

CHAPTER 8

Control properties of motor units

Evolving concepts

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INTRODUCTION

This review deals with two evolving concepts which describe and attempt to unify various observations concerning the behavior of motor units that has been reported during the past decade. The two concepts are: (1) the *common drive* which describes the behavior 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 to accurately decompose the myoelectric signal into the constituent motor unit action potential trains. For details refer to LeFever and De Luca (1982), Mambrito and De Luca (1983, 1984).

To understand the strategies which the nervous system uses to control motor units for the purpose of generating and modulating the force of a muscle, three 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 behavior of firing rates of active motor units? (3) Is there any interaction between recruitment threshold and firing rate? The first question has received considerable attention (Henneman et al., 1965, 1974; Desmedt and Godaux, 1977a,b, 1978a,b). The other two questions have been less well documented, possibly due

to the technical complexity of the experimental approach to them.

THE CONCEPT OF THE COMMON DRIVE

To address properly the question concerning the behavior of the firing rate it is necessary to observe it as a function of time and force of contraction. Several reports (Leifer, 1969; Person and Kudina, 1972; Milner-Brown et al., 1973; Tanji and Kato, 1973a,b; Monster and Chan, 1977; Kanosue et al., 1979; Monster, 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 motoneuron pool increases the firing rates of all the active motor units.

This commonality in the behavior of the firing rates was studied in detail by De Luca et al. (1982b). We observed the behavior 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. Also, the firing rates of 11 consecutively active motor units have been studied in more recent works.

The studies of De Luca et al. (1982a,b) described a unison behavior 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 motoneurons 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 motoneuron pool. This is the same concept which comfortably explains the recruitment of motor units according to the size principle. Since our initial report, other independent reports of the common drive have been published (Stashuk, 1985; Nordstrom et al., 1986; Stashuk and De Bruin, 1988).

Fig. 1A provides an example of the behavior 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 behavior 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 in 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 fibers. 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-

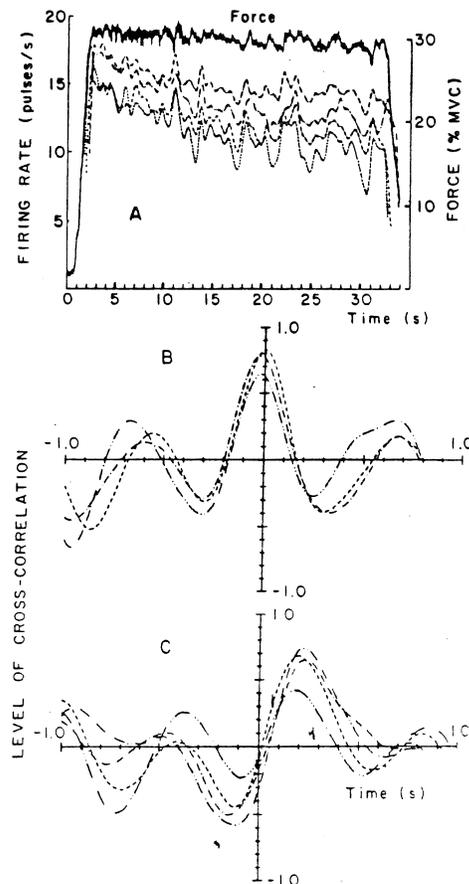


Fig. 1. A: firing rate records of four concurrently active motor units (dash lines) are shown superimposed on the force output (continuous line) recorded during a constant-force isometric abduction of the deltoid. The force level is given in percent of maximal voluntary contraction (MVC) at right. B: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

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 yet. But, 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. The observation has been made by several investigators using a variety of paradigms (Crochetiere et al., 1967; Cogshall and Bekey, 1970; Gottlieb and Agarwal, 1971; Soechting and Roberts, 1975; Solomonow and 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 behavior is seen during force-increasing and force-decreasing contractions (Fig. 2). In this

