Hz), sampled, and compressed by eliminating parts of the signal

preset threshold level.

third section consists of a signal decomposition technique where action potential trains are extracted from the EMG signal highly computer-assisted interactive algorithm. The algorithm continuously updated template matching routine and firing statistics. MUAPs in the EMG signal. The templates of the MUAPs updated to enable the algorithm to function even when a specific MUAP undergoes slow variations.

section deals with ways of displaying the results. The more representation formats are:

MUAP waveshapes

representing motor unit firings

time intervals between successive firings of the same motor vs. time of the muscle contraction where the estimated time-varying mean firing rate of the is plotted vs. time of the muscle contraction firing rates which indicate the amount of common drive

functions which provide an indication of the amount of motor unit discharges

system has been tested in terms of:

obtained by different operators

EMG signal

by comparing results pertaining to the same signals which were independently and simultaneous electrodes

Control Properties of Motor Units

This chapter will deal with those properties of motor units which describe their recruitment and firing behavior during the process of force generation. These properties will be referred to as the *control properties*, because it is through these modes that the central and peripheral nervous systems affect the performance of a muscle or a group of muscles. Motor unit properties such as biochemical structure, twitch response, physical dimensions, etc. may be considered to be properties which specify the identity of the scheme(s) that the nervous system employs to involve (or possibly take advantage of) the different types of muscle fibers. These latter properties will not be addressed directly in this chapter.

Prior to embarking on a detailed description of the control properties of the motor units, it is useful to review the function and potential involvement of peripheral and central mechanisms.

THE PERIPHERAL CONTROL SYSTEM

There are a variety of apparently specialized receptors located in the muscles, tendons, fascia, and skin which provide information to appropriate parts of the central nervous system concerning the state of the force and length characteristics of muscles. A nonreceptor system, the Renshaw system, which resides completely in the anterior horn of the spinal cord will also be described in this section. Although according to the classical anatomical distinction of central and peripheral, the Renshaw system is physically located in the central nervous system. However, as will be seen later in this chapter, some aspects of the Renshaw system are intimately associated with the peripheral feedback mechanisms. Thus, from a control point of view it is advantageous to consider the performance of the Renshaw system in association with the peripheral nervous system. Together, they may be considered to form the output stage of the motor system, or the *peripheral control system*.

An overview of the interactions of the major components of the peripheral control system is presented schematically in Figure 5.1. For completeness, the suprasegmental and supraspinal input are also included in this figure. The representation in Figure 5.1 is purposely arranged to emphasize details of the peripheral control system which are reasonably well understood and accepted. The schematic representation is directed at presenting the behavioral characteristics of the peripheral control system rather than describing anatomical details. Thus, it should not be viewed as a wiring diagram, but rather as a block diagram.
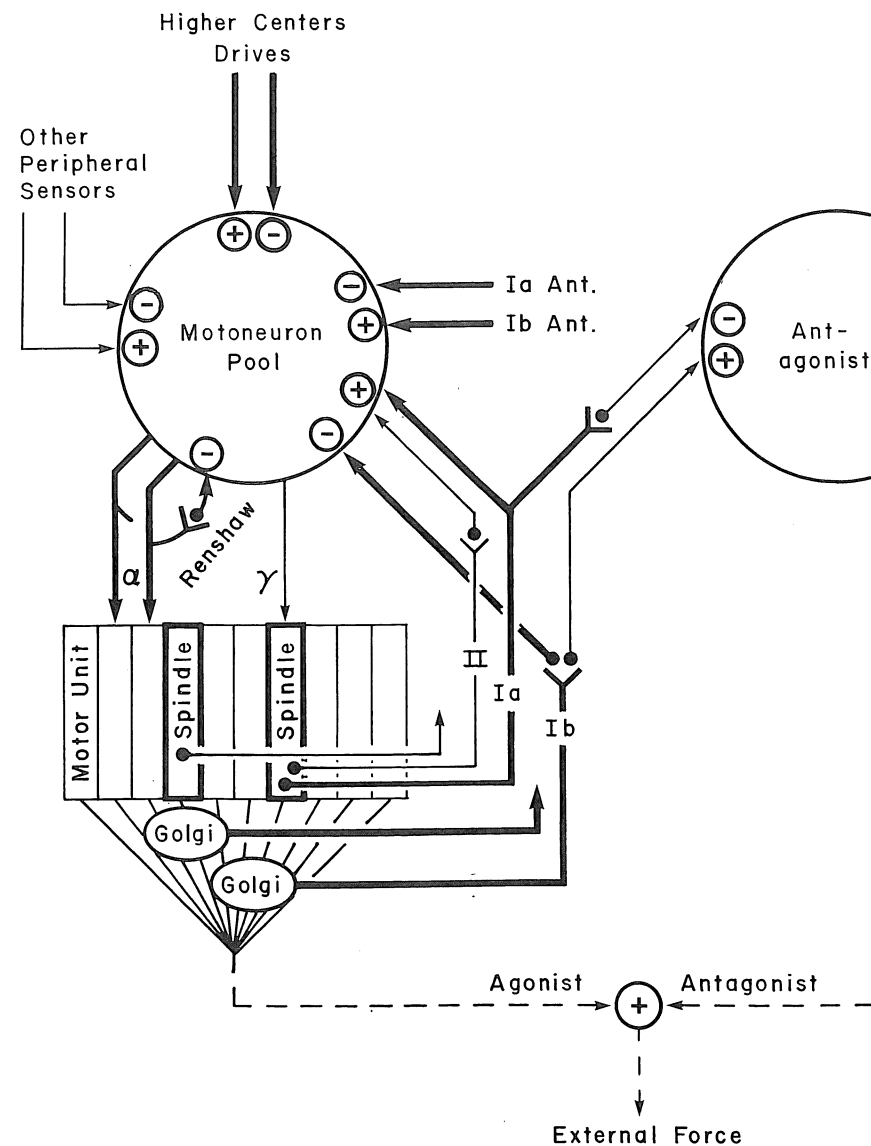
Figure 5.1. A simplified schematic representation of most of the components of the peripheral control system which interact with a muscle. The *arrows* and *signs* indicate excitatory (+) and inhibitory (−) actions on the pool. The *thickness* of the *lines* indicates the dominance of the contributions. The diagram is by no means complete but does contain the more dominant interactions. The *broken lines* represent force interactions. Note that when a spindle is slackened during a muscle contraction, the Ia and II afferent fiber discharge decreases, thus the effect on the motoneuron pool will be disfacilitatory and not excitatory as represented in this diagram.

Note that the concept of the peripheral control system evolves around an entity referred to as a motoneuron pool. This motoneuron pool may be thought of as an aggregate of interacting neurons, located in the anterior horn of the spinal cord, whose joint behavior is associated with the control of a function in either one muscle or a specific group of muscles. The output of the motoneuron pool consists of the (efferent) information transmitted down the α-motoneuron, γ-motoneuron and, possibly, β-motoneuron. The presence of the latter in man remains to be clearly established and, hence, it has not been included in the diagram. The input to the motoneuron pool consists of the (afferent) information from the peripheral receptors, the Renshaw system, and the drive from the higher centers. Note that all the inputs to the motoneuron pool are expressed as either having an excitation (+) or an inhibition (−). An excitatory contribution will increase either the disposition of an α- and γ-motoneuron to begin discharging (recruitment) or to increase its firing rate if it is already active. An inhibitory contribution has the opposite effect.

Let us now proceed to a description of the sensory systems. The forthcoming description is purposely brief. For more specific details the reader should refer to any of the numerous books dealing with mammalian muscle receptors, for example, the chapter Mammalian Muscle Receptors by Hasan and Stuart in *Handbook of the Spinal Cord* (1984).

The Muscle Spindle

The muscle spindle is by far the most studied muscle sensor organ. It is located within the body of the muscle. The spindle consists of a capsule having a fusiform shape, attached at both ends to muscle fibers. It is generally believed to be arranged in parallel with the adjacent muscle fibers. The architectural arrangement is apparently designed to favor the monitoring of muscle length and changes in length. Inside the spindle capsule are located "intrafusal" muscle fibers. These may number from 2 to 25. These fibers have contractile characteristics similar to those of the normal or "extrafusal" muscle fibers and are separable into three categories distinguished on the basis of the arrangement of the nuclei in the middle portion of the intrafusal fiber and, contrary to the depiction in most textbooks, not on the basis of their shape (Matthews, 1972). These fibers are referred to as "bag 1," "bag 2," and "chain" fibers. Bag and chain fibers are distinguishable on the basis of their mechanical properties, with the bag fibers being more dynamic. Whereas bag 1 and bag 2 fibers differ mostly in their content of elastic strands (Banks et al, 1981) and innervation, these intrafusal fibers are innervated by two distinct types of efferent motoneurons: the gamma dynamic, innervating the bag 1 fibers, and the gamma static, innervating the bag 2 and chain fibers. The γ-motoneurons are considerably smaller (2 to 8 μm) than their functionally synonymous α-motoneurons. Wrapped around each

of the intrafusal fibers are the endings of two groups of afferent nerve fibers, the larger group Ia and the smaller group II. The Ia afferent fibers connect with a monosynaptic (direct contact) excitatory projection on the motoneuron pool of the same muscle and with a disynaptic (through an interneuron) inhibitory projection on the motoneuron pool of the antagonist muscle(s). It has also been shown that this pathway of "reciprocal inhibition" is accompanied by longer pathways of "reciprocal excitation" via delayed oligosynaptic excitatory and inhibitory Ia projections (Jankowska et al, 1981a and b). The group II afferent fibers also impinge on the motoneuron pool of the same muscle with an excitatory projection but with a disynaptic contact. There is no clear evidence indicating the presence of a group II pathway to the antagonist muscle. A third type of afferent, the β-motoneurons, have been shown to exist in some mammalian subprimate animals. The β-motoneurons innervate both intrafusal and extrafusal fibers. Their presence in human muscles remains speculative and, as such, their role will not be discussed in the context of this chapter.

It is now generally agreed that the Ia and II group fibers modify their discharge rate as the mechanoreceptor endings of these fibers are elongated. *The mechanoreceptor endings may be elongated*, either by stretching the muscle which stretches the spindle capsule and thus the intrafusal fibers, or by contracting the intrafusal fibers via γ fiber excitation. As the mechanoreceptors become elongated, the discharge rate of the receptors increases; as they shorten, the discharge rate decreases. It is also generally agreed that rate of length change of the muscle (fibers) modifies the discharge characteristics of the afferent fibers. Numerous experiments have shown that the Ia afferents respond to length and velocity and the II afferents mainly to length. Thus, the II afferents may be viewed as mainly static sensors and the Ia afferents as both static and dynamic sensors. This distinction is convenient from an analytical point of view, but physiologically the distinction cannot be made so clearly. Several investigators (Houk and Rymer, 1981; Rack, 1981; and others) have further categorized the response of the Ia fibers by demonstrating that they are nonlinear sensors; being much more sensitive to small displacements than to large displacements, thereby keeping the gain of the stretch reflex low when the muscle length changes appreciably. They are more sensitive to lengthening (stretch) than to shortening. Houk et al (1981) have also demonstrated that the dynamic component of the spindle response is proportional to the 0.3 power of velocity. This suggests that spindle Ia afferents are better suited for motion detection (change in velocity) rather than for signaling the precise velocity of the muscle (fibers).

It is a commonly accepted view that the α and γ-systems are coactivated during a muscle contraction, that is, when the motoneuron pool of a

muscle is excited, both the extrafusal and the intrafusal fibers contract. It can be reasonably assumed that this coactivation has, as one of its main functions, the task of setting the length of the spindle appropriately with respect to the length of the contracting muscle fibers. This task is equivalent to setting the operating point of the Ia mechanoreceptors, so that their sensitivity remains high over the length variability of the extrafusal muscle fibers. Any length and velocity perturbation applied to the muscle spindles from the adjacent muscle fibers will modify the discharge of the afferent fibers. Note that these perturbations may occur locally within the muscle, even during attempted isometric contractions, because the mechanical disturbances caused by the individual extrafusal muscle fibers may not be (and in all likelihood are not) symbiotic.

