CONTROL PROPERTIES OF MOTOR UNITS

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SUMMARY

This review will deal with two evolving concepts which describe and attempt to unify various observations concerning the behaviour of motor units that have been reported during the past decade. The two concepts are: (1) The common drive which describes the behaviour of the firing rates of motor units, and appears to provide a simple schema for controlling motor units; and (2) the firing rate/recruitment interaction which appears to enhance the smoothness of the force output of a muscle.

The evolution of these concepts has been expedited by the development of recent techniques such as our decomposition technique which enables us accurately to decompose the myoelectric signal into the constituent motor unit action potential trains. For details refer to LeFever & De Luca (1982), Mambrito & De Luca (1983) and Mambrito & De Luca (1984).

THE CONCEPT OF THE COMMON DRIVE

To understand the strategy (or strategies) which the nervous system uses to control motor units for the purpose of generating and modulating the force of a muscle, two central questions arise. (1) Is there a strategy or are there rules which govern the process of motor unit recruitment? (2) Is there a strategy or are there rules which govern the behaviour of firing rates of active motor units? The first question has received considerable attention. Notable contributions have been made by Henneman and his colleagues. The second question has not engaged a comparable level of excitement, possibly due to the technical complexity of the experiments necessary to address it.

To address properly the question concerning the behaviour of the firing rate it is necessary to observe it as a function of time and force of contraction. Occasional reports in the literature provide the beginning of an indication of firing rate as a function of force. Several reports (Leifer, 1969; Person & Kudina, 1972; Milner-Brown, Stein & Yemm, 1973; Tanji & Kato, 1973a,b; Monster & Chan, 1977; Monster, 1979; Kanosue, Yoshida, Akazawa & Fujii, 1979) have all demonstrated that the firing rates of active motor units increase proportionally with increasing force output. This implies that increased excitation to the muscle motoneurone pool increases the firing rates of all the active motor units.

Key words: Motor unit, firing rate, recruitment.

This commonality in the behaviour of the firing rates was studied in detail by De Luca, LeFever, McCue & Xenakis (1982*b*). We observed the behaviour of the firing rates of up to eight concurrently active motor units in the first dorsal interosseous and deltoid muscles during various types of isometric contractions: attempted constant force, linear force increasing and force reversals. Since that study, we have performed similar investigations on the flexor pollicis longus, extensor pollicis longus, tibialis anterior, extensor carpi ulnaris and extensor carpi radialis longus.

The studies of De Luca *et al.* (1982*a*,*b*) described a unison behaviour of the firing rates of motor units, both as a function of time and force. This property has been termed the *common drive*. Its existence indicates that the nervous system does not control the firing rates of motor units individually. Instead, it acts on the pool of the homonymous motoneurones in a uniform fashion. Thus, a demand for modulation of the force output of a muscle may be represented as a modulation of the excitation and/or inhibition on the motoneurone pool. This is the same concept which comfortably explains the recruitment of motor units according to the size principle.

The presence of the common drive provides an avenue for studying the commonality of different muscles involved in a task. Fig. 1A provides an example of the behaviour of the firing rates of four motor units during an attempted constant-force contraction of the deltoid muscle. The firing rates have been filtered with a 400-ms Hanning window. Note the common behaviour of the fluctuations of all the firing rates. This commonality becomes more apparent in Fig. 1B, which presents the cross-correlations of the firing rates. The high correlation values and the lack of any appreciable time shift with respect to each correlation function indicates that the modulations in the firing rates occur essentially simultaneously and by similar amounts in each motor unit. If the firing rates of the motor units are cross-correlated with the force output of the muscle, an appreciably high cross-correlation is also evident (Fig. 1C). The peaks of the cross-correlation functions occur at a time corresponding to the time delays of the force built up after excitation in the muscle fibres. This testifies to the fact that the fluctuations in the force output are causally related to the fluctuations in the firing rates.

