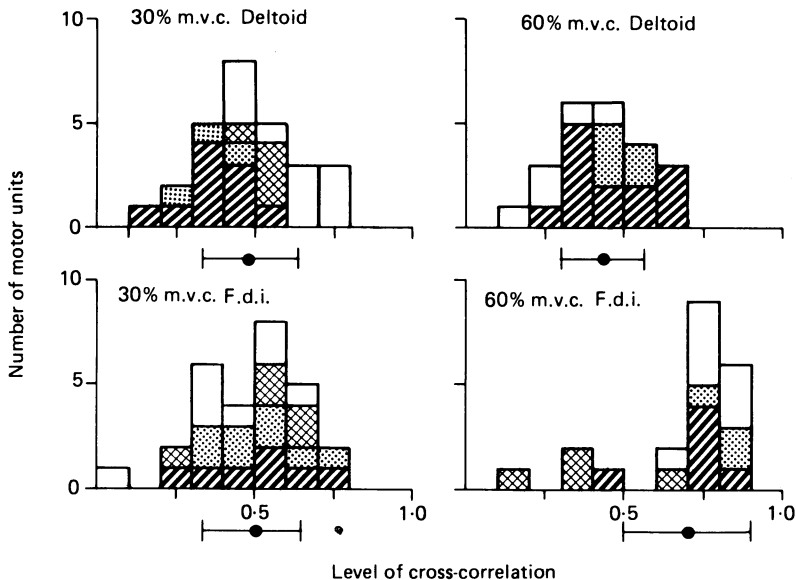


Fig. 3. Maximal cross-correlation levels obtained between firing-rate activity and force output during a 5 sec interval (as shown in Fig. 1 C). Means and standard deviations for all levels of contraction are provided at the base of each histogram. The relatively high cross-correlation levels (means > 0.4) indicate that force fluctuations at 1-2 Hz are caused by simultaneous modulation of motor-unit firing rates. See Fig. 2 legend.

Few data were available from powerlifters, but their mean firing-rate lead was not found to be significantly different from the control group.

Force-varying contractions. Fig. 5A shows a force-output record from a triangular force-varying isometric contraction of the f.d.i. at a force-rate of 20% m.v.c./sec, together with the firing-rate records of five concurrently active motor units. A total

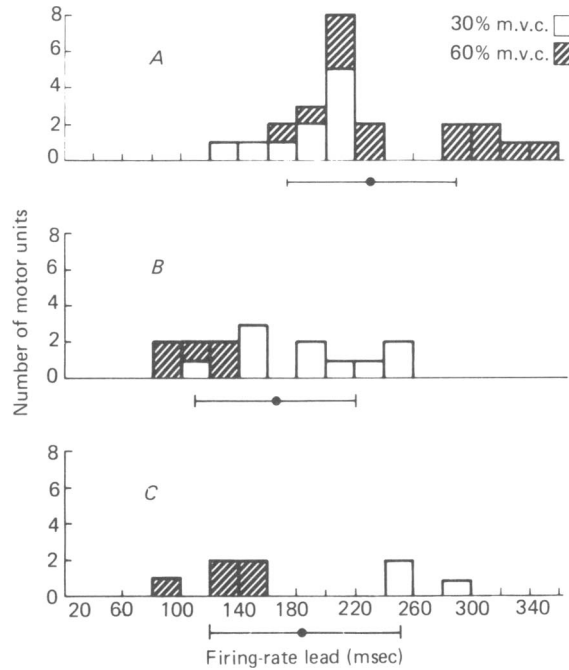


Fig. 4. Firing-rate leads of motor units in the deltoid obtained by cross-correlating between firing-rate activity and force output for long-distance swimmers (A), normal subjects (B), and powerlifters (C). Means and standard deviations are provided at the base of each histogram. Long-distance swimmers had a significantly longer mean firing-rate lead than normals ($P < 0.002$).