The classical approach to conceptualizing the function of the muscle spindle has been to consider it as a servocontroller for compensation of loads applied to the tendon of a muscle. This notion was an outgrowth of the experimental work involving investigations concerning reflexes. In such experiments the whole muscle or limb was commonly perturbed, and the resulting neuroelectric response was monitored.

More recently, a series of studies have addressed the question of the sensitivity of the muscle spindle to the mechanical disturbances of the individual motor unit contractions (Binder et al, 1976; Binder and Stuart, 1980; Cameron et al, 1980 and 1981; McKeon and Burke, 1983). All these investigators recorded the activity of the muscle spindle afferents and the activity of the MUAPTs simultaneously. The time course and magnitude of motor unit contractions were extracted from the force record using spike-triggered averaging techniques. It was found that both group Ia and II afferent activity was strongly coupled to the contractions of some motor units located near the spindle and was more or less indifferent to the contractions of other remotely located motor units. These results support the proposition that muscle receptors (see analogous findings in section on Golgi tendon organ) generate a "sensory partitioning" of the muscles.

Schwestka et al (1981) and Windhorst and Schwestka (1982) showed that the influence exerted by one motor unit on the spindle discharges was more or less strongly affected by the action of other motor units, dependent on the relative timing of their contractions. Windhorst et al (1982) also showed that the muscle spindle is particularly sensitive to "doublet" activations of motor units (successive firing of the same motor unit within 10 ms).

The Golgi Organ

The Golgi organs are located in the relatively stiff aponeuroses extending from the tendon. Thus, these receptors provide almost no information concerning muscle length. They are, instead, sensitive to

muscle tension. They are fusiform in shape, approximately 650 μm long and 50 μm in diameter in midsection. They are innervated by the group Ib afferent fibers which, through a disynaptic connection, have an inhibitory effect on the motoneuron pool of the homonymous muscle and a less pronounced but nonetheless measurable excitatory effect on the motoneuron pool of the antagonist muscle(s) (Watt, 1976).

For several decades it was believed that the Golgi organs had a high-force threshold, restricting their involvement to that of a safety valve. Houk and Henneman (1967) showed that discharge of the Golgi organs was highly sensitive to minute increases of the tension applied to the tendon. Subsequently, it has been shown by Binder et al (1977) that the Golgi organs are sensitive to individual motor unit twitches. In fact, the architecture of the muscle fiber insertion into the tendon is structured so that muscle fibers of several (5 to 25) motor units attach to any one Golgi organ. This apparent distribution of motor unit impingement to the Golgi organs serves the purpose of spatially integrating the force emanating from the quasirandomly generated force twitches from the motor units. This arrangement provides the Golgi sensor with the capability of responding to the force contribution of individual motor units, as well as to a more global force contribution from the muscle as a whole.

Behavior of Muscle Spindle and Golgi Organs during a Contraction and a Stretch

The Golgi tendon is essentially a force sensor; therefore, it will respond in a fashion similar to an externally applied tension (during stretch) or an internally applied tension (during a voluntary contraction). The spindle, on the other hand, is sensitive to length and velocity; thus, it will respond differently, depending on whether it is being elongated during a stretch or shortened during a voluntary contraction. The conjoint involvement of the two sensory systems is displayed in a schematic fashion in Figure 5.1.

When an external load applied to a muscle stretches the muscle, probably all (certainly most) of the spindles in a muscle are stretched and respond by providing an excitatory influence on the motoneuron pool of the stretched muscle and an inhibitory influence on the motoneuron pool of the antagonist muscle. The Golgi organs will also be stimulated, and they respond by contributing an inhibitory influence on the moto-neuron pool of the agonist muscle and an excitatory influence on the motoneuron pool of the antagonist muscle. In this operating condition, the spindle and the Golgi organ responses conflict. However, if the applied stretch is brisk, that is, if the rate of force applied to provide the perturbation displacement is considerable, a reflex contraction response counteracting the displacement will result. This indicates that under such

conditions the Ia afferent fiber stimulation provides the dominant effect, an interpretation which is consistent with the known fact that the Ia fiber endings detect motion changes. This mechanism is the well-known stretch reflex. Thus, viewed from the perspective of external disturbances, the spindle provides a mechanism for load or displacement compensation.

When a muscle is contracted, either under voluntary control or via electrical stimulation, the spindles are slackened as the muscle fibers around it shorten. However, unlike the case of a rapid externally applied stretch, only some of the spindles throughout the muscle will be disturbed at any given force level. (All the spindles will be disturbed only when all the motor units in the muscle are excited.) Thus, the discharge of the spindles will be decreased, providing a reduction in the excitatory influence (which is at times referred to as disfacilitation) on the agonist motoneuron pool and a decrease in the inhibitory influence on the antagonist motoneuron pool. However, the Golgi organs will respond to the increasing tension and increase their discharge appropriately. Thus, they will provide an inhibitory effect on the homonymous muscle and an excitatory effect on the antagonist muscle(s). Hence, during a voluntary contraction, the behavior of the muscle spindle and the Golgi organs is complementary.

Renshaw Cells

Renshaw (1946) discovered that antidromic impulses in motoneuron axons (moving towards the cell body) inhibited neighboring motoneurons, and that such impulses caused discharges of interneurons of the ventral horn, which have since been called Renshaw cells. The Renshaw cells receive collateral branches from the motoneuron axons while the Renshaw cells' axons terminate on the motoneurons themselves. This forms a feedback circuit with "recurrent inhibition" whose significance is not yet fully understood.

It has been reported that Renshaw cells are more strongly excited by collaterals of large motoneurons than collaterals of small ones (Ryall et al, 1972; Pompeiano et al, 1975; Friedman et al, 1981; and others). It also has been shown that Renshaw cells mutually inhibit other Renshaw cells (Ryall, 1970), the γ-motoneurons (Ellaway, 1971), and the interneurons mediating group Ia reciprocal inhibition (Ryall and Piercey, 1971). Renshaw cells may be activated by the discharge of a single motoneuron (Ross et al, 1975), and their discharge rates are nonlinearly related to the motoneuron discharge rate (Ross et al, 1976; Hultborn and Pierrot-Deseilligny, 1979; Cleveland et al, 1981).

It should be noted that the morphological and physiological evidence for the presence of Renshaw cells has been obtained mainly from the lumbarsacral part of the spinal cord of cats. Reports of their existence in man are much scarcer. Pierrot-Deseilligny and Bussel (1975) have pro-

vided an elegant demonstration of their activity in the soleus muscle of man.

It is difficult to identify a clear functional role of the Renshaw cells because of their apparent multiple actions. Hultborn et al (1979) have suggested that the supraspinal inputs which converge on Renshaw cells enable the recurrent inhibition to serve as a variable gain regulator at the motoneuronal level. Hultborn et al (1979) also argued that Renshaw cell action on the Ia inhibitory pathway and on the γ-motoneurons is meaningful since all these neurons act together as a functional unit, forming an "output stage" of the motor system.

Other Muscle Receptors

Muscles contain a variety of sensory fibers in addition to those mentioned in the previous sections. Afferent fibers with free nerve endings and having a wide range of diameters (groups II, III, and IV) have been identified. A few Pacinian corpuscles (specific skin sensors sensitive to touch and pressure) are supplied by fibers of group I and II. Joint capsule receptors are also innervated by sensory fibers. Prolonged muscular contractions in conjunction with blood occlusion produce discharges of the unmyelinated C fibers, which also seem to be sensitive to light touch or slight changes in temperature (see Mendell and Henneman, 1980).

Although the actions of most of these receptors are not clearly identified, several withdrawal reflexes which may arise in response to the possibility of injury seem to originate in these types of receptors. It has also been shown (Sabbahi and De Luca, 1981, 1982; and others) that cutaneous afferents may have important inhibitory effects on the α-motoneurons.

BEHAVIOR OF MOTOR UNITS

All the sensory mechanisms, along with the suprasegmental and supraspinal contributions, converge on the soma of the α-motoneurons and contribute to its disposition to discharge. The discharge behavior of the α-motoneurons may be conveniently studied by observing the discharges of the motor units in the muscle.

Interpulse Intervals

When MUAPTs can be properly identified, it is possible to measure the time between adjacent discharges of a motor unit, i.e., the interpulse interval (IPI). The IPI has been observed to be irregular, and can be described as a random variable with characteristic statistical properties (De Luca and Forrest, 1973a).

The most general characterization of the IPI is a histogram, which is a discrete representation of the probability distribution function. The histogram should only be computed for relatively short durations of the MUAPT (less than 10 s). Two common parameters of the probability

distribution function, or the histogram, are the mean and the standard deviation. These two parameters have been used to describe the IPIs. Tokyzane and Shimazu (1964) suggested that it might be possible to differentiate between two categories of motor units (tonic and kinetic) by plotting the mean vs. the standard deviation of the IPIs. Their report presented two distinguishably different relationships. Leifer (1969), Person and Kudina (1972), De Luca and Forrest (1973a), and Hannerz (1974) found no such distinction. They, instead, found a continuous range of mean vs. standard deviation relationship.

The shape of the IPI histogram, as reported by various investigators, is not consistent. Buchthal et al (1954b), Leifer (1969), Clamann (1970), and others have reported that the shape has a Gaussian distribution. De Luca and Forrest (1973a and b), Person and Kudina (1972), and others have reported an asymmetric distribution with positive skewness. It is now known that the shape of the IPI histogram will vary as a function of time during a sustained contraction (De Luca and Forrest, 1973a) and as a function of firing rate. Figure 5.2 presents histograms of the IPIs during six consecutive equilength segments of 5 s of a MUAPT detected during a constant force contraction from the deltoid muscle. Note that as the time of contraction progresses, the mean value and standard deviation of the IPI both increase, and the shape of the histogram changes. The MUAP used in Figure 5.2 corresponds to that whose firing rate is displayed as the first recruited motor unit in Figure 5.8. When a motor unit is recruited, the IPIs have a relatively large coefficient of variation. But as the firing rate increases, usually associated with an increase in the force output of the muscle, the coefficient of variation decreases as the motor unit discharges become more regular. This property is demonstrated in Figure 5.3. The *top section* presents the force profile of an isometric contraction of the deltoid muscle superimposed on the IPI values of three MUAPTs which were detected during the contraction. The *bottom section* presents the IPI histograms of four consecutive segments of MUAPT no. 3. The first part of the contraction was maintained at the recruitment level of motor unit no. 3, the second part of the contraction at a higher force level. Note that the IPI values of motor unit no. 3 are highly irregular when it is discharging near its threshold but become considerably more regular as the force output is increased by a small amount (4%). This modification in the IPI behavior is reflected in the histograms.