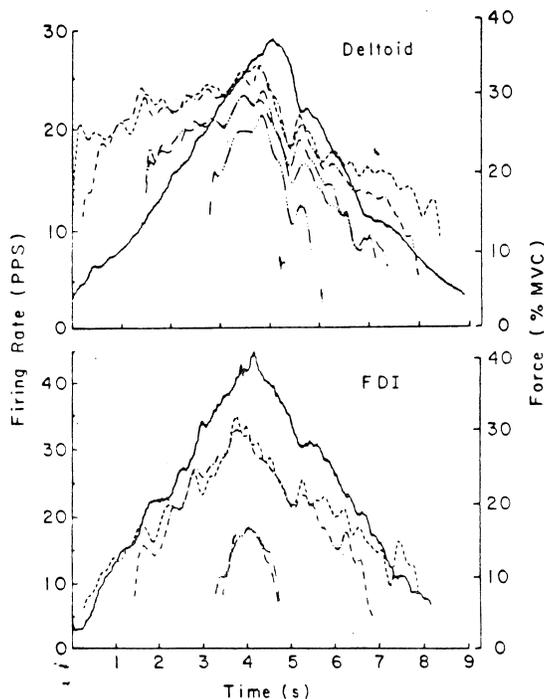


Fig. 2. Firing rate records of concurrently active motor units (dash lines) are shown superimposed on the force output (continuous line) recorded during triangular force-varying contractions of the deltoid and first dorsal interosseous (FDI). Force levels are given in percent of maximal voluntary contraction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

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 the lower force-threshold, slower-twitch counterparts. Recently this behavior has also been observed in the human masseter muscle by Miles and Turker (1987). This arrangement indicates a peculiarity of motor unit control during voluntary contractions. That is, the firing rate behavior is not complementary 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. (1982a) calculated that in some cases the faster-twitch motor units never achieved a fused contraction during voluntary effort. This behavior provides a basis for the concept that in man, the full force generation potential of the muscle fibers may not normally be utilized during voluntary contractions. Conceivably, it may be held in abeyance for occasional dramatic displays of force. The relatively lower firing rates of the fast fatiguing motor units provide for the precautionary employment of these motor units, making them able to sustain their force generating ability longer.

The examples of 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 and in motor units of slow-twitch and fast-twitch fibers. The reader interested in quantitative assessments is referred to De Luca et al. (1982b).

The *common drive* has also been observed in an agonist-antagonist set of muscles simultaneously. In a recent study involving the flexor pollicis

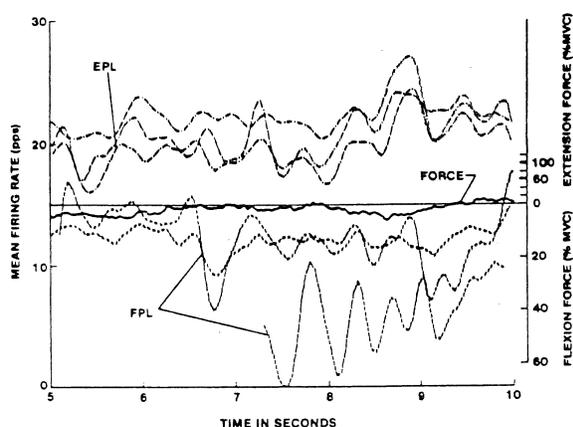


Fig. 3. Example of motor unit firing rate behavior during thumb phalangeal joint stiffening. FORCE line denotes the force (or torque) output from the joint; the FPL lines represent the firing rates of motor units in the flexor pollicis longus; the EPL lines represent the firing rates of motor units in the extensor pollicis. These two muscles are the sole controllers of the joint.

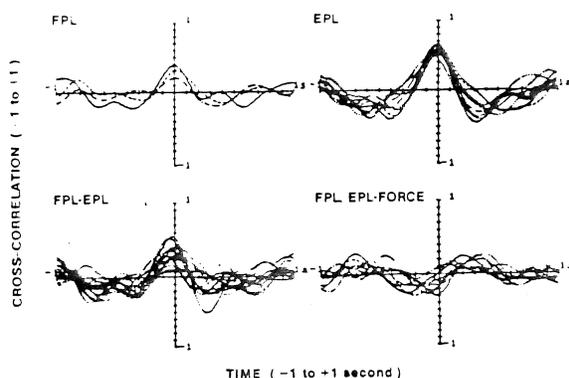


Fig. 4. Examples of cross-correlation functions of the firing rates of the motor units during coactivation (joint stiffening) within the flexor pollicis longus (FPL), within the extensor pollicis longus (EPL), between the motor units in both muscles, and between the firing rates of flexor motor units and force and the firing rates of extensor motor units and force. Note that the cross-correlation functions of the firing rates peak at approximately *time zero*, indicating that there is essentially zero time shift between the fluctuations in each of the firing rates. That is, the fluctuations are produced simultaneously. This behavior has been called *common drive*.