of 115 motor units were examined in this segment of the study. In general, smaller firing-rate fluctuations present in constant-force isometric contractions are also superimposed upon large firing-rate changes seen in force-varying contractions. For the purpose of this analysis, however, these smaller fluctuations have been smoothed out, permitting the larger firing-rate variations to be examined more readily. While similar firing-rate behaviour was seen at all force rates in a particular muscle, differences were observed between the general firing-rate behaviour of the deltoid and the f.d.i.; these have been discussed extensively in the previous paper (De Luca *et al.* 1982). In both muscles, however, the firing rates of all motor units increased with increasing force, and then began to decline at different times prior to the force reversal. An estimate of this time period (firing-rate reversal lead) was obtained by cross-correlating between the force record and firing-rate record of each motor unit (see Methods). The shaded area in Fig. 5A illustrates graphically the concept of

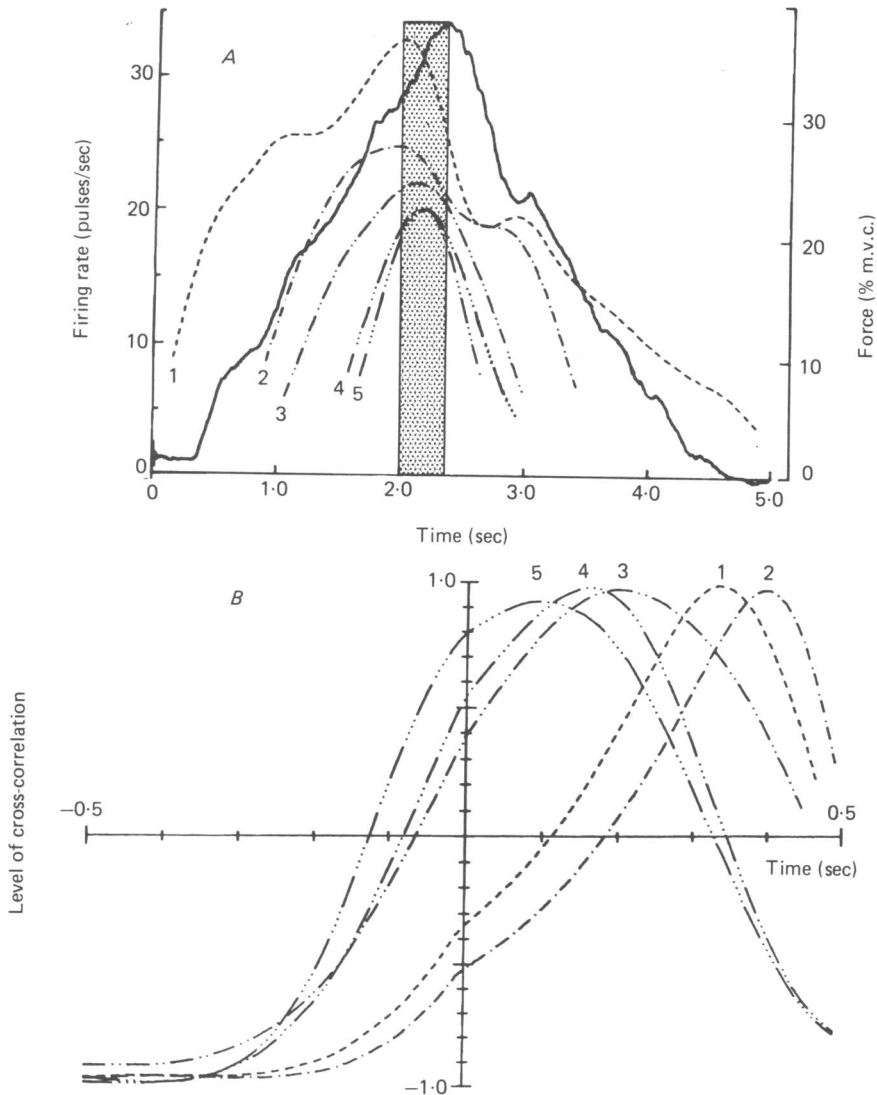


Fig. 5. *A*, firing-rate records of five concurrently active motor units (dashed lines) are shown superimposed on the force output (continuous line) recorded during a triangular force-varying contraction of the f.d.i. Width of shaded area illustrates the concept of firing-rate reversal lead for the lowest threshold motor unit. (Note the presence of separate vertical scales for each of the displayed parameters. Firing rate and force values are related through the time axis.) *B*, functions obtained by cross-correlating between the firing-rate and force records for each motor unit shown in *A*. Horizontal positions of peaks are estimates of firing-rate reversal leads.