The high level of cross-correlation between the firing rates and the force output (Fig. 1C) points strongly to the fact that a muscle is incapable of generating a pure constant-force contraction under isometric conditions. The fluctuations in force which are ever present during attempted constant-force contractions are a manifestation of the low-frequency oscillations which are inherent in the firing rates of motor units. The dominant frequency of this oscillation is approximately 1·5 Hz. The source of this oscillation has not been identified. However, it is interesting to note that the transfer function of the stimulation frequency and mechanical output of a nerve-muscle unit is a low-pass filter having a 3-dB point at approximately 1–2 Hz. This observation has been made by several investigators using a variety of paradigms (Crochetiere, Vodovnik & Reswick, 1967; Coggshall & Bekey, 1970; Gottlieb & Agarwall, 1971; Soechting & Roberts, 1975; Solomonow & Scopp, 1983). Therefore, it would be functionally useful to 'drive' the muscle near the 'critical' frequency of the muscle contractile characteristics. In this fashion, the 'drive' to the muscle is

continuously poised to affect changes in the force output in the shortest period of time without any overshoot (errors).

Similar behaviour is seen during force-increasing and force-decreasing contractions (Fig. 2). In this case, the firing rate fluctuations are superimposed on a 'bias' firing rate value. This bias value displays the common and proportional association with force output which has been documented by several investigators. That is, as an increase in the force output of a muscle is required, all the active motor units increase their firing rates proportionally. Given that the initial (or minimal) firing rates of motor units at recruitment are quite similar, it follows that the higher force-threshold, faster-twitch motor units will always have lower firing rates than their lower force-threshold, slower-twitch counterparts. This arrangement indicates a peculiarity of motor unit control during voluntary contractions. That is, the firing rate behaviour is not
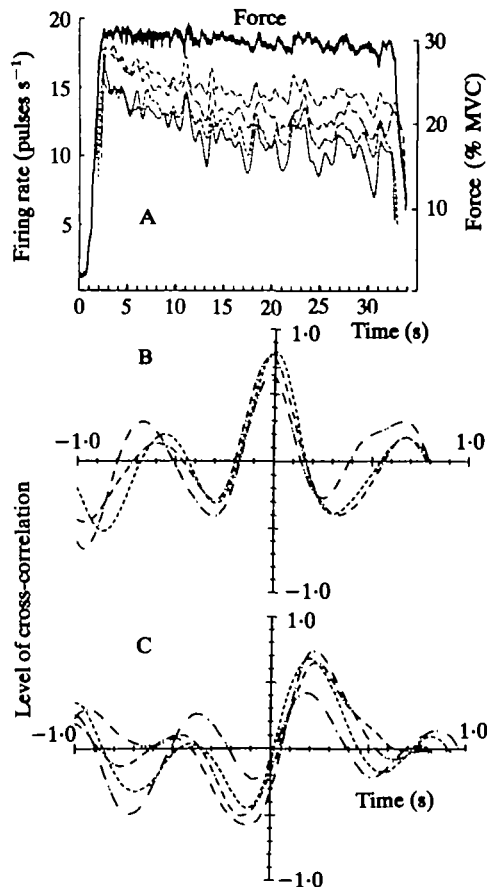

Fig. 1. (A) Firing-rate records of four concurrently active motor units (dashed lines) are shown superimposed on the force output (continuous line) recorded during a constant-force isometric abduction of the deltoid muscle. The force level is given as percentage of maximal voluntary contraction (MVC) on the 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.

complimentary to the mechanical properties of the motor units. Higher threshold motor units tend to have shorter contraction times and twitch durations, and thus require higher firing rates to produce fused contractions. De Luca *et al.* (1982*a*) calculated that in some cases, the faster-twitch motor units never achieved a fused contraction during voluntary effort. This behaviour provides a basis for the concept that in man, the full force generation potential of the muscle fibres may not normally be utilized during voluntary contractions. Conceivably, it may be held in abeyance for occasional dramatic displays of force.

The examples in Figs 1 and 2 are representative of observations seen in the firing rates of motor units in all the upper and lower limb muscles investigated to date. It has been seen in relatively small and relatively large muscles; in motor units of slow-twitch and fast-twitch fibres. The reader interested in quantitative assessments is referred to De Luca *et al.* (1982*b*).