The rapid decrease of the standard deviation with increasing firing rate after recruitment is found in the data of Hannerz and of Person and Kudina. The latter investigators proposed that after-hyperpolarization may be responsible for reducing the standard deviation and thus increasing the regularity of the intervals. Considerable modifications in
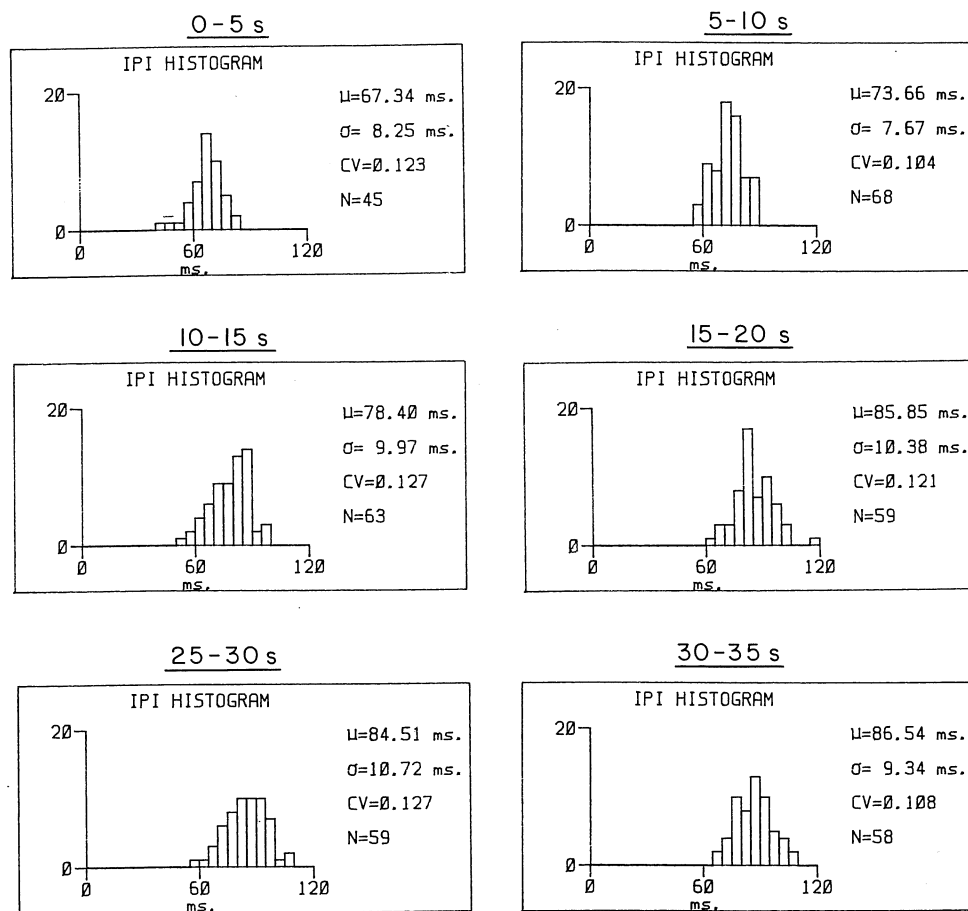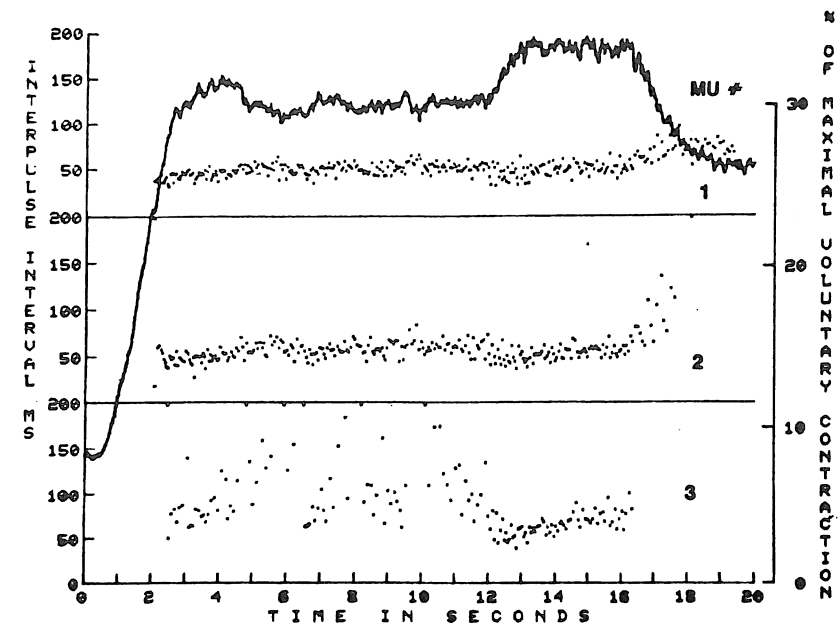
0–5 s

IPI HISTOGRAM

μ=67.34 ms.
σ= 8.25 ms.
CV=0.123
N=45

5–10 s

IPI HISTOGRAM

μ=73.66 ms.
σ= 7.67 ms.
CV=0.104
N=68

10–15 s

IPI HISTOGRAM

μ=78.40 ms.
σ= 9.97 ms.
CV=0.127
N=63

15–20 s

IPI HISTOGRAM

μ=85.85 ms.
σ=10.38 ms.
CV=0.121
N=59

25–30 s

IPI HISTOGRAM

μ=84.51 ms.
σ=10.72 ms.
CV=0.127
N=59

30–35 s

IPI HISTOGRAM

μ=86.54 ms.
σ= 9.34 ms.
CV=0.108
N=58

Figure 5.2. Histograms of the IPI of six consecutive segments (each 5 seconds long) of a MUAPT detected from the deltoid muscle during a constant-force isometric contraction at 30% of maximal voluntary contraction. This MUAPT corresponds to the first recruited motor unit in Figure 5.8. Note that as the time of the contraction progresses, the mean, standard deviation and shape of the histogram of the IPI change.
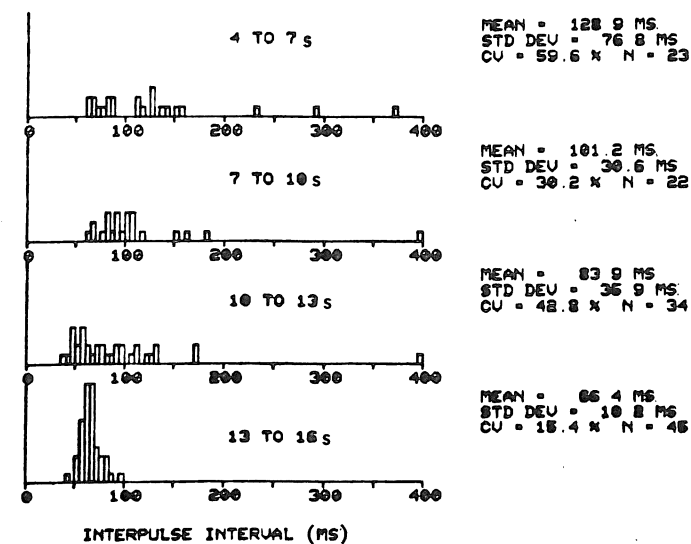
Histograms of MU #3

4 TO 7 s

MEAN = 128.9 MS.
STD DEV = 76.8 MS.
CV = 59.6 % N = 23

7 TO 10 s

MEAN = 101.2 MS.
STD DEV = 30.6 MS.
CV = 30.2 % N = 22

10 TO 13 s

MEAN = 83.9 MS.
STD DEV = 35.9 MS.
CV = 42.8 % N = 34

13 TO 16 s

MEAN = 86.4 MS.
STD DEV = 10.8 MS.
CV = 15.4 % N = 46

INTERPULSE INTERVAL (MS)

Figure 5.3. (*Top*) The interpulse intervals of three concurrently active motor units during an isometric contraction of the deltoid muscle having the displayed force profile. Note the decreased variability of the interpulse intervals of the third motor unit when the force output increases. (*Bottom*) Histograms of the interpulse intervals of the third motor unit at various time intervals of the contraction. Note the dramatic change in the shape.

the shape of the IPI histograms have also been reported from patients afflicted with supraspinal motor disturbances (Freund et al, 1973).

As the force increases, the rate of discharge of the motor unit increases, and the IPIs become shorter, which is evident in Figure 5.3. This diminution of the IPIs is accentuated during "ballistic" contractions, i.e., those which are performed as fast as possible. During such contractions, IPIs less than 10 ms in duration are present (Desmedt and Godaux, 1978; Bawa and Calancie, 1982).

Gurfinkel' et al (1964) reported several influences on the standard deviation for the IPIs of individual motor units. In patients with disturbances of joint perception, the standard deviation was considerably reduced compared to that of a normal individual, but in patients with cerebellar disturbances, no differences were seen. They also found a tendency for the standard deviation to decrease when normal subjects used surrogate means of control (audio or visual feedback) in addition to proprioception. Although Holonen (1981) reports no discernible difference in the regularity of the IPI between audio and visual feedback, Sato (1963) found that the coefficient of variation for motor units from the dominant hand of right-handed subjects tended to be lower than that of the left hand. Voluntary oscillations were more regular when performed with the right hand. This suggests that a lower coefficient of variation corresponds to greater capability of precision control.

Interdependence. Another statistical parameter of interest for describing the IPIs of a motor unit is their interdependence. The greatest amount of dependence (if any) should occur between adjacent intervals. Dependence may be tested by plotting the values of the adjacent IPIs against each other in the form of a scatter diagram. If the adjacent IPIs are independent and the random process is stationary (time invariant), the points on the scatter diagram will be randomly distributed in a fashion determined by the probability distribution function of the IPIs. In case of dependence, the points on the scatter diagram will have statistically dependent coordinates. An alternative test for dependence is serial correlation. If the average product of the adjacent IPIs is equal to the square of the average of the IPIs, then the serial correlation is zero, and the IPIs are linearly independent. Lesser values indicate a negative serial correlation and the tendency of short IPIs to be followed by long IPIs, and vice versa. If the IPI random process is not stationary, the above tests may indicate dependence, when none exists. Therefore, measurements for IPI dependence must be performed over sufficiently short time periods, to reduce time-varying effects.

Several authors have noted weak, negative correlations between adjacent IPIs of single motor units. Kranz and Baumgartner (1974) found some motor units that exhibited negative serial correlation, some weakly positive, and some with no significant serial correlation in most cases.

Person and Kudina (1971, 1972) found negative serial correlation only for motor units firing at rates above 13 pulses/second (pps). At these firing rates they found a constant small standard deviation (5 ms) and symmetric IPI histograms. They attributed these results to the effect of afterhyperpolarization. De Luca and Forrest (1973a) used a chi-square test on the joint interval histogram for adjacent intervals of MUAPTs detected during constant-force isometric contractions. No dependence of any statistical significance was found.

Few authors report having made calculations from the IPI data of single motor units to test for higher order interval dependence. The 2nd through 10th order serial correlation coefficients computed by Kranz and Baumgartner (1974) were of lesser magnitude than the first order coefficients, and the chi-square test on the 3rd order joint interval histogram computed by De Luca and Forrest (1973a) revealed no dependence.

Synchronization. Synchronization, the tendency for two or more motor units to discharge at a fixed time interval with respect to each other. This includes, but is not limited to, MUAPTs which are phase-locked or entrained. In a mathematical sense, synchronization can be defined as dependence between MUAPTs. A useful technique for observing the synchronous activity among the discharges of pairs of motor units has been described in Chapter 4. It consists of calculating the "intensity function," which is an operation similar to obtaining a cross-correlation function of two discrete variables.

The interest in this property of motor unit discharge has its roots in the observations of Piper (1907, 1908), who noted that on occasions, the surface EMG signal displayed oscillatory (grouped) activity. This occurrence has been accepted as an indication of synchronization of motor unit discharges. Such an interpretation has often been contested and still remains to be proven.

Evidence of the symptoms of synchronization has been reported by several authors. Lippold et al (1957, 1970) found that the MUAPTs from different motor units tended to group at the rate of approximately 9 bursts/second. This grouping became more evident when the muscle became fatigued. Missiuro et al (1962) and others have claimed to observe synchronization by noting the appearance of large periodic oscillations in the EMG signal as the muscle fatigued. Direct evidence was noted by Mori (1973), who observed that motor unit discharges in the soleus muscle synchronized during quiet stance in man. In a later study, Mori and Ishida (1976) demonstrated that the discharge of motor units would indeed become synchronized if the feedback from the muscle spindle in the muscle was sufficiently large.