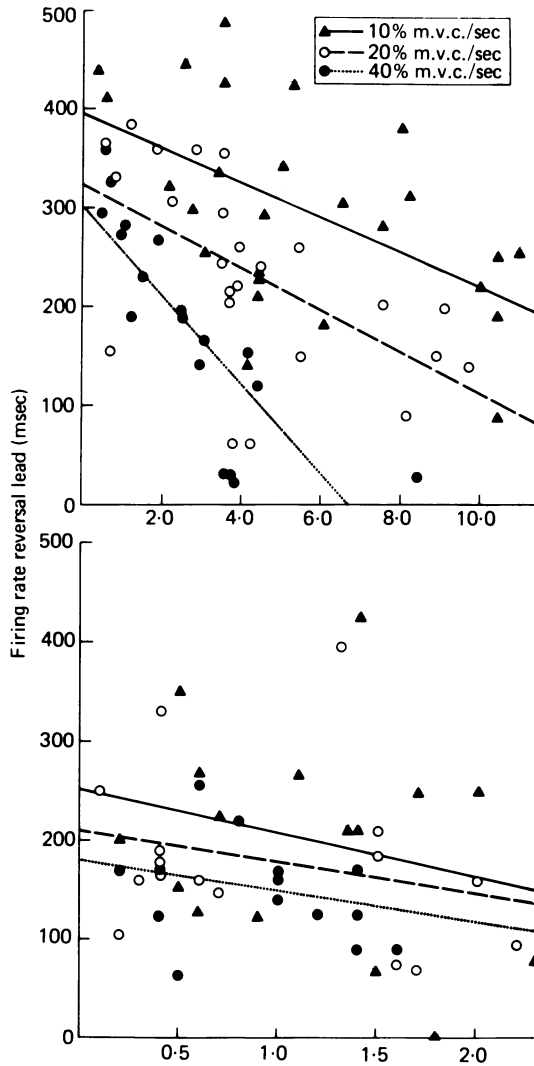


Fig. 6. Relationship between firing-rate reversal lead and the threshold force for recruiting each motor unit in the deltoid (*A*), and f.d.i. (*B*). A linear regression analysis was performed on the data at the force rates 10, 20 and 40 % m.v.c./sec respectively; resulting linear regression co-efficients are lower for the f.d.i. (0.25, 0.25, 0.27) than for the deltoid (0.54, 0.56, 0.81).

reversal lead, while Fig. 5*B* illustrates the result of the cross-correlation process. Firing-rate reversal leads were found to range from 0 to 500 msec, with generally larger values for the deltoid (248 ± 108 msec; mean \pm s.d. of an observation; $n = 67$) than for the f.d.i. (179 ± 86 msec; $n = 48$).

The firing-rate reversal leads of motor units from contractions at different force rates are plotted in Fig. 6 as a function of threshold force for recruiting each motor unit. A linear regression analysis was performed on the data at the force rates 10, 20 and

40% m.v.c./sec respectively; resulting linear regression co-efficients are lower for the f.d.i. (0.25, 0.25 and 0.27) than for the deltoid (0.54, 0.56 and 0.81). These data indicate that slow-twitch motor units, recruited early in a contraction at low force levels, tend to reduce their firing rates before fast-twitch motor units recruited at higher force levels. As the force rate increases, the lines are shifted to smaller reversal leads and lower recruitment thresholds, a result which can be accounted for by several possible mechanisms (see Discussion).