The *common drive* has also been observed to exist in an agonist–antagonist set of muscles simultaneously. In one of our recently completed studies involving the flexor
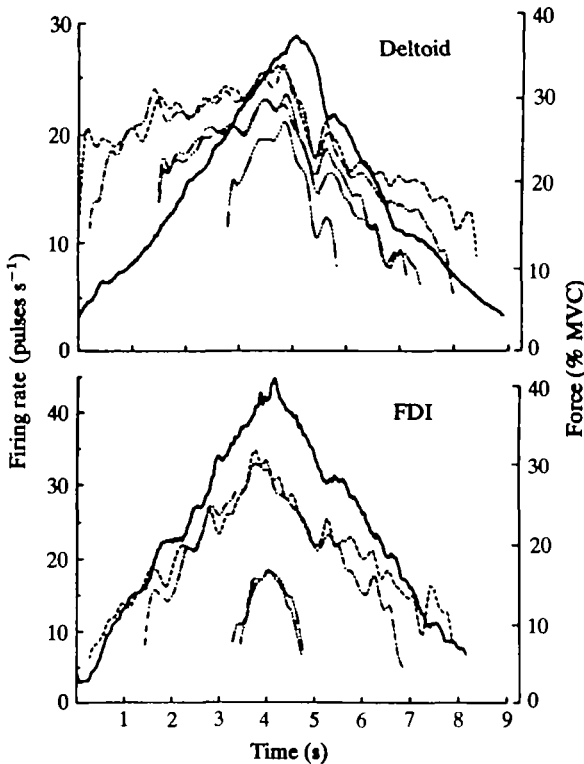

Fig. 2. Firing-rate records of concurrently active motor units (dashed lines) are shown superimposed on the force output (continuous line) recorded during triangular force-varying isometric contractions of the deltoid and first dorsal interosseous (FDI) muscles. Force levels are given in percentage of maximal voluntary contraction (MVC) on the 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 % MVC). Note the presence of separate vertical scales for each of the displayed parameters. Firing rate and force values are related through the time axis.

pollicis longus and the extensor pollicis longus, the sole controllers of the inter-phalangeal joint of the thumb, De Luca and colleagues have noted the *common drive* in both muscles. During voluntary stiffening of the inter-phalangeal joint, the firing rates of motor units in the two muscles were highly correlated with essentially no time shift. An example of this behaviour is provided by Fig. 3. Note that although the force or torque output is approximately zero, the *common drive* exists and is evident even among motor units of the two muscles. This particular example points to the necessity of associating the behaviour of the motor unit control to the effect on the motoneurone pool rather than on the output of the joint. The same study also indicated that during random flexion-extension isometric contractions of the inter-phalangeal joint, the firing rates of the antagonist motor units were negatively highly cross-correlated. This implies the existence of an ordered modulation of the firing rates of motor units in the two muscles; when the firing rate increased in one it decreased in the other and *vice versa*.

These observations of the *common drive* indicate that when two antagonist muscles are activated simultaneously to stiffen a joint, the nervous system views them as one unit and controls them in like fashion. In this case, the homonymous motoneurone pool consists of the motoneurone pools of both muscles. However, when the force output of the joint alternates from flexion to extension or *vice versa*, the two pools are
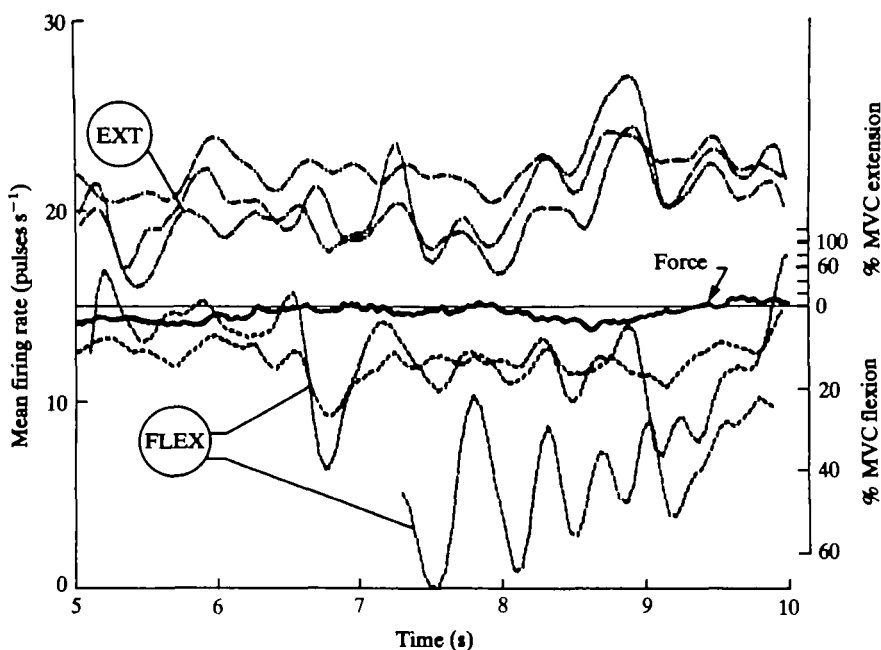
Fig. 3. Example of motor unit firing rate behaviour during thumb phalangeal joint stiffening. Force line denotes the force (or torque) output from the joint; the FLEX lines represent the firing rates of motor units in the flexor pollicis longus; the EXT lines represent the firing rates of motor units in the extensor pollicis. These two muscles are the sole controllers of the joint. MVC, maximal voluntary contraction.