Kranz and Baumgartner (1974) and Shiavi and Negin (1975) performed a cross-correlation analysis between the MUAPs of simultane-

ously recorded MUAPTs. They concluded that during nonfatiguing, constant-force, isometric contractions of the first dorsal interosseous, flexor digitorum profundus, extensor digitorum indicis, and tibialis anterior, there was no significant cross-correlation. However, Buchthal and Madsen (1950) and Dietz et al (1976), using the same technique, did find evidence of weak cross-correlation in normal muscles. The amount of the cross-correlation increased in diseased muscles. The degree of cross-correlation also increased as the amplitude of the physiological tremor increased. Milner-Brown et al (1975) reported that it might be possible to accentuate synchronization by exerting large forces for short periods of time.

The phenomenon of motor unit synchronization has not been analyzed and documented as fully as other motor unit properties. Data have been reported which indicates that motor units tend to synchronize when the muscle is fatiguing, during physiological tremor, and in some disease states. However, no detailed description of the behavior of synchronization as a function of measurable parameters such as force and time has been given. This has mainly been due to limitations in the detection and analysis techniques that have been used. Also, a major disadvantage of the studies on synchronization which use indirect measurements from the raw EMG signal is that parameters other than synchronization may cause apparent oscillations in the amplitude of the raw EMG signal.

Firing Rate

Due to the pseudorandom nature of the IPIs, it is useful to measure the discharges of a motor unit in terms of an average firing rate, which is the reciprocal of the average IPI. However, for the firing rate to be meaningful, it should be measured over a representative time interval of 400 to 1000 ms. Measurements made over shorter time intervals may lead to unrepresentatively large firing rate values, and measurements made over larger time intervals may obscure meaningful trends in the firing rate. For details on techniques for calculating the firing rates, refer to Chapter 4.

The procedure of averaging (or filtering) the firing rates over the 400 to 1000 ms time is comparable to the filtering effect which the muscle tissue has on the pulse train from the α-motoneurons which excite it. Solomonow and Scopp (1983) have provided clear evidence that the mechanical response of muscle tissue to the pulse frequency of the electrical stimulation applied to its innervating nerves has the response of a low-pass filter with a 3 dB point in the neighborhood of 1.5 to 2.5 Hz. Thus, the recommended averaging (filtering) interval of 400 to 1000 ms allows the observer to "see" the firing rate in a fashion analogous to the way the muscle tissue "sees" the firing rate.

The first reported study on the firing rates of motor units was that of Adrian and Bronk (1928, 1929), who properly noted that in man, the upper limit of the motor unit firing rate was approximately 50 pps. This was confirmed by other early studies by Smith (1934) and Lindsley (1935).

Firing Rate as a Function of Force. The force dependence of firing rate during an isometric contraction has been studied by many investigators.

In the rectus femoris muscle, Person and Kudina (1972) found that the low threshold motor units began firing at 5 to 11 pps and reached 18 to 21 pps at 45% MVC. They also found that the higher the recruitment threshold of the motor unit, the less the motor unit increased its firing rate with increasing force.

A frequently studied human muscle is the biceps brachii. Clamann (1970) found that the firing rate of motor units recruited at the lowest force levels was 7 to 12 pps. The firing rate increased with increasing isometric force to a maximum of approximately 20 pps. The minimal firing rate of a motor unit increased linearly with the threshold of recruitment. Almost no motor units fired above 20 pps, even near 100% maximal voluntary contraction (MVC), and no recruitment was observed above 75% MVC. Clamann (1970) also found that motor units near the muscle surface had higher thresholds of recruitment than those deep in the muscle.

Leifer (1969), also working with the biceps brachii, found that all motor units fired at approximately 11 to 16 pps throughout the entire range of contraction force. After a motor unit was recruited, its firing rate increased slightly with increasing force and then remained constant at a preferred rate. He found that this preferred rate increased slightly with increasing threshold of recruitment. As the force level decreased, the firing rate decreased to 30 to 40% of the preferred rate before becoming inactive.

Also working with the biceps brachii, Gydikov and Kasarov (1974) found that all motor units had a firing rate of 6 to 10 pps when they were recruited. Minimal recruitment occurred above 60% MVC. For some motor units, the firing rate increased to approximately 13 pps and then remained constant with increasing force, whereas for other motor units, the firing rate increased linearly with force up to 100% MVC. The former were generally recruited at lower force levels than the latter. Based on their data, they proposed the existence of two types of motor units, tonic and kinetic. However, their small sample source (a total of 30 motor units from 15 subjects) limits the significance of their proposal. Clamann (1970) and Leifer (1969) did not describe two types of motor units in the biceps brachii; however, the firing rate characteristics found by these two investigators appear to differ slightly.

Kanosue et al (1979) studied the motor unit firing rate properties of the brachialis muscle, a synergist to the biceps branchii. Their results were in general agreement with those of Leifer (1969) in the biceps brachii. Kanosue et al (1979) provided support for the nonlinear increase of the firing rate as a function of force. However, unlike Gydikov and Kasarov, they did not conclude that two distinctly different categories of motor units are present in brachialis, based on their firing rate characteristics. Kanosue et al (1979) also reported that as the force output of the muscle increased to approximately 75% MVC, the firing rates of some motor units increased dramatically.

Hannerz (1974) and Grimby and Hannerz (1977), working with the tibialis anterior and short toe extensors, reported that the minimal firing rate of motor units recruited below 25% MVC was 7 to 12 pps and the maximal firing rate was 35 pps. For motor units recruited above 75% MVC the minimal firing rate was 25 pps, and the maximal firing rate was 65 pps in the tibialis anterior and 100 pps in the short toe extensors. Thus, both the average firing rate and the initial firing rate at recruitment increased with force. These firing rates are notably higher than those reported by other investigators. This discrepancy may be due to the method used to estimate the firing rate. They also found that all motor units recruited above 80% MVC discharged in bursts with pauses of 1 second or more at constant force levels. In a complementary study on the toe extensor, Borg et al (1978) found that motor units which could be driven continuously at firing rates below 10 pps had axonal conduction velocities between 30 and 40 m/s; those that could be driven only in higher firing rates bursts had higher axonal conduction velocities.

Monster and Chan (1977), working with the extensor digitorum communis in the forearm, demonstrated that the rate of increase of the firing rate increased with the voluntary force output of the muscle for higher threshold motor units. This behavior is consistent with that found by Kanosue et al (1979) in the brachialis muscle. However, it must be noted that the force levels studied by Monster and Chan (1977) was considerably less in terms of percentage MVC than those studied by Kanosue et al (1979).

Tanji and Kato (1973a and b), working with a smaller muscle, the abductor digiti minimi, found that motor units began firing at approximately 8 to 9 pps. They also reported that the earlier recruited motor units had the capability of increasing the firing rate to much higher values than latter recruited motor units during linear force increasing contractions. The firing rate at the beginning of the contraction was noted to increase as the force-rate of the contraction increased.

Milner-Brown et al (1973a) studied the activity of single motor units in the first dorsal interosseous muscle contracting at force levels below

50% MVC. They found that when recruited, motor units began firing at 8.4 ± 1.3 pps and increased their firing rate 1.4 ± 0.6 pps for each 100 g of force output, independent of the force at which each motor unit was recruited. They also found that a change in the force rate affected this result. At slow rates of increasing force (100 g/s), the firing rate had a tendency to reach a plateau, while at faster rates of increasing force (1000 g/s) motor units were recruited at lower force levels but with higher initial firing rates. This difference was not apparent during decreasing voluntary contraction.

Freund et al (1975) also performed an extensive investigation of single motor unit activity in the first dorsal interosseous muscle. They found that all motor units, regardless of their recruitment threshold, began firing at approximately the same rate (6.8 ± 1.4 pps). However, the lower threshold motor units increased their firing rates with increasing force much faster than the higher threshold units. The firing rates increased with force asymptotically to a maximal rate which also depended on recruitment threshold. These maximal rates varied from approximately 25 to 10 pps for low to high threshold motor units, respectively. However, none of the studied motor units were recruited above a force of 700 g. The rate of force increase tested by Freund et al (1975) was slower than that tested by Milner-Brown et al (1973a). This difference might account for some of the observed discrepancy.

Firing Rate as a Function of Muscle. It is now apparent that two distinct behaviors of the firing rate of motor units as a function of force output of the muscle have been reported by several investigators. The behavior is muscle dependent. In smaller muscles, such as those in the hand, the firing rates of motor units reach relatively higher values than the firing rates of motor units in larger limb muscles. Comparable data for highlighting this point has been presented by De Luca et al (1982a), as well as by Kukulka and Clamann (1981). The latter investigators studied the firing rate behavior of motor units in the biceps brachii and the adductor pollicis in the same subjects. De Luca and colleagues investigated the first dorsal interosseous and the deltoid of the same subjects.

De Luca et al (1982a and b), employing the recording and decomposition system described in Chapter 4, were able to study the behavior of up to eight concurrently active motor units. The subjects were requested to generate triangular force-varying isometric contractions up to 80% MVC. The experiments were performed on four categories of subjects: normal sedentary individuals, world class long distance swimmers, world class powerlifters, and world class concert pianists. An example of the results is presented in Figure 5.4, which presents the continual value of the mean firing rate (averaged over 800 ms) and the force produced by
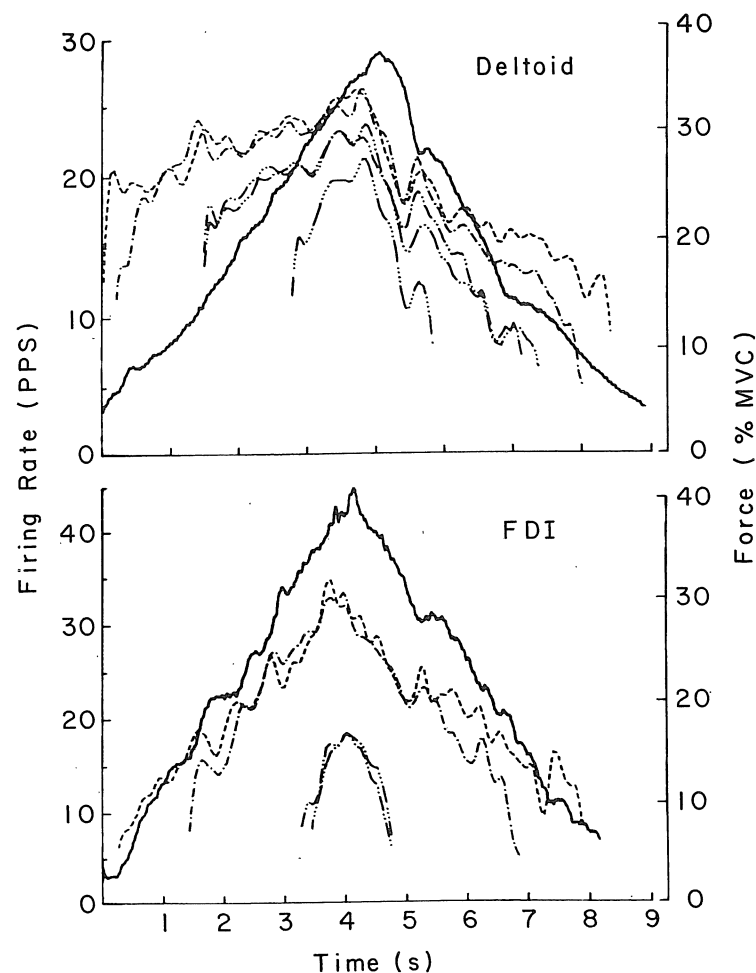

Figure 5.4. Firing-rate records of concurrently active motor units (*dashed lines*) are shown superimposed on the force output (*continuous line*) recorded during triangular force-varying contractions of the deltoid and first dorsal interosseous (*FDI*). Force levels are given in percent of maximal voluntary 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.

the muscle (about a joint) as functions of the time of the contraction. (The *heavy solid line* represents the force.) Note that in the deltoid muscle the firing rate rises steeply after recruitment, reaches an apparent plateau, and subsequently decreases less rapidly than it increased, although the force rate on the rising and falling phases is somewhat similar. The

first dorsal interosseous muscle on the other hand presents a strikingly different behavior during a similar force task. In this case, the firing rates are nearly linearly related to the force and do not display the plateau or asymmetry with force which is evident in the deltoid data. All the subjects clearly demonstrated this distinction in the firing rate behavior.