DISCUSSION

Constant-force isometric contractions. The observed firing-rate behaviour (Figs. 1 and 2) provides graphic evidence for a homogeneous input to human motoneurone pools. During constant force isometric contractions, each motoneurone may be driven by a separate input, or each may respond to a common input with its own intrinsic 'firing rate-current' relationship (Monster, 1979); both of these mechanisms can produce the distribution of mean (bias) firing rates seen in Fig. 1A. However, the simultaneous, low-frequency fluctuations superimposed on these bias rates must be attributed to the modulation of a common synaptic input. These results expand upon the findings of Mendell & Henneman (1971) that all motoneurons in a single pool may receive excitation from each muscle spindle afferent. Because our experiments were carried out under isometric conditions, the contribution of muscle spindle (Ia) afferents was presumably small, pointing to an evenly distributed supraspinal or Ib afferent input.

As a mechanical consequence of this omnipresent behaviour, our data (Fig. 3) point strongly to the fact that a muscle is incapable of generating purely isotonic contractions under isometric conditions. Small, low-frequency fluctuations in isometric force output mentioned by Milner-Brown, Stein & Yemm, (1973a) can now be seen as the manifestation of an underlying common drive to all concurrently active motor units. The purpose for this slowly fluctuating synaptic drive is not obvious, although an attractive idea emerges from work on the frequency response of motor-unit tension development (Stein, French, Mannard & Yemm, 1972). These investigators showed that as the average firing rates increase in the cat soleus, the responsiveness of the muscle to high frequency components of the input is reduced, while the response to low frequency components (less than 3 Hz) is enhanced. Small, compensatory firing-rate changes of 1–2 Hz are consequently more effective at regulating force output than larger firing-rate variations at faster frequencies. It would seem that the mechanisms affecting motor-unit firing rates may have evolved to complement the mechanical responses of the end organs.

While the firing-rate fluctuations remain highly correlated as a contraction progresses, the bias firing rates begin to decline with no corresponding decline in force output (Fig. 1A). Person & Kudina (1972) attributed this effect to additional recruitment as the contraction progressed. No such newly recruited units were seen either here or in a past study (De Luca & Forrest, 1973); this behaviour is more likely to be due either to post-tetanic twitch potentiation (as discussed by De Luca, 1979), or to a concurrent reduction in the force output of agonist and antagonist muscles, which maintains the monitored force output of a joint constant. Motor-unit firing

rates have been shown to decline immediately and drastically following the onset of a maximal voluntary contraction (Bigland-Ritchie, 1980). Stimulation experiments indicate that the rapidity of this effect may help to preserve muscle excitability during repetitive firing, while accompanying a slowing of contractile speed during strenuous contractions (Edwards, Hill & Jones, 1975).

The variability of this effect at different force levels was not examined here, but the rapidity of firing-rate decline (Fig. 1A) points out the limitations on most past investigations of firing rate-force relationships. As observed here, firing rates generated during linearly increasing isometric contractions will differ from those determined at increasing levels of static force (Kosarov & Gydikov, 1976). This may help to explain why these investigators observed maximal firing rates of 18 pulses/sec in the f.d.i. at 100% m.v.c. while we have observed rates above 50 pulses/sec at 80% m.v.c. To obtain values indicative of normal voluntary effort, it is important to determine firing rate-force profiles in a dynamic fashion.

Due to size-related differences in the firing rate-current relationships of each motoneurone, the existence of a common synaptic drive does not result in motor unit synchronization, an effect discussed extensively in the literature (for a review, see De Luca, 1979). Synchronization is properly defined as the tendency of motor units to regularly discharge at or near (within a few msec) the time that other motor units discharge. It is equivalent to phase-locking or entrainment. When motor-unit activities modulate about unequal bias firing rates, they are highly cross-correlated, but their discharges do not consistently occur adjacently in time. On rare occasions, motor units examined in the present study exhibited entrained synchronous activity for periods of less than 1.5 sec.

A tendency toward synchronized activity during isometric contractions has been reported (by indirect observation) to increase with physical training in the f.d.i. (Milner-Brown *et al.* 1975); enhancement of supra-spinal reflexes was proposed as an explanation for this effect. Since data presented here indicate that firing rates modulate simultaneously, the type of synchronization previously reported may occur if bias firing rates converge toward some preferred level, possibly by the response of associated tensoreceptors and resulting reflex mechanisms. However, we were unable to detect any significant trend toward this behaviour in the athletes or pianists studied.