longus and the extensor pollicis longus, the sole controllers of the inter-phalangeal joint of the thumb, De Luca and Mambrito (1987) 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 behavior is provided by Fig. 3. Cross-correlation functions of firing rates between motor unit pairs and cross-correlation functions of firing rates and force are presented in Fig. 4. In that study, a total of 121 cross-correlation functions were calculated. The accumulated maximal values of the cross-correlation functions of the firing rates within the extensor pollicis longus, within the flexor pollicis longus, and between the extensor pollicis longus and flexor pollicis longus muscles are represented in the histograms of Fig. 5. 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 behavior of the motor unit control to the effect on the motoneuron pool rather than on the output of the joint. The same study also reported 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;

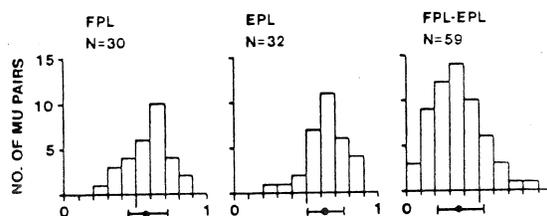


Fig. 5. Histograms of the cross-correlation maximal values (at time 0 ± 10 ms) among firing rates during the coactivation contractions of the thumb phalangeal joint: (left) among motor units in the flexor pollicis longus (FPL) muscle (0.58 ± 0.14); (middle) among motor units in the extensor pollicis longus (EPL) muscle (0.63 ± 0.14); and (right) between motor units from both muscles (0.37 ± 0.16).

when the firing rate increased in one it decreased in the other and vice versa.

There remains the concern that the cross-correlation observed in the flexor pollicis longus and the extensor pollicis longus may be partially due to the common origin of the major portion of their efferent nerve fibers, the C_8 root. The anatomical proximity of the two motoneuron pools might facilitate the interaction of the firing rates. To dispel this concern, Kamen and De Luca studied the right and left tibialis anterior muscles which were simultaneously coactivated isometrically at 30% maximal voluntary level (MVC). The cross-correlation of the firing rates of the motor units between the two muscles is presented in Fig. 6A. In this case, the motoneuron pools do not share physical proximity. Similar experiments by

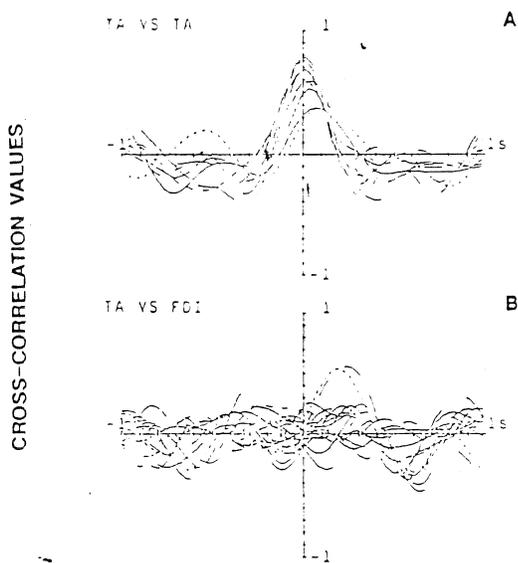


Fig. 6. A: cross-correlation functions of motor unit firing rates from right and left tibialis anterior (TA) muscles. Both muscles were simultaneously performing a 30% maximal level isometric dorsiflexion contraction. Note the considerable cross-correlation at or near zero time. B: cross-correlation function of motor unit firing rates from the right tibialis anterior (TA) muscle and the right first dorsal interosseous (FDI) muscle. Both muscles were simultaneously performing a 30% maximal level isometric contraction. The FDI was attempting abduction and the TA dorsiflexion. Note the lack of cross-correlation among the firing rates.

Kamen, Solar and De Luca involving the ipsilateral first dorsal interosseous and tibialis anterior muscles showed no evidence of cross-correlation of the motor unit firing rates in four subjects. An example is presented in Fig. 6B.