Another interesting observation that can be made in Figure 5.4 concerns the properties of the firing rate at recruitment and at decruitment. In the deltoid muscle, the recruitment and decruitment firing rates are higher than in the first dorsal interosseous. In the deltoid the decruitment firing rate is lower than the recruitment firing rate. This distinction is not apparent in the first dorsal interosseous. Figure 5.5 presents the results of the grouped data from the separate categories of subjects. The distinction in the behavior of the absolute values of the recruitment and decruitment firing rates is now apparent. Note the relatively minor distinction among subject categories, compared to the distinction between the two muscles. This data provides circumstantial evidence for the adaptation of motoneuronal properties, such as the time course of afterhyperpolarization, during a sustained contraction. It also indicates that the process of adaptation is executed with varying emphasis in different muscles.

The dynamics of the firing rates also differed between the two muscles. Figure 5.6 presents the maximal firing rate values of the motor units at the 40% and 80% MVC level as a function of recruitment force. In the deltoid the firing rate of all the motor units increased only by approximately 16 pps. This increased "swing" in the firing rate range of the first dorsal interosseous muscle is also visible in Figure 5.4.

A comparison of the firing rate properties of the first dorsal interosseous and deltoid muscles is presented in Table 5.1.

This minimal firing rate, or firing rate at recruitment, is generally assumed to be governed by the duration of the motoneuron afterhyperpolarization. Zwaagstra and Kernell (1980) have reported a negative correlation between the size of the motoneuron cell body and the duration of the afterhyperpolarization, indicating that the earlier recruited smaller motoneurons should have a lower initial firing rate. To date, numerous investigations have not revealed a distinct increase in the minimal firing rate as a function of recruitment threshold. (The works of Hannerz (1974) and Grimby and Hannerz (1977) are an exception.) Thus, it is reasonable to conclude that the minimal firing rate is determined by additional factors, possibly the recurrent inhibition of the Renshaw system. This latter suggestion is speculative but nonetheless attractive.

Figure 5.5 and the above table present a clear indication that the firing rate at recruitment is much more variable among motor units in different
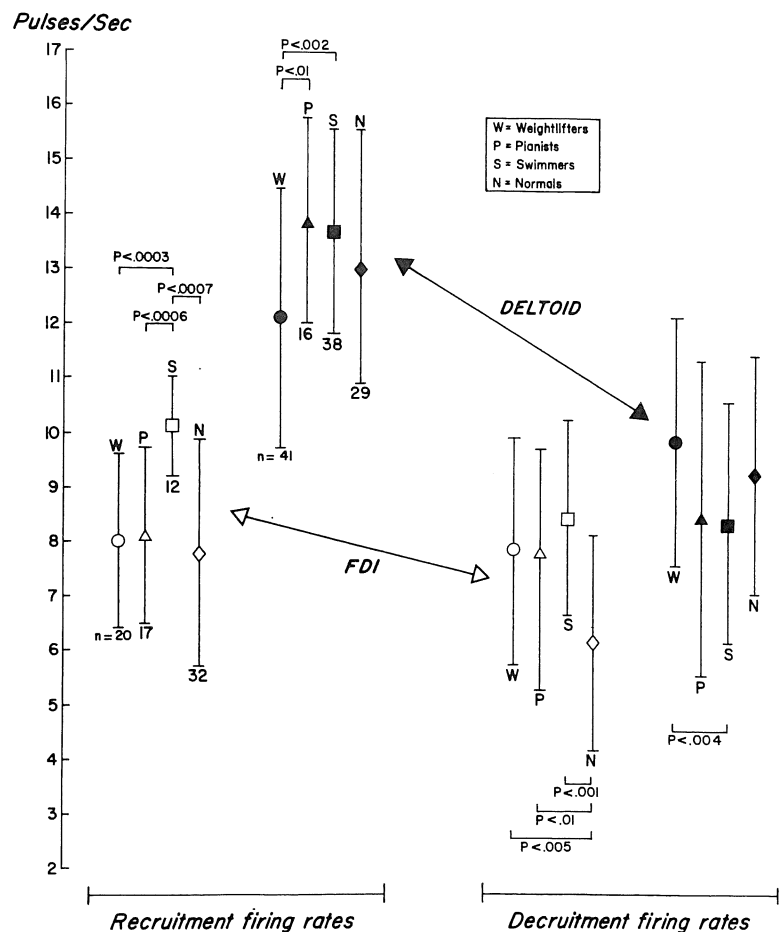
Figure 5.5. The distribution of motor-unit firing rates at initiation (recruitment) and cessation (decruitment) of continuous activity during triangular force-varying contractions reaching 40% MVC. In general, decruitment firing rates are lower than recruitment firing rates, but both of these parameters are greater in the deltoid than in the first dorsal interosseous (FDI). Significant differences between subject groups are indicated by bars showing the upper limits of the P values. (From C.J. De Luca et al, © 1982a, *Journal of Physiology*.)
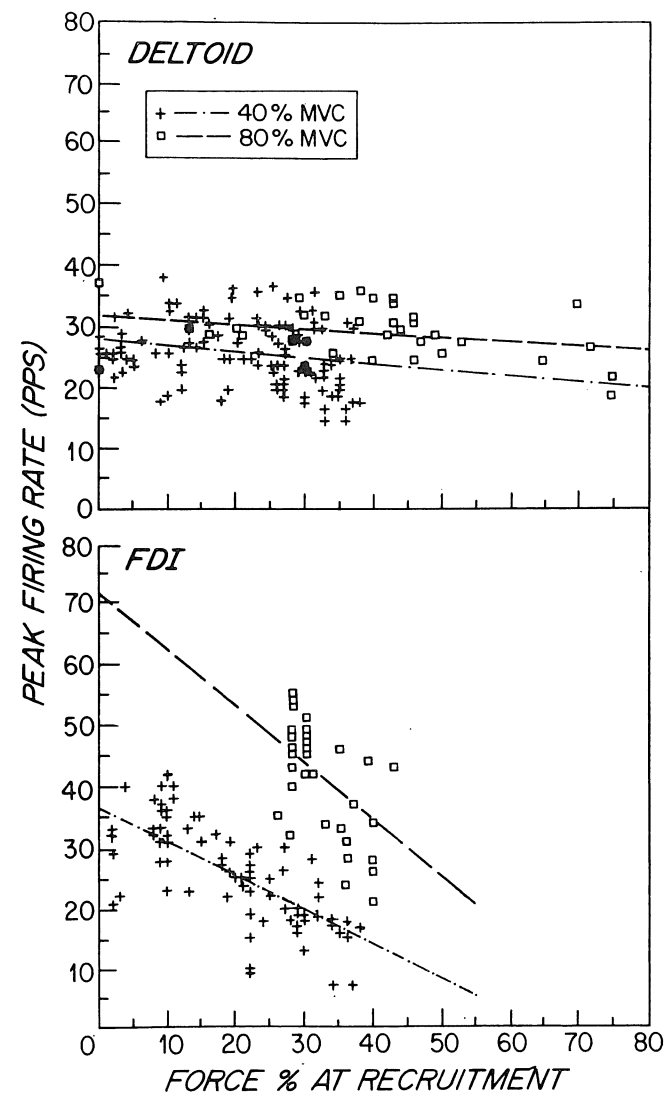
Figure 5.6. Peak firing rates achieved during triangular contractions reaching 40 and 80% MVC as a function of recruitment-force threshold. The computed least-squares linear regressions in the first dorsal interosseous (FDI) show strong negative correlations (linear regression coefficients > 0.56). In the deltoid, the linear regressions had slopes significantly different from zero at 40% MVC ($p <$ 0.008), but not at 80% MVC ($p <$ 0.08). (From C.J. De Luca et al, © 1982a, *Journal of Physiology*.)

Table 5.1
Motor-Unit Firing Rates in Two Different Muscles[a]

Muscle	Recruitment rate (pulses/s)	Decruitment rate (pulses/s)	Peak rate at 40% MVC (pulses/s)	Peak rate at 80% MVC (pulses/s)
FDI	8.9 ± 2.2[a] (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)

[a] In each case the mean $\pm$ SD of an observation is listed with the number of observations (n) in parentheses.

muscles than among motor units within a muscle. It is also apparent that training does not significantly affect the firing rate value at recruitment.

Firing Rate during Strenuous Contractions. Another interesting property of the firing rates of motor units has been observed by Kanosue et al (1979) in the brachialis and by De Luca et al (1982a and b) in the first dorsal interosseous during extremely strenuous isometric contractions. The observations of De Luca et al (1982a) are presented in Figure 5.7. The firing rates of relatively high threshold motor units abruptly double from 30 to 60 pps. Such behavior was only seen occasionally, partly due to the extremely difficult task of accurately identifying motor unit action potential during these strenuous contractions. This phenomenon may also account for the distinction in motor unit behavior noted by Gydikov and Kosarov (1974) in the biceps brachii.

This behavior may represent a means of tapping the force reserves in a muscle. The type of contraction in which this phenomenon is clearly seen (10% MVC/s) is important, since these strenuous contractions were the only type in which the subject reported definite effects of fatigue on performance. As force output slowly increases toward 80% MVC, muscular fatigue causes the actual level of maximal voluntary effort to fall below that possible in a nonfatigued state. During the contraction shown in Figure 5.7, the individual (a normal subject) actually reported the sensation of reaching maximal voluntary contraction at the time of the firing-rate bursts.

Brief firing-rate bursts of 50 pps have been reported in single units during maximal voluntary contractions of the human quadriceps muscles (Warmolts and Engels, 1972) but only in patients with chronic low-grade motor neuropathies. Muscle biopsy revealed that this behavior was only seen in homogeneous fields of fast-twitch fibers (greater than 96%), apparently arising as the result of collateral reinnervation. Because of the difficulties inherent in separating the activities of several rapidly firing motor units, we were unable to determine whether all units displayed this bursting activity or whether large units were activated preferentially. The mechanical contribution of smaller units would pre-
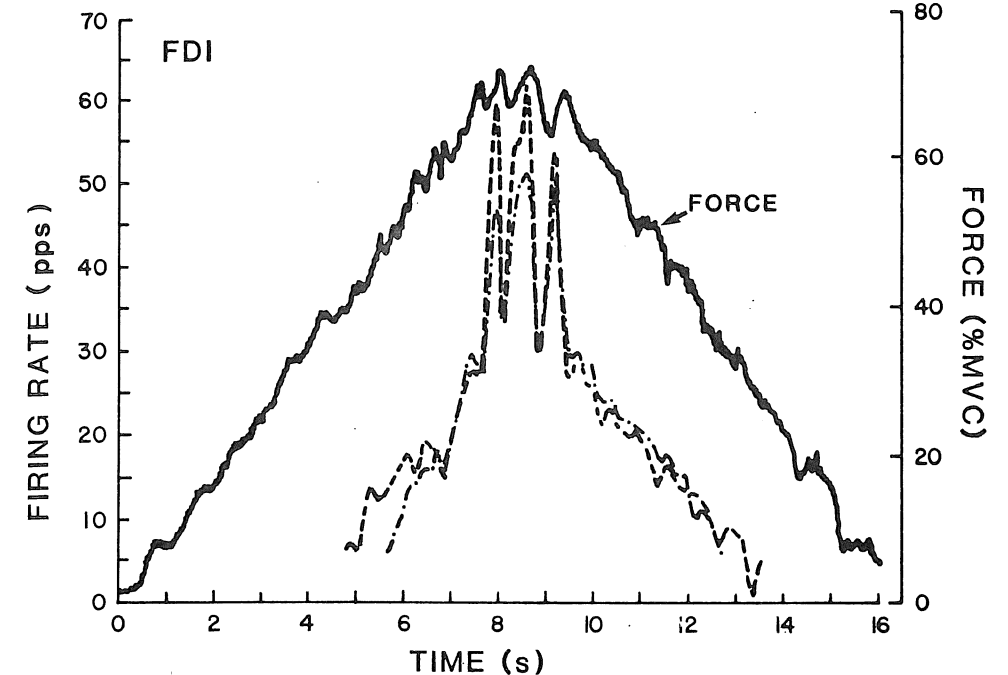
Figure 5.7. Firing-rate activity of two high force-threshold motor units (*dashed lines*) superimposed on the force output (*continuous line*) during a triangular force-varying contraction of the first dorsal interosseous (FDI). The highest rate is achieved by the lower threshold motor unit (recruitment-force thresholds for the two units were 31 and 42% 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. (From C.J. De Luca et al, © 1982a, *Journal of Physiology.*)

sumably be small, however, since most are probably fused at the relatively high firing rates observed prior to the bursts (approximately 30 pps).