The extent to which a motor unit's activity is correlated with force output should increase with the size of the motor unit and decrease with the number of active motor units in the muscle. Thus, it is not surprising that the firing rates of athletes (long-distance swimmers and powerlifters) are less correlated with force in muscles like the deltoid (Fig. 3, 30% m.v.c.). This effect probably results from examining small motor units in a bulky muscle with numerous active motor units. No such discrepancy is seen at 60% m.v.c. once larger motor units have become active. Similarly, higher force-firing rate correlations seen at 60% m.v.c. in the f.d.i. are probably due to a sampling bias consistently present in experiments of this kind. Larger m.u.a.p.s are easier to discriminate and are thus chosen preferentially for myoelectric recording; they also tend to be associated with motor units having large twitch responses (Olson, Carpenter & Henneman, 1968). Because the f.d.i. has a relatively small number of motor units (approximately 120; Feinstein, Lindegard, Nyman & Wohlfart, 1955)

each detected motor unit contributes substantially to the force output, resulting in high cross-correlation levels.

As illustrated in Fig. 4, the technique of digital cross-correlation permits an estimation of the temporal relationship between firing rate and force development (firing-rate lead) in each motor unit. Due to wide differences in the mechanical responses of different fibre types, the chance of detecting motor units with longer firing-rate leads should increase directly with the percentage of slower-twitch fibres present in a muscle. Consequently, the significant difference in mean firing-rate lead observed between long-distance swimmers and normal subjects (Fig. 4) provides electromyographic support for the results of Gollnick, Armstrong, Saltin, Saubert, Sembrowich & Shepherd (1973), who reported a statistically significant difference in the percentage of non-fatiguing, slow-twitch fibres in the deltoid of swimmers (range of 66–85 % with a mean of 74 %) and weightlifters (range of 43–67 % with a mean of 53 %). Interestingly, another study (Johnson, Polgar, Weightman & Appleton, 1973) found the percentage of slow-twitch fibres in the deltoid of normal subjects to be 53.3 ± 9.4 % (mean \pm s.d. of an observation). The lack of significant firing-rate lead shift in the powerlifters studied could therefore be expected. However, strict criteria applied to select only the most reliably decomposed m.u.a.p. trains during a minimum 5 sec interval of stable force output resulted in insufficient data to draw definitive conclusions from this group of athletes. Pianists contributed little constant-force cross-correlation and firing-rate lead data for similar reasons. Additional experiments were impossible to carry out due to the limited availability of these elite performers.

Force-varying isometric contractions. Because it was impossible to obtain more than eight reliably separated motor units from a single contraction (usually three to four), data plotted in Fig. 6 were collected from all subjects at the specified force rates. Grouping data in this manner almost inevitably obscures clear relationships. Thus, the low linear regression co-efficients calculated for the f.d.i. (Fig. 6B) may have resulted because the distribution of *firing-rate reversal leads* was smaller for the f.d.i. than for the deltoid, reducing the likelihood of detecting a trend. Lest this explanation be construed as justification for a non-existent relationship, it should be pointed out that the contraction of Fig. 5A was obtained from the f.d.i. Consequently, there is evidence for a negative correlation between *firing-rate reversal lead* and threshold force in both muscles.

Several recent studies have emphasized the influence of mechanical events on control schemes governing motor-unit firing-rate behaviour. For example, Budingen & Freund (1976) have shown that during linearly force-varying isometric contractions of the extensor indicis, increases in force rate accelerate the timing of firing onset for each motor unit, so that the peak of each first twitch contraction occurs at approximately the same force level (irrespective of force rate). As elegantly stated by Henneman (1980): 'It is the mechanical events in muscle that should be the centre of attention. The motoneurone pool must be organized to achieve precise timing of these events in single motor units and to bring about optimal combination of them for all types of behaviour.'