controlled reciprocally with one being inhibited or disfacilitated while the other is excited.

At this point, a cautionary note is in order. The presence of the high level of cross-correlation in the firing rate cannot be interpreted as evidence of motor unit discharge synchronization. It simply means that the average pulses per epoch of time discharged by one motor unit behave similarly to those of all the other active motor units in the same epoch of time. It is, therefore, an indication of the control of motor units over a larger time scale than that which affects the properties of synchronization that relate to individual discharges of motor units.

If the same data is studied by analysing the cross-correlation function of the interpulse intervals of pairs of motor unit action potential trains (one from each muscle) no evidence of consistent synchronization is seen.

Firing rate at force reversal

The concept of the *common drive* raises a concern over the control scheme necessary to increase the force output to a precise value and then decrease the force, as would be the case in the execution of an accurate triangular force trajectory required in a skilled task. If the firing rates of all the motor units (slow-twitch and fast-twitch) are modulated simultaneously, how is an accurate force value generated prior to a force reversal when the contraction times of the different motor units (or muscle fibres) vary from 30 to 150 ms? This question is answered by the data in Fig. 2. Note that the earlier recruited (slower-twitch, longer contraction time) motor units decrease their firing rates *before* the later recruited (faster-twitch, shorter contraction time) motor units. Clearer and more detailed examples of this phenomenon may be found in De Luca *et al.* (1982*b*). This magnificent orchestration of firing rate reversals apparently considers the mechanical properties of the motor units so as to synchronize their contribution to obtain an accurate force output.

The ordered firing rate reversals cannot be explained by differences in axonal conduction velocities. In fact, the conduction velocity gradation is organized in the opposite direction to that required. One explanation for this behaviour would be that the nervous system keeps track of the particular mechanical response of each motor unit and delays the firing rate of each motor unit by an appropriate amount. Such an explanation is inconsistent with the *common drive* which is in effect during other force generation modalities. In addition, it would require a tremendous amount of processing in the central nervous system. It is indeed highly unlikely in the light of other possibilities.

There remain two other possible explanations: a selective sensitivity to a reduction in excitation and/or a selective sensitivity to an increase in inhibition to the motoneurone pool. The possibility of the combined events is particularly attractive since experimental evidence obtained by Clamann, Gillies & Henneman (1974) suggests that interaction between excitation and inhibition processes might be expressed as simple algebraic values. Lusher, Ruenzel & Henneman (1979) have also demonstrated that in anaesthetized cats, inhibition apparently proceeds according to the size principle, with the smaller motoneurones being affected first.

The sequence of events 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 IPSPs are produced in smaller motoneurones, 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 augments the firing rate decrease. This simple scheme combines the known electrical responses of motoneurones 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.

Thus, the concept of the *common drive* is not violated because the excitation and inhibition act on the motoneurone pool without regard to the individual moto-neurones. The specific ordered response is a property of the motoneurone pool architecture and structure.