Within one muscle, existence of *common drive* could be partially explained by the widespread homogeneous influence of the stretch reflex mechanism, especially the arborization of the Ia fibers (Luscher et al., 1984). However, the reciprocal arrangement of the Ia and Ib fibers with the alpha motoneuron fibers of antagonist muscles does not favor formation of zero-time shift firing rate fluctuations between the motoneuron pools of the two muscles. This concept is supported by the data of Fig. 5, which show that during coactivation, the average value of the maximal cross-correlation of the firing rates of motor units among antagonist muscles is significantly ($P < 0.0001$) lower, approximately 60% that of the motor units in the individual muscles.

The existence of the *common drive* among the antagonist muscle set during co-activation may be used to argue for a functional association or mechanical linkage between the muscles. Their cross muscle behavior was investigated further by cross-correlating the firing rates of motor units in the right and left first dorsal interosseous muscle when they were contracting in a mechanically coupled fashion (the two index fingers abducting against each other) and when they were not in contact. The *common drive* was seen only when the index fingers were in contact. This latter observation argues for the need for a mechanical linkage between two muscles for the *common drive* to exist. However, another set of experiments performed on simultaneously dorsiflexing but not touching tibialis anterior right and left muscles did show *common drive*. In this case, the *common drive* cannot be attributed to mechanical coupling, and is most likely due to tightly coupled spinal connectives which are more prevalent in lower limbs than in upper limbs.

The notion that the *common drive* may be, at least in part, of central origin is supported by the

observations of Fetz and Cheney (1980) and Cheney and Mewes (1986). They reported the existence of corticomotoneuronal cells in the premotor cortex and rubromotoneuronal cells whose activity was noted to be correlated to motor unit action potentials in groups of simultaneously active muscles in the forearm of primates executing coordinated volitional contractions. Their results suggest that individual cortical cells have a connection to motor units in separate muscles. Such an arrangement could be exploited as a mechanism for imparting the *common drive*. However, more direct proof is required for a convincing argument.

The role of suprasegmental versus segmental sources for the *common drive* remains to be clarified.

The common drive is not due to synchronization

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 synchronization of motor unit discharges were studied by cross-correlating the interpulse intervals directly, synchronization may or may not be seen. A study currently in progress in our Center is beginning to show that synchronization of discharges occurs sporadically during a substantial contraction. The reader is referred to a previous chapter by Stashuk and De Luca for an example of discharge synchronization. The fact that the firing rates of motor units calculated over a window of 400 ms, or approximately 6–8 pulses, are cross-correlated, while the pulse-to-pulse discharge does not necessarily show any evidence of synchronization implies, that the nervous system transmits information through groupings of discharge rather than by individual discharges. In fact, studies in-

volving only the analysis of individual discharges may reveal more about the connections of the neurons rather than the information transmitted through them.

These observations suggest that the anterior horn in the spinal cord behaves as a low-pass filter which demodulates the low-frequency from the discrete discharges of the numerous neural inputs that converge upon it. It is this low-frequency (1–2 Hz) information in the firing rates which modulates the force output of the muscle. The muscle fibers cannot respond mechanically to the individual discharges. Thus, it follows that the low-pass operation performed to calculate the firing rates reveals behavioral information, such as the *common drive*, of the motoneuron discharges.

Firing rate at force reversal

The concept of *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 fibers) 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. (1982b). 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 behavior 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 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 motoneuron pool. The possibility of the combined events is particularly attractive since experimental evidence obtained by Clamann et al. (1974) suggests that interaction between excitation and inhibition processes might be expressed as simple algebraic values. Luscher et al. (1979) have also observed that in anesthetized cats, inhibition apparently proceeds according to the size principle, with the smaller motoneurons 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 motoneuron pool which competes with the increasing excitatory input in progress. Larger IPSPs 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 augments the firing rate decrease. 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.

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

Properties of the common drive

In general, during isometric contraction, the concept of the *common drive* embodies the following behavioral properties:

- (1) the average firing rates of all motor units are modulated simultaneously, or with a relative delay of a few milliseconds;
- (2) the average firing rates of motor units vary in proportion to the net excitation present in the motoneuron pool, with the earlier recruited motor units having greater average firing rates than the latter recruited motor units;
- (3) during force diminution, the earlier-recruited faster-firing motor units decrease their average firing rate before the later-recruited slower-firing motor units; this behavior complements the mechanical properties and provides a control strategy which enables all the motor units to provide their force contribution effectively;
- (4) the modulation of the average firing rates of the motor units causes a modulation in the force output of a muscle; consequently, the force cannot be strictly isometric;
- (5) the unison behavior of the average firing rates of motor units may exist among the motor units of functionally linked muscles.