Although intermittent firing-rate bursts have been observed using single-unit recording, Figure 5.7 is the first evidence of a bursting phenomenon in continuously active motoneurons during nonballistic contractions. Whether these rapidly increasing firing rates result from a sudden increase in synaptic excitation is difficult to determine. However, evidence of this type of nonlinearity is well documented in cat spinal motoneurones subject to increased levels of current injection (Kernell, 1965). Baldisseria et al (1978) have accounted for this effect (the so-called secondary range of motoneuron firing) by a model based on the time course of motoneuronal afterhyperpolarization, indicating that it may well be a passive response to high levels of synaptic current injection. This effect may also account for the extremely rapid firing-rate bursts

(60 to 120 bursts/s) seen by Desmedt and Godaux (1977a and b) during ballistic contractions of the tibialis anterior, where high levels of synaptic current are necessary.

In contrast, no evidence of a firing-rate burst response was seen during voluntary contractions of the deltoid up to 80% MVC. Because of the "tonic" behavior observed in the deltoid, motor-unit firing rates remained much lower than those reached in the first dorsal interosseous. Refer to the previous table for details. If twitch contraction times are comparable for motor units in the two muscles, most fast-twitch deltoid units are probably unfused even at 80% MVC. Interestingly, a recent study of single motor units in the neighboring human brachialis muscle (Kanosue et al, 1979) has demonstrated behavior similar to that seen here in the deltoid but with an increased reliance on rate coding above 70% MVC. De Luca et al (1982a and b) did not investigate the force range between 80 and 100% MVC; however, the presence of unfused motor units indicates that rate coding has a tremendous potential for increasing force output up to (and even beyond) maximal voluntary levels in muscles like the deltoid. If the central nervous system were to increase firing rates or generate firing-rate bursts in the large fast-twitch motor units of the deltoid (such as those seen in the first dorsal interosseous), extraordinary force levels could be achieved for short periods of time. This mechanism may indeed be the explanation for many of the incredible feats performed by humans under high stress conditions and during hypnotic states.

Firing Rates in Abnormal Muscles. Much fewer investigations studying the behavior of the firing rate of abnormal muscles have been performed. However, it appears that interest in this area is increasing as new techniques and equipment develop. Companion reports by Andreassen and A. Rosenfalck (1980) and A. Rosenfalck and Andreassen (1980) have shown that the mean firing rate of motor units in spastic muscles is a reduced firing rate, compared to that of motor units from the corresponding muscle in normal subjects. Kranz (1981) drew similar conclusions in patients with clinically mild lesions of the central nervous system. Conversely, Holonen et al (1981) report that the average firing rate tends to be greater than normal in muscles with myopathic disorders.

Firing Rate as a Function of Time

During sustained contractions of healthy muscles, the firing rate of motor units has a tendency to decrease independently of the force output of the muscle. This behavior appears to be a reflection of motoneuronal adaptation processes and/or a decrease in the excitation to the muscle. This phenomenon was first reported to occur in constant force contractions by Person and Kudina (1972) in the rectus femoris, independently

by De Luca and Forrest (1973a) in the deltoid and, more recently, in the first dorsal interosseous by De Luca et al (1982b). An example of this behavior during constant-force contractions is evident in the time progression of the characteristics of the IPI histograms of Figure 5.2 and in the firing rate curves of Figure 5.8. Grimby et al (1981) also observed a decrease in the firing rate. Kranz (1981) observed similar behavior in the first dorsal interosseous, extensor digitorum communis, and flexor digitorum profundus in patients with clinically mild lesions of the central nervous system.

This phenomenon has also been observed during force-varying isometric contractions. Figure 5.4 and Table 5.1 clearly show that the firing rate at decruitment is less than that at recruitment during a force-varying contraction.

Kernell and Monster (1981) investigated the property by injecting a constant current into the motoneurons of the gastrocnemius muscle of cats. They succeeded in continuously exciting motoneurons which they were able to classify as slow-twitch (fatigue resistant) and fast-twitch (fast-fatiguing). Their results clearly indicated that the firing rates of the fast-twitch (fast-fatiguing) motoneurons decreased, whereas those of the slow-twitch (fatigue-resistant) motoneurons did not alter under similar stimulation of constant-current injection. Thus, it is apparent that the firing rate adaptation is at least in part a motoneuronal property, possibly associated with a modification of the afterhyperpolarization characteristics.

Twitch Potentiation

The decrease in the firing rate during a sustained contraction appears to occur concomitantly with another phenomenon, twitch potentiation, that is, an increase in the twitch tension produced by a motor unit. This phenomenon was first observed in mammalian muscles by von Euler and Swank (1940). Subsequent studies by Stondaert (1964), Nystrom (1968), and Burke et al (1976) have investigated the posttetanic potentiation in the *in vivo* soleus and gastrocnemius muscle of the cat. Substantial potentiation was always evident in the gastrocnemius muscle, in contrast to relatively little potentiation in the soleus muscle. In the cat, the soleus muscle consists almost entirely of slow-twitch fibers, whereas the gastrocnemius contains both slow-twitch and fast-twitch fibers. Thus these results are consistent with and supportive of the observations of the firing rate decrease in fast-twitch fibers made by Kernell and Monster (1982).

Muscles of humans have also been reported to display twitch potentiation. Gurfinkel' and Levik (1976) noted such behavior in the forearm flexor muscles. Vandervoort et al (1983) also demonstrated potentiation of the twitch response of the tibialis anterior and plantar flexor muscles
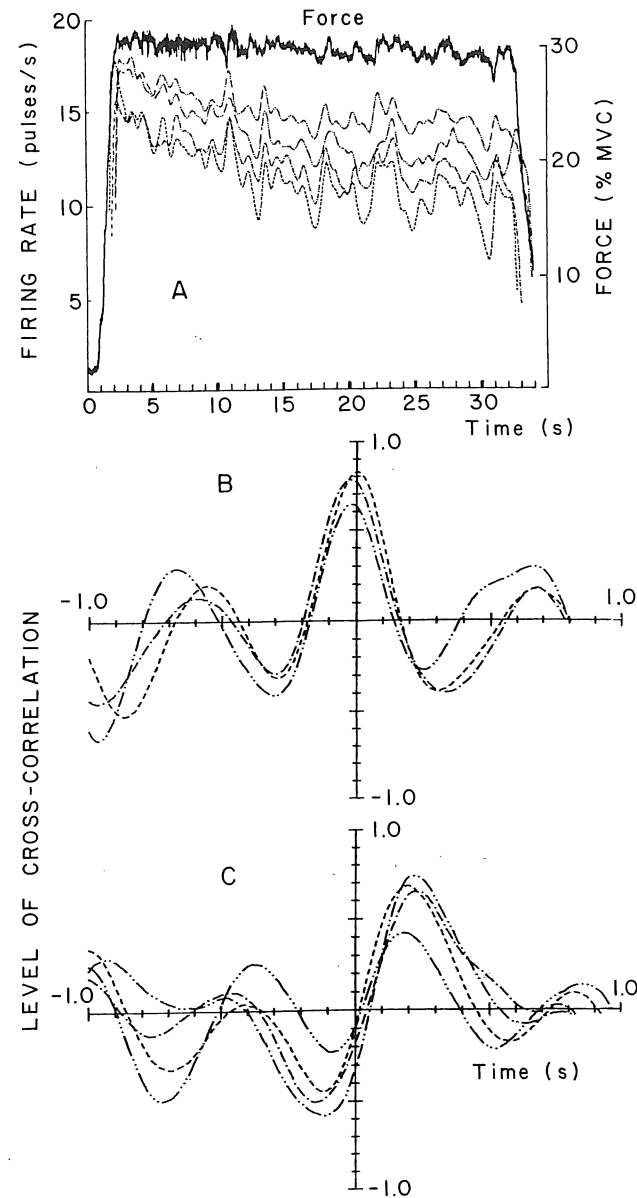
Figure 5.8. (A) Firing-rate records of four concurrently active motor units (dashed lines) are shown superimposed on the force output (continuous line) recorded during a constant-force isometric abduction of the deltoid. The force level is given in percent of maximal voluntary contraction (MVC) at right. (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. (From C.J. De Luca et al, © 1982b, Journal of Physiology.)

of the leg. They noted that the twitch potentiation was always more evident in the tibialis anterior than in the plantar flexors, and that it was only evident in contractions greater than 50% MVC. These observations support the notion that the faster-twitch fibers, which are more abundant in the tibialis anterior and are recruited at relatively higher force levels, are more susceptible to potentiation. They further noted that the potentiation effect was dependent on muscle length and time of contraction. It was greatest after contractions lasting approximately 10 s and in muscles in shortened positions. They speculated that the twitch potentiation was in some fashion related to the normally incomplete activation of the contractile elements in the muscle fibers.

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 behavior of firing rates of active motor units? The first question has received considerable attention. Notable contributions have been made by Henneman and his colleagues. Details of this question will be addressed in a subsequent section. The second question has not engaged a comparable level of excitement, possibly due to the technical complexity of the experiments necessary to address it.

In order to address the question concerning the behavior of the firing rate properly it is necessary to observe the firing rate as a function of time and force of contraction. The occasional reports in the literature provide the beginning of an indication of the firing rate behavior as a function of force. Several reports (Leifer, 1969; Person and Kudina, 1972; Milner-Brown et al, 1973a; Tanji and Kato, 1973a and b; Monster and Chan, 1977; Monster, 1979; Kanosue et al, 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). They 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.

The studies of De Luca et al (1982a and 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 homonymous 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.

Figure 5.8*A* 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 Figure 5.8*B*, 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 indicate 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 (Figure 5.8*C*). 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. 5.8*C*) 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 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 to 2 Hz. This observation has been made by several investigators using a variety of paradigms. (Crochetiere et al, 1967; Coggshall and Bekey, 1970; Gottlieb and Agarwall, 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).

Referring back to Figure 5.4, a similar behavior is seen during force-

increasing and force-decreasing contractions. 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 considerably 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. This arrangement indicates a peculiarity of motor unit control during voluntary contractions, that is, the firing rate behavior is not 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 (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 physical force generation potential of the muscle fibers may not be utilized during voluntary contractions. Conceivably, it may be held in abeyance for occasional dramatic displays of force.

The examples of Figures 5.4 and 5.8 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 fibers.