FIRING RATE AND RECRUITMENT INTERACTION
Interaction within a muscle

Considerable anatomical and functional coupling exists among the motor units within a muscle. This behaviour has been studied extensively in decerebrate animal preparations by providing foreign electrical and mechanical stimuli to sensory receptors in the muscle. The reader is referred to Binder *et al.* (1976), Binder, Kroin, Moore & Stuart (1977), Binder & Stuart (1980), Cameron *et al.* (1980) and Lucas & Binder (1984). Such an interaction was also found during voluntary contractions by Broman, De Luca & Mambrito (1985) and is displayed in Fig. 4. In this study it was found that when a motor unit is recruited during slow force increasing (1–2 % $MCV s^{-1}$) isometric contraction (MVC = maximal voluntary contraction), it was often observed that previously activated motor units were disfacilitated. This was noted as a *decrease* in the firing rates of previously activated motor units as the firing rate of the newly activated motor unit increased and the force output of the muscle increased. The decrease in the firing rate is accentuated when the new motor unit is recruited with a doublet (first two discharges within 10 ms). The phenomenon has been observed in several muscles (large and small) located in both the upper and lower limb.

This interaction between recruitment and firing rate may be explained by consider-ing the known behaviour of the stretch reflex and the Renshaw recurrent inhibition.

The following sequence of events would explain the phenomenon. As the muscle fibres of a newly recruited motor unit contract, they shorten. If these muscle fibres are located near a spindle, the spindle will slacken and the discharge of the Ia and II fibres will be reduced, thus decreasing the excitation to the homonymous motoneurone pool. The contracting muscle fibres will also apply tension to the Golgi organs, which will increase the discharge of the Ib fibres, thus producing an increase in the inhibition

to the homonymous motoneurone pool. Both effects will disfacilitate the pool and thus decrease the 'drive' to the active motoneurones which is noted as a decrease in the firing rates of the motor units.

The stretch reflex, however, fails to explain two aspects of the interaction: (1) the firing rate increase of the newly recruited motor unit and (2) the slowness of the decrease in the firing rates. Therefore, the involvement of an additional mechanism, complementing the stretch reflex feedback is proposed; that is, the Renshaw-cell-mediated recurrent inhibition. It has been shown that Renshaw cells can be activated by the discharge of a single motoneurone (Ross, Cleveland & Haase, 1975), and that Renshaw cells are more strongly excited by collaterals of large motoneurones than small ones (Ryall, Piercey, Polosa & Goldfarb, 1972; Pompeiano, Wand & Sontag, 1975). Consequently, if the Renshaw cell inhibitory action on the alpha-motoneurone pool is achieved in a size-related fashion (small diameter motoneurones being affected more than large diameter ones), this complementary mechanism could have the desired selective property of preferentially slowing down the motor units which are already active. That is, those having motoneurones with smaller diameter and are recruited earlier at lower force levels.

The compound effect of the inhibition provided by the Renshaw recurrent inhibition and the stretch reflex inhibition interacting with the common drive excitation on the motoneurone pool is represented schematically in Fig. 5. In this figure the thickness of the lines expresses the magnitude of the influence.
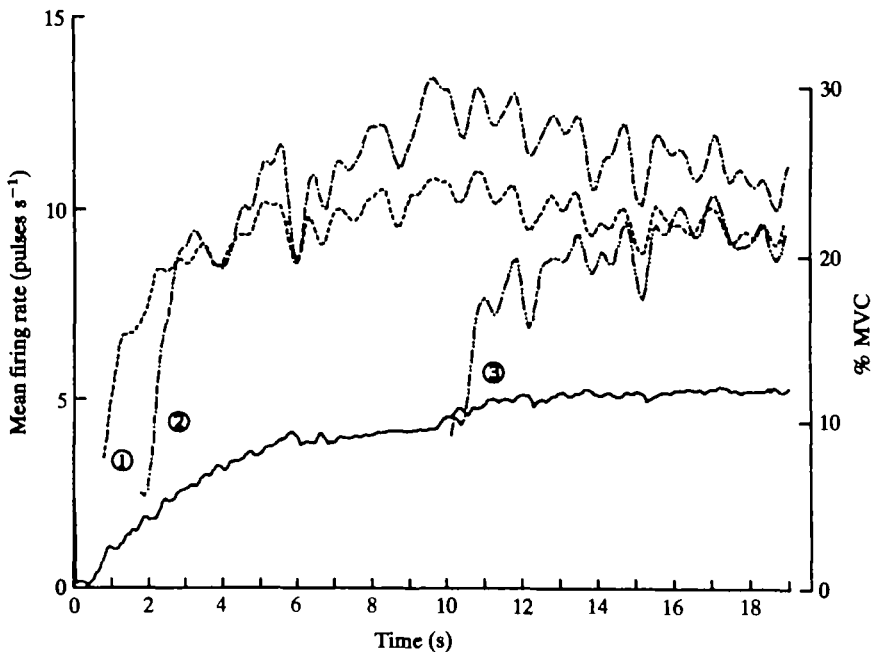