FIRING RATE AND RECRUITMENT INTERACTION

Interaction within a muscle

Considerable anatomical and functional coupling exists among the motor units within a muscle. This behavior 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. (1977), Binder and Stuart (1980), Cameron et al. (1980), Lucas and Binder (1984). Such an interaction was also found during voluntary contractions by Broman, De Luca and Mambrito and is displayed in Fig. 7. In this study it was found that when a motor unit is recruited during slow force

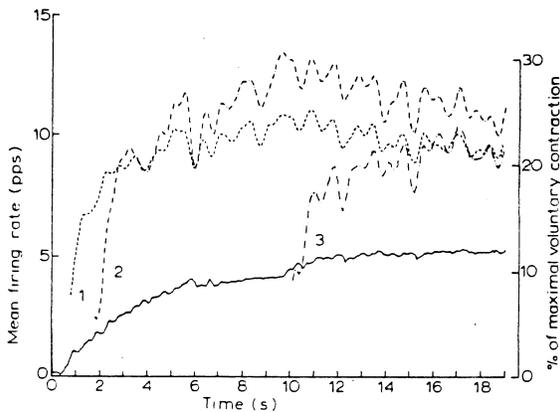


Fig. 7. Firing rates (broken lines) of three concurrently active motor units of the tibialis anterior muscle recorded during an isometric contraction. The force (solid line) is presented as a percentage of the maximal voluntary contraction (right scale). Note the gradual decrease of the firing rates of the top two tracings as the third motor unit is recruited.

increasing (1–2% MVC/s) isometric 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 considering the known behavior of the stretch reflex and the Renshaw recurrent inhibition.

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

of the Ib fibers; thus producing an increase in the inhibition to the homonymous motoneuron pool. Both effects will disfacilitate the pool and thus decrease the 'drive' to the active motoneurons 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, complimenting 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 motoneuron (Ross et al., 1975), and that Renshaw cells are more strongly excited by collaterals of large motoneurons than small ones (Ryall et al., 1972; Pompeiano et al., 1975). Consequently, if the Renshaw cell inhibitory action on the alpha motoneuron pool is achieved in a size-related fashion (small diameter motoneuron 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 motoneurons with smaller diameter and are recruited earlier and at a lower force level.

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 motoneuron pool is represented schematically in Fig. 5. In this figure the thickness of the lines expresses the magnitude of the influence.

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 more smooth 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.

A second example of interaction between recruitment and firing rate of the motor units can be found in the work of De Luca et al. (1987). In this work (in progress) the behavior of the motor units in the first dorsal interosseous muscle were studied before and after a topical anesthetic (10% xylocaine) was applied to the skin over the hand and

wrist. The recruitment force threshold and the firing rate values of the motor units were studied during a ramp and constant force contraction. The results of one experiment are presented in Fig. 8. In this figure, the time scale expresses the amount of time elapsed since the application of the anesthetic. The force threshold of motor units recruited below 20% MVC increased while their average firing rates (which are among the largest in value) decreased. On the contrary, the force threshold level of motor units recruited above 25% MVC decreased while their average firing rates (which were among the lowest in value) increased. In other words, the dynamic ranges of recruitment thresholds and firing rates became narrower after skin desensitization. Control studies (without application of anesthesia) revealed no significant change of the recruitment threshold or the average firing rates.

The interconnected compensatory relationship between recruitment threshold and firing rate is consistent with the behavior of the motor units that is observed during normal recruitment. That is, the motor units that are recruited at increasingly higher force levels have the increasingly lower firing rates (see Fig. 2). Apparently, the recruitment threshold and the firing rates are dependent, at least in the limb muscles that have been studied thus far.

The concepts of the *common drive* and firing rate/recruitment interaction are explained diagrammatically in Fig. 9. In this figure, the latest recruited motor unit (n) affects the performance of previously recruited motor units [$n-1$, $n-2$, . . . , 1] as specified by the wiring arrangements and gain settings of the stretch reflex and Renshaw cells. The *common drive* is presented as a process which is activated, but the accumulated excitatory and inhibitory effects of the anterior horn level. The motor units are increasingly sensitive to excitation or inhibition in the order of their recruitment [1, 2, . . . , $n-1$, n], but all the active motor units receive the net excitement or the net inhibition which accumulates at the anterior horn cell.