The *common drive* has also been observed to exist in an agonist-antagonist set of muscles simultaneously. In a recent study involving the flexor pollicis longus and the extensor pollicis longus, the sole controllers of the interphalangeal joint of the thumb, De Luca and colleagues have noted the *common drive* in both muscles. During voluntary stiffening of the interphalangeal joint, the firing rates of motor units in the two muscles were highly correlated with essentially no time shift (see Fig. 5.9 for details). Note that although the force or torque output is approximately zero, the *common drive* remains. 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 the output of the joint. The same study also reported that during random flexion-extension isometric contractions of the interphalangeal 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.
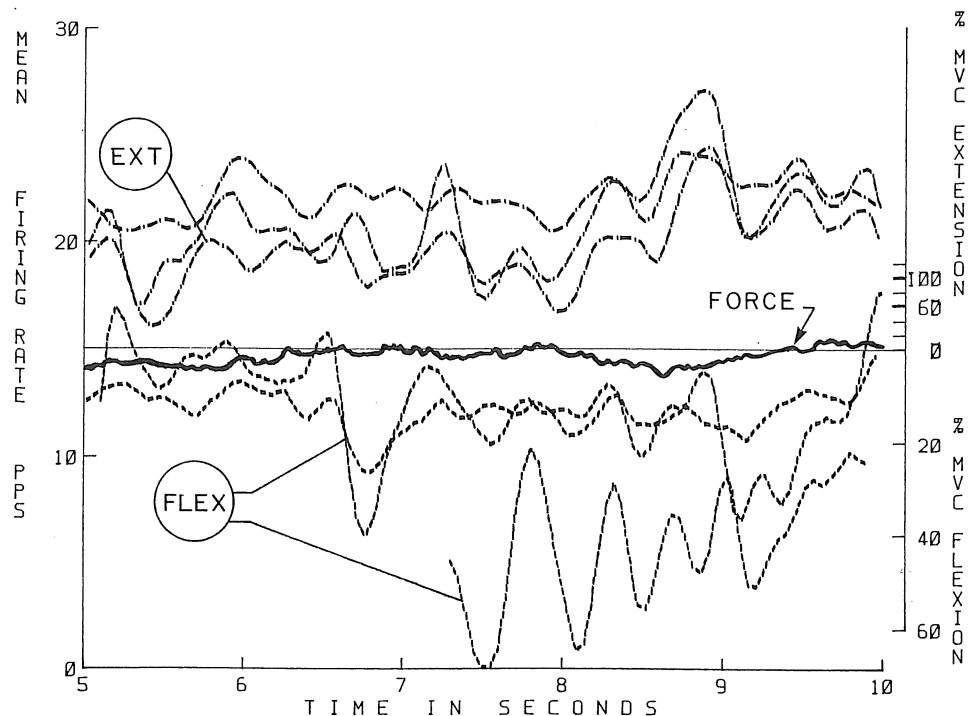
Figure 5.9. Example of motor unit firing rate behavior during thumb phalangeal joint stiffening. FRC line denotes the force (or torque) output from the joint; the *FLEX* lines represent the firing rates of motor units in the flexor pollicis longus; the *EXT* lines represent the firing rates of motor units in the extensor pollicis. These two muscles are the sole controllers of the joint.

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 motoneuron pool consists of the motoneuron pools of both muscles. However, when the force output of the joint alternates from flexion to extension, or vice versa, the two pools are 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 considerably 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 effects

the properties of synchronization that relate to individual discharges of motor units.

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 fibers) vary from 30 to 150 ms? This question is answered by the data in Figure 5.10. In this particular case the firing rates were filtered with a window of 800 ms in order to emphasize the "bias" firing rate, which is related to the force output. The *shaded area* prior to the force reversal emphasizes the fact that the earlier recruited (slower-twitch, longer contraction time) motor units decrease their firing rates *before* the latter recruited (faster-twitch, shorter contraction time) motor units. The *bottom* of the figure presents the cross-correlation functions of the firing rates and the force, providing a clearer expression of the *lead-time* between the firing rate reversal and the force reversal. 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. Lusher et al (1979) have also demonstrated 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
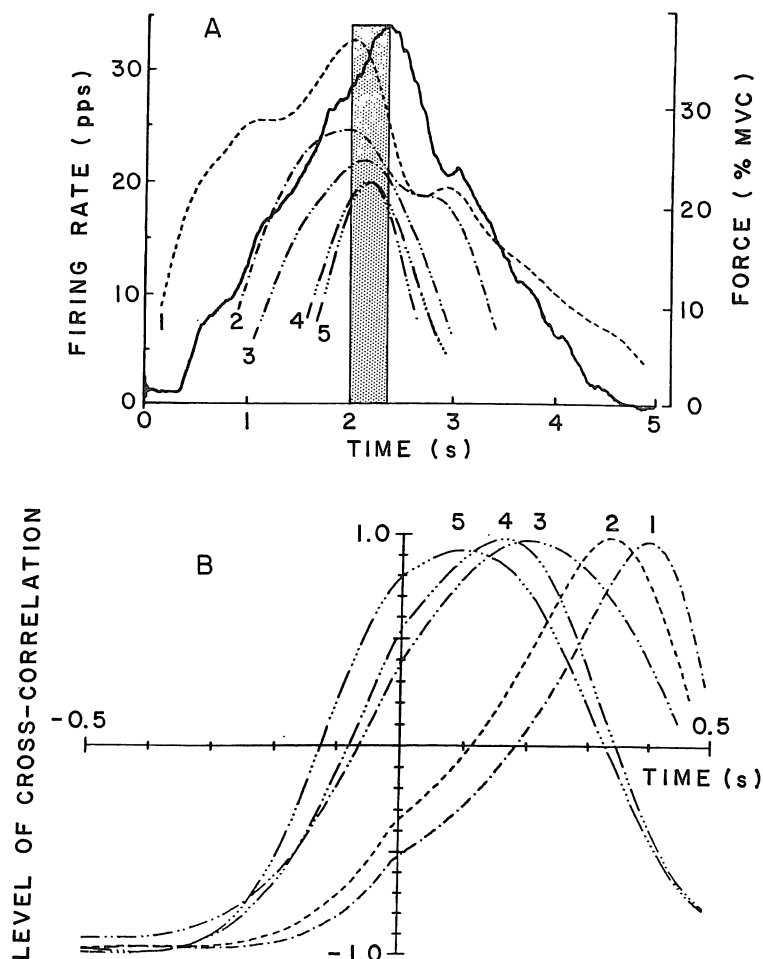
Figure 5.10. (A) Firing-rate records of five concurrently active motor units (*dashed lines*) are shown superimposed on the force output (*continuous line*) recorded during a triangular force-varying contraction of the first dorsal interosseous. Width of *shaded area* illustrates the concept of firing-rate 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. (From C.J. De Luca et al, © 1982b, *Journal of Physiology*.)

the motoneuron pool which competes with the increasing excitatory input in progress. Larger inhibitory postsynaptic potentials 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.

Recruitment

Ordered Progression. The behavior of the process which controls the recruitment of motor units has received considerable attention. One of the most consistent observations of motor unit behavior reported in the literature concerns the order of recruitment as a function of size. For over two decades Henneman and his colleagues, working with decerebrate cats, have compiled considerable data directed at describing a "size principle." This size principle states that the recruitment order within a motoneuron pool progresses from the smallest to the largest motoneuron. The most convenient *in situ* measure of the motoneuron size in a contracting muscle has been found to be the conduction velocity of the axon. And in fact, Henneman and his colleagues have used this measure (as well as others) to argue their case.

The choice or description of the invariant parameter which describes the recruitment of motoneurons (or motor units) has been questioned by Fleshman et al (1981). In a series of related publications, they have been persistent in arguing that the motor unit type, classified according to the electrical-mechanical properties (or fatigue characteristics), has a dominant involvement in the behavior of the recruitment order. Kernell and Monster (1981), working with anesthetized cats, injected a current in α-motoneurons and confirmed that the axons with lower conduction velocities were consistently more excitable than those with faster conduction velocities. However, among fast-twitch motoneurons of about the same size, as measured by their axonal conduction velocity, the average threshold current was about twice as high for cells innervating fatigue-sensitive muscle fibers than for those supplying more fatigue-resistant ones.

These caveats are not necessarily contrary to the basic concept of the size principle because it is generally accepted that motor unit size and twitch tensions are represented as a continuum in the fiber type classifications. In fact, it is conceivable that the nervous system follows a recruitment order strategy which may reflect the orderly increase of the mechanical contribution of the motor units within a muscle.

Freund et al (1975), working with humans, measured the axonal conduction velocities and found that the slower conduction velocities, and thus the smaller axons, were associated with the lower threshold motor units. Clark et al (1978), working with rhesus monkeys, have also confirmed that motor units recruited at lower force levels have longer contraction times and produce smaller twitch tensions than higher threshold motor units. By averaging the force output of the muscle as each action potential from a single motor unit occurred, Milner-Brown et al (1973b) were able to determine the twitch tension of some motor unit. They found a linear relationship between twitch tension and recruitment force, suggesting that the fractional increment in force ($\Delta F/F$) is constant. Goldberg and Derfler (1977), investigating the masseter muscle, found that motor units with high-recruitment thresholds tend to have larger amplitude MUAPs and twitches with greater peak tension than with motor units recruited at lower force levels.

Experiments directed at studying the recruitment order of motor units during relatively fast force increasing contractions, including ballistic contractions, have been performed by Tanji and Kato (1973a), Budingen and Freund (1976), Desmedt and Godaux (1977b, 1978), and De Luca et al (1982a). All these reports with the exception of Tanji and Kato stated that the recruitment order remained invariant as a function of force output and force rate. Tanji and Kato (1973a), Budingen and Freund (1976), and Desmedt and Godaux (1977b, 1978) all noted that the firing onset of a motor unit occurred earlier as the rate of the force output increased. This phenomenon is particularly evident during ballistic or near-ballistic contractions. This *apparent downshift* in force threshold of recruitment was correctly interpreted by Budingen and Freund (1976), who pointed out that in contrast to firing onset, the peak of the force of a motor unit twitch occurs at approximately the *same* muscle tension, regardless of the force rate.

This latter observation indicates that the time of recruitment of a motor unit must be considered as the time when the motor unit contributes to the force output, not the time at which the action potential is noted. This should serve as a reminder that the action potential is an *artifact* of the contractile process, albeit a useful one for investigatory purposes.