Firing-rate changes associated with rapid force reversals have never been analysed carefully. Given the widely disparate mechanical and temporal responses of the individual motor units in a single muscle, can a simple reduction in synaptic

excitation to the motoneurone pool produce such an exquisitely timed event? Near the force peak, we have seen firing rates of early recruited motor units decline, while the firing rates of later recruited units continue to increase for a substantial period of time (Fig. 5A). Since the order of reversal and the relatively long firing-rate reversal leads (up to 500 msec) cannot be explained by differences in axonal conduction velocities, the explanation may lie with the underlying mechanisms governing synaptic excitation and inhibition of the motoneurone pool.

The firing-rate behaviour observed in Fig. 5A argues for the existence of either: (1) a selective reduction in excitation, (2) a selective increase in inhibition or (3) a brief homogeneous inhibitory input, coupled with a selective (size-related) sensitivity to inhibition. While none of these possible mechanisms can be completely eliminated, a tremendous amount of spinal processing would be necessary to effect a selective process (Henneman, Clamann, Gillies & Skinner, 1974). The third possibility is especially attractive since it has been suggested (Clamann, Gillies & Henneman, 1974) that (1) the interaction between excitation and inhibition is a simple algebraic process and (2) the density of inhibitory inputs is equal for all motoneurons in a pool. Further, evidence presented here (Figs. 1, 2) and previously (De Luca *et al.* 1982) supports the existence of a size-related sensitivity to homogeneous excitation in both the deltoid and f.d.i. A reflex study in cats (Luscher, Ruenzel & Henneman, 1979) has suggested a possible presynaptic basis for these differences: afferent impulses may fail to invade the extensive arborizations of fibres going to large motoneurons as effectively as the smaller branchings synapsing on smaller cells. A higher percentage of synaptic endings are subsequently activated on small motoneurons, resulting in larger e.p.s.p.s and greater excitability. Since this effect does not relate to the type of synaptic transmitter, it is not difficult to imagine a similar effect on inhibitory inputs to the motoneurone pool.

The sequence of events produced by this mechanism might be as follows: As the subject plans or anticipates a force reversal, an increasing inhibitory input is applied to the motoneurone pool which competes with the increasing excitatory input in progress. Larger i.p.s.p.s are produced in smaller motoneurons, effectively overcoming the excitation and resulting in ordered firing-rate reversals. Either prior to or as the force peak is reached, a reduction in excitatory input rapidly reduces all firing rates and produces the ordered decruitment described previously (De Luca *et al.* 1982). This simple scheme combines the known electrical responses of motoneurons with the varied mechanical responses of individual motor units to produce sharp force reversals: firing rates of small units with slow-twitch responses are reduced earlier than larger units with fast-twitch responses, effectively synchronizing the mechanical relaxation of the entire motor-unit population.

Since the subjects were provided with visual feed-back, the question arises as to whether this apparent mechanism is visually controlled. Fortunately, the fastest of these contractions (40% m.v.c./sec) were at a rate beyond a subject's capability for visual tracking, necessitating a pre-programmed response. A linear relationship between firing-rate reversal lead and recruitment threshold was found in the deltoid during such rapid contractions (correlation co-efficient = 0.81).

Shifts toward lower recruitment thresholds observed in Fig. 6 at higher force rates may well be the result of the accelerated firing onset described by Budingen & Freund

(1976). Another possibility is an adjustment in the intensity of inhibition to reduce firing-rate reversal leads during faster contractions. Further work is needed to clarify which, if either, of these mechanisms is responsible for the consistent shift seen as force rate increases.

The results of this analysis have provided considerable support for the suggestion that simple mechanical behaviour of a muscle can be achieved through homogeneous inputs (common drive) to size-structured motoneurone pools. These conclusions were based primarily on experiments involving direct insertion of electrodes into motoneurons, a procedure difficult to perform on humans. With the further development of highly stable electrodes and improvements in existing recording methods, our decomposition technique promises to compensate partially for this handicap without sacrificing the advantages of human experimentation.

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