Fig. 4. Firing rates (broken lines) of three concurrently active motor units of the tibialis anterior muscle recorded during an isometric contraction. The force (solid line) is presented as a percentage of the maximal voluntary contraction (MVC) (right scale). Note the gradual decrease of the firing rates of the top two tracings as the third motor unit is recruited.

This interaction between recruitment and firing rate provides an apparently simple strategy for providing *smooth* force output. Upon recruitment of a new motor unit it may be desirable to produce an increase in muscle force which is less than the minimal incremental contribution of the new motor unit. One way to achieve this goal is to decrease the firing rates of the motor units which are already active, so as to diminish their contribution to the total force output when the new motor unit is recruited. Thus, compensatory decreases of the firing rates of previously activated motor units will enable the muscle to produce a smoother force output during recruitment. This effect becomes more important as the newly recruited motor units provide an increasingly stronger twitch contribution. Thus, in general, motor units recruited later should have a stronger effect on the firing rates of previously-activated motor units, as may be noted in Fig. 5.

Interaction in different muscles

The weight of the evidence from several recent studies suggests that small muscles, such as those in the hand, are controlled by different firing rate-recruitment schemes

- = Disfacilitation   S = Stretch reflex

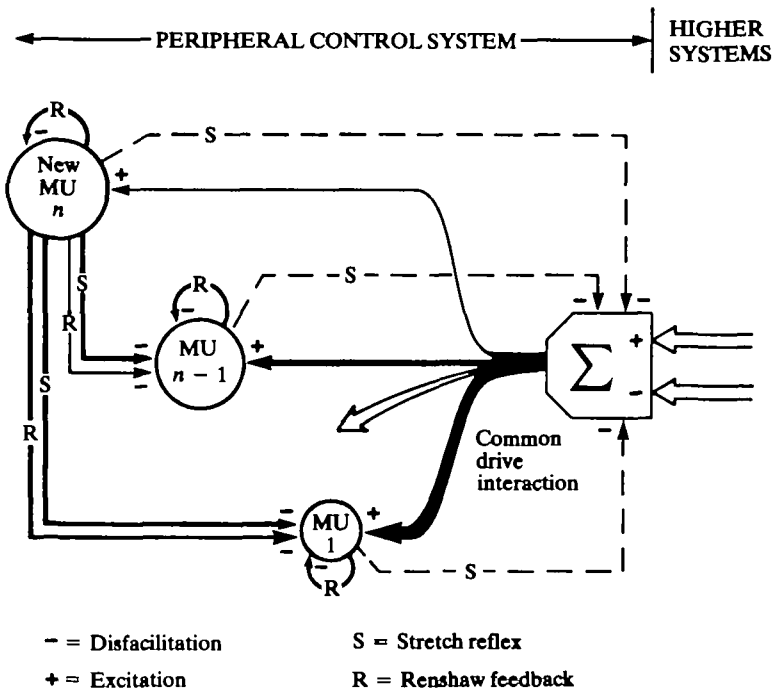+ = Excitation   R = Renshaw feedback

Fig. 5. Schematic diagram describing the concept of the common drive and phenomenon of recruitment/firing rate interaction during a voluntary contraction. In this representation the excitatory and inhibitory inputs from sources other than the peripheral control system are shown to act on the motoneurone pool as a unit. The increase or decrease in the excitation (+) to each motoneurone has a common origin and is interdependent. The thickness of the line indicates the sensitivity to a change in the state of excitation or inhibition for each motoneurone. The size of the motoneurone (or motor unit, MU) is represented by the size of the circles. Motor unit 1 is the first recruited and motor unit *n* is the last recruited. The stretch reflex inhibition (−) is represented by the connection S, and the recurrent inhibition by R (Renshaw feedback).