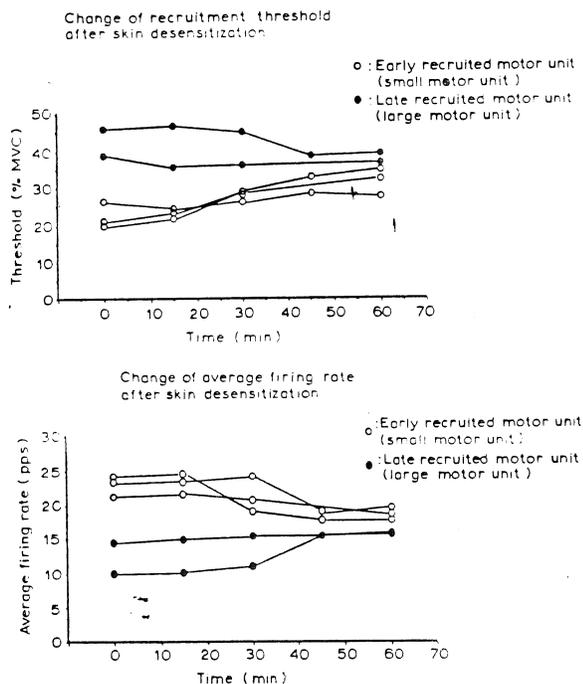


Fig. 8. The recruitment threshold and average firing rate value (at 50% MVC) of motor units from the first dorsal interosseous muscle. The time scale indicates the elapsed time since the skin of the corresponding hand and wrist were anesthetized with 10% xylocaine (topically applied). The contractions were isometric. The same motor units were identified in each contraction.

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 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 (Milner-Brown et al., 1973; Kukulka and Clamann, 1981; De Luca et al., 1982a). The firing rates of these muscles continuously increase with the force output reaching values as high as 60 pulses/s. 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, and tend to demonstrate a plateau effect (Desmedt and Godaux, 1977a,b, 1978; Grimby and Hannerz, 1977; Kanosue et al., 1979; De Luca et al., 1982a). 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 behavior 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., 1982a) when recruitment is absent or scarce.

The explanation for the need of these con-

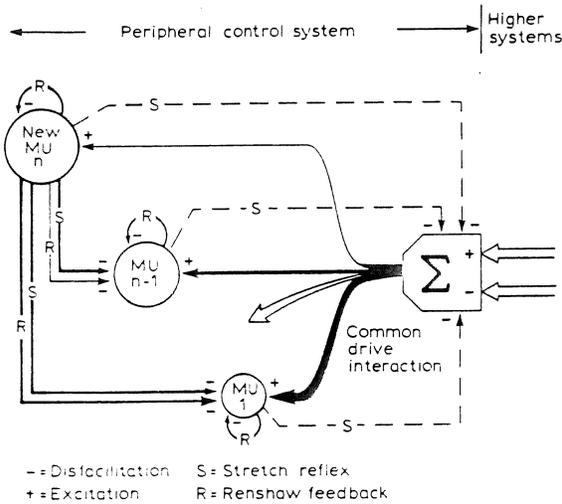


Fig. 9. Schematic diagram describing the concept of the common drive and phenomenon of recruitment/firing rate interaction during a voluntary contraction. In this representation the excitatory and inhibitory inputs from sources other than the peripheral control system are shown to act on the motoneuron pool as a unit. The increase or decrease in the excitation (+) to each motoneuron 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 motoneuron. The size of the motoneuron (or motor unit) 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.

TABLE 1

In each case the mean ± SD of an observation is listed, with the number of observations (*n*) in parentheses

| Muscle | Recruitment rate (pulses/s) | Derecruitment rate (pulses/s) | Peak rate at 40% MVC (pulses/s) | Peak rate at 80% MVC (pulses/s) |
|---------------------------|-----------------------------|-------------------------------|---------------------------------|---------------------------------|
| First dorsal interosseous | 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) |

trasting 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 et al., 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 be incapable of producing a smooth increasing contraction. As force increased, the orderly addition of larger motor units would produce a 'staircase' effect in the force 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 behavior of the firing rate is to some extent molded by the performance required from the muscle and the number of motor units which comprise the muscle. It appears that the nervous system is configured 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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