than larger muscles, such as those in the leg or arm. Smaller muscles recruit their motor units within 0–50 % MVC and rely exclusively on firing rate increase to augment the force output between 50–100 % MVC (De Luca *et al.* 1982*a*; Kukulka & Clamann, 1981; Milner-Brown *et al.* 1973). The firing rates of these muscles continuously increase with the force output, reaching values as high as 60 pulses s^{-1}. Larger muscles recruit motor units at least to 90 % MVC, and possibly higher. Their firing rates have a relatively smaller dynamic swing, generally peak at 35–40 pulses s^{-1} and tend to demonstrate a plateauing effect (De Luca *et al.* 1982*a*; Kanosue *et al.* 1979; Grimby & Hannerz, 1977; and others). Thus, smaller muscles rely primarily on firing rate and larger muscles rely primarily on recruitment to modulate their force. A comparison of these two properties for the first dorsal interosseous and deltoid muscles is provided in Table 1.

The inhibitory interaction between recruitment and firing rate described above may, in fact, explain the different behaviour of the firing rates in muscles with notably different recruitment schemes. A newly recruited motor unit would decrease the firing rate of the motor units which are already active, and the global effect would be to prevent large firing rate increases as long as recruitment occurs. This is consistent with the relatively high increases in firing rate observed above 70 % MVC in the brachialis muscle (Kanosue *et al.* 1979) and above 50 % MVC in the first dorsal interosseous (De Luca *et al.* 1982*a*) when recruitment is absent or scarce.

The explanation of the need for these contrasting force generation mechanisms may be found by considering the anatomy and function of the muscles. In the human body, smaller muscles are generally involved in performing accurate movements; such movements require small incremental changes in force. In contrast, large muscles are generally involved in either producing large forces or in controlling posture.

Small anatomically confined muscles have relatively few motor units; for example, the first dorsal interosseous contains approximately 120 (Feinstein, Lindegard, Nyman & Wohlfart, 1955). When a new motor unit is activated, the average quantal force increase would be 0·8 %. If recruitment were the only (or even principal) means by which additional force were developed, small muscles would have limited capability for producing a smoothly increasing contraction. As force increases, the orderly addition of larger motor units would produce a 'staircase' effect in the force

Table 1. *Firing rate statistics of motor units from a small and large muscle*

Muscle	Recruitment rate (pulses s^{-1})	Decruitment rate (pulses s^{-1})	Peak rate at 40 % MVC (pulses s^{-1})	Peak rate at 80 % MVC (pulses s^{-1})
First dorsal interosseus	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. MVC, maximal voluntary contraction.

output. Yet, generally the function of small muscles is to produce small, accurate movements requiring fine force-gradations. By recruiting its motor units during the first 50 % MVC, the average quantum of force augmented by the activation of a new motor unit is one-half the value which would have been increased if the recruitment range extended to 100 % MVC. The force above the 50 % MVC is generated by the highly dynamic firing rates of motor units in small muscles. As a secondary contribution, the highly dynamic firing rates also assist in smoothing the 'staircase' effect.

Large muscles have many more motor units; for example, the biceps brachii contains approximately 770 (Christensen, 1959). Thus, by setting the recruitment to span the full range of force generation, the activation of a new motor unit would provide an average quantal increase of 0·12 %. Large muscles generally do not require finer force gradation to accomplish their task. Thus, the firing rates of such muscles do not require continual regulation and do not possess the highly dynamic characteristics seen in smaller muscles.

This interpretation is consistent with the notion that recruitment is the more basic mode of force generation. The behaviour of the firing rate is to some extent moulded by the performance required from the muscle and the number of motor units which comprise the muscle. It appears that the nervous system is constructed to 'balance' the contribution of firing rate control and recruitment control, so as to enhance the *smoothness* of the force output of the muscle.

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