De Luca et al (1982a) verified, in human muscles, that when the force output of a muscle is voluntarily decreased, motor units are *decruited* in the opposite order in which they were recruited. This result had been known to occur in decerebrated cats. The observation implies that disfacilitation of the motoneuron pool obeys a principle of ordered behavior also. The ordered decruitment behavior may be usefully associated with thresholds in the diminishing force. Figure 5.11 presents the
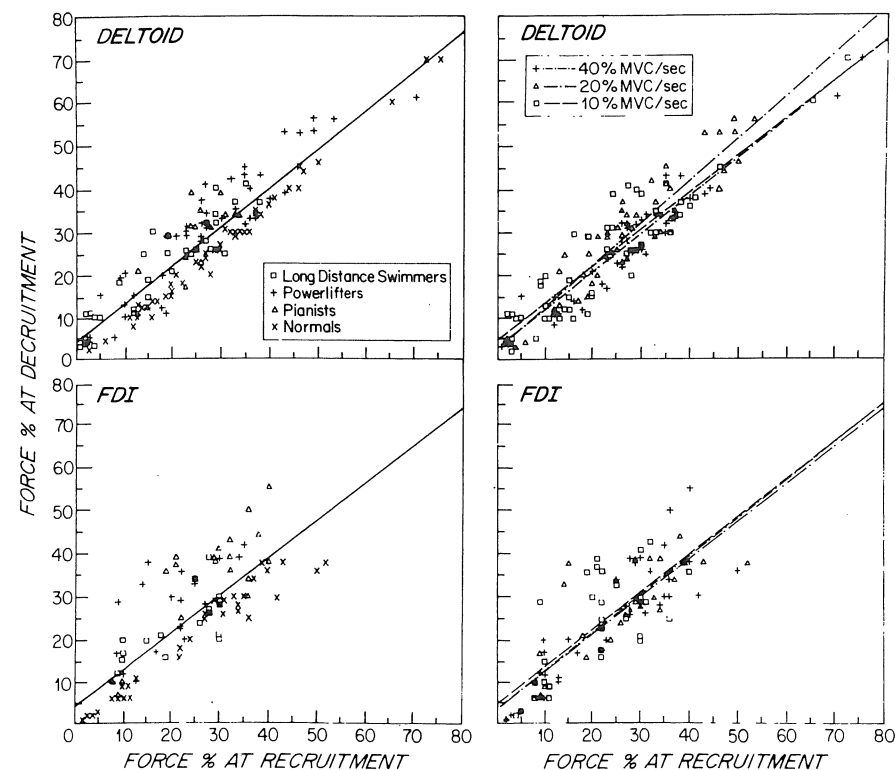
Figure 5.11. Force levels, given as percent maximal voluntary contraction (*MVC*) associated with motor-unit recruitment and decruitment. The linear relationship observed for both muscles (regression coefficients > 0.8; all data grouped) was consistent across all subject groups (*A* and *B*) and was invariant at the three force rates examined (*C* and *D*). Recruitment was only observed up to 52% MVC in the first dorsal interosseous (*FDI*) but was seen as high as 80% MVC in the deltoid. (From C.J. De Luca et al, © 1982a, *Journal of Physiology*.)

force at recruitment plotted against the force at decruitment for motor units which were active during linearly force-increasing and linearly force-decreasing contractions of deltoid and first dorsal interosseous muscle of normal subjects and highly trained athletes. Positive linear correlations were observed in both muscles ($r = 0.94$ for deltoid, $r = 0.83$ for first dorsal interosseous). No significant deviation from this relationship was seen among the four subject groups. Furthermore, Figure 5.11 illustrates invariant behavior across the force rates (nonballistic) of the contractions. This relationship points to a highly ordered recruitment and decruitment scheme which remains invariant with muscle, training, and force rate (nonballistic).

Small upward shifts observed in the regression lines of Figure 5.11 indicate that motor units, in general, have a tendency to cease firing at relatively higher force levels than those at which they began. This effect has also been reported by Milner-Brown et al (1973b). It may simply be an expression of the fact that the force developed by a motor unit lags its discharge.

Modification of Ordered Progression. There have been some reports which have argued that the orderly progression of motor unit recruitment is altered under some conditions.

Tanji and Kato (1973a) reported that the recruitment order is not rigidly fixed among motor units with nearly similar force thresholds. Such observations have also been made in our laboratory. There are at least two possible explanations for such observations. One concerns the instantaneous force-rate at the time of recruitment. If the contractions are not repeated with the identical force rates in the neighborhood of the recruitment thresholds, it is conceivable that the order of two somewhat similarly sensitive motor units may be altered if the rise time of the twitches of the two motor units differs. The other explanation concerns the properties of motoneuron adaptation and/or twitch potentiation. During repeated contractions the twitch responses may be altered so that their mechanical characteristics coincide with the need for an altered recruitment order.

Person (1974) reported that the recruitment order was stable for a given movement task but could be altered when the muscle performed a different movement task. Thomas et al (1978) noted that recruitment order reversal occurred during markedly different orientations in multifunctional muscles such as the abductor pollicis brevis and extensor digitorum; none was seen in the first dorsal interosseous. Desmedt and Godaux (1981), however, did report order reversal in the first dorsal interosseous. Romeny et al (1982), working with the biceps brachii, also reported observing changes in the recruitment order, depending on the function (flexion or supination) performed by the muscle. All three reports stated the reversal was not consistent. Desmedt and Godaux reported a reversal between motor unit pairs only in 11.2% of the motor units which they observed. All three of these investigations used fine-wire electrodes to detect the signals. The reader is referred to the discussion on detection techniques in Chapter 2. Note that a relative movement of 0.1 mm between the detection surfaces of the electrodes and the active fibers may cause considerable modifications in the shapes of the MUAPs, the parameter that is used to determine if a new motor unit is recruited. Considering that the reversal has been noted almost exclusively during contractions of markedly different orientations, any claim for recruitment reversal must first prove that the electrode does

not migrate into the territory of other motor units. None of the published studies addresses this question. This necessary query shows that the inquisitiveness of an investigator should be tempered with the technicality of an engineering approach. The reported reversal may in fact occur, but it is yet to be proven.

An unquestionable reversal of the recruitment order of motor units has been artificially induced in the first dorsal interosseous by Stephens et al (1978). They noted that prolonged electrical stimulation of the digital nerves of the index finger induced a reversal of recruitment order. This phenomenon persisted for some time after the stimulation ended. Similar results have been obtained by Mizote (1982) working with the lumbricals of anesthetized cats.

Recruitment as a Function of Muscle. An overview of the available literature reveals that the recruitment scheme varies among muscles. In some muscles all the motor units are recruited at force levels well below maximal while in others, recruitment continues up to maximal. A clear example of this phenomenon may be seen in Figure 5.11, where in the first dorsal interosseous, all the motor units were recruited below 50% MVC, whereas in the deltoid, recruitment persisted up to nearly 80% MVC and may have been present even at higher force values. Milner-Brown et al (1973a) reported similar observations for the first dorsal interosseous. Kukulka and Clamann (1981) reported that in the biceps brachii, recruitment was observed up to 80% MVC, whereas in the adductor pollicis none was observed above 50% MVC. Kanosue et al (1979) found recruitment up to at least 70% MVC in a relatively large muscle, the brachialis.

The accumulation of the above individual pieces of evidence indicates that small muscles, such as those found in the hand, recruit all their motor units below 50% MVC and larger muscles found in the limbs recruit motor units throughout the full range of voluntary force. A possibility may exist that in some muscles such as the soleus and gastrocnemius, not all the motor units are activated during perceived maximal efforts (Belanger and McComas, 1981). Although in a smaller muscle, the adductor pollicis, both Merton (1954) and Bigland-Ritchie (1982) reported that all the motor units do become activated. However, in the latter case it has been correctly pointed out by Belanger and McComas (1981), that the thenar musculature contributing to adduction of the thumb is complex and is not all innervated by one nerve, thus complicating the rationale for comparing the force output during perceived voluntary maximal contractions and tetanic electrical stimulation of muscles via their innervation.

Recruitment as a Function of Time. It is now generally accepted that human muscles contain motor units which have a continuum of mechan-

ical characteristics. The faster-twitch muscle fibers which comprise the motor units that are recruited at higher force-thresholds decrease their mechanical output at a faster rate than earlier recruitment slower-twitch muscle fibers. Thus, a question arises concerning the possibility of motor units being recruited during a sustained contraction.

Several investigators have reported that during a constant-force iso-metric contraction, new motor units ought to be recruited throughout the duration of the contraction. (Edwards and Lippold, 1956; Vrenden-bregt and Rau, 1973; Person, 1974; Maton, 1981; and Kato et al, 1981). In fact we have made observations in our own laboratory which could be construed as supporting this position. However, such an interpretation must be cautioned. All experiments to date which have addressed this question have been restricted to relating the time-dependent behavior of recruitment to the torque measured at the affected joint. This torque is the result of the individual torques of all the agonists minus that of all the antagonist muscles. Thus, it is conceivable that the monitored torque output remains constant while the separate contributions from the ago-nist and antagonist muscles vary linearly. An extreme example of this complication is presented by Figure 5.9. In this case the joint is stiff, the torque output is approximately zero, and several motor units are active in the agonist and the antagonist.

It is clear that much more work is required on this problem before a generalized statement may be made.

Firing Rate and Recruitment Interaction

Interaction within a Muscle. At the beginning of this chapter a descrip-tion of the peripheral systems which affect the control properties of motor units was presented. Referring to that text and to Figure 5.1, it may be seen that considerable anatomical and functional coupling exists among the motor units within a muscle. Such an interaction was indeed found by Broman et al (1984) and is displayed in Figure 5.12. In this study it was found that when a motor unit is recruited during slow force 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 discharge 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.
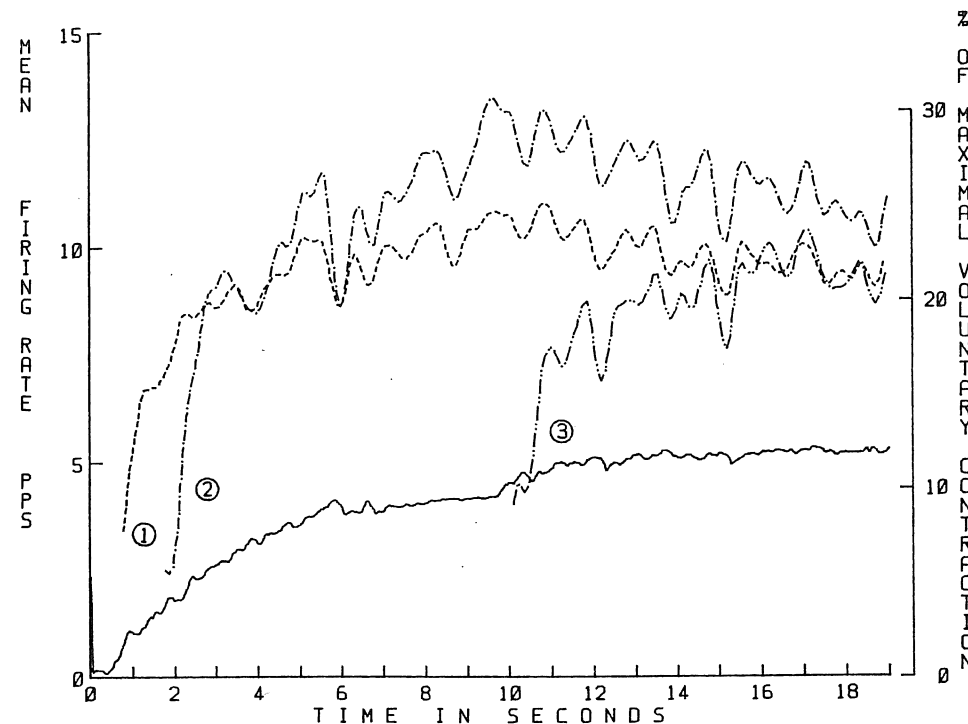
Figure 5.12. Firing rates (*broken lines*) of three concurrently active motor units of the tibialis anterior muscle recorded during an isometric contraction. The force (*solid line*) is presented as a percentage of the maximal voluntary contrac-tion (*right scale*). Note the gradual decrease of the firing rates of the top two tracings as the third motor unit is recruited.

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 dis-facilitate the pool and thus decrease the "drive" to the active motoneu-rons, 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 inter-action: (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, complement-ing 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 by small ones (Ryall et al, 1972; Pompeiano et al, 1975). Consequently, if the Renshaw cell inhibitory action on the α-motoneuron pool is achieved in a size-related fashion (with the small diameter motoneuron being affected more than the 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 which 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 are represented schematically in Figure 5.13. 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, later recruited motor units should have a stronger effect on the firing rates of previously activated motor units, as may be noted in Figure 5.13.

Interaction in Different Muscles. It is apparent 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 to 50% MVC and rely exclusively on firing rate increase to augment the force output between 50 and 100% MVC. The firing rates of these muscles continuously increase with the force output reaching values as high as 60 pps. 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 to 40 pps, and tend to demonstrate a plateauing effect.

Smaller muscles rely primarily on firing rate, and larger muscles rely primarily on recruitment to modulate their force. For an example of this phenomenon, refer to Figures 5.6 and 5.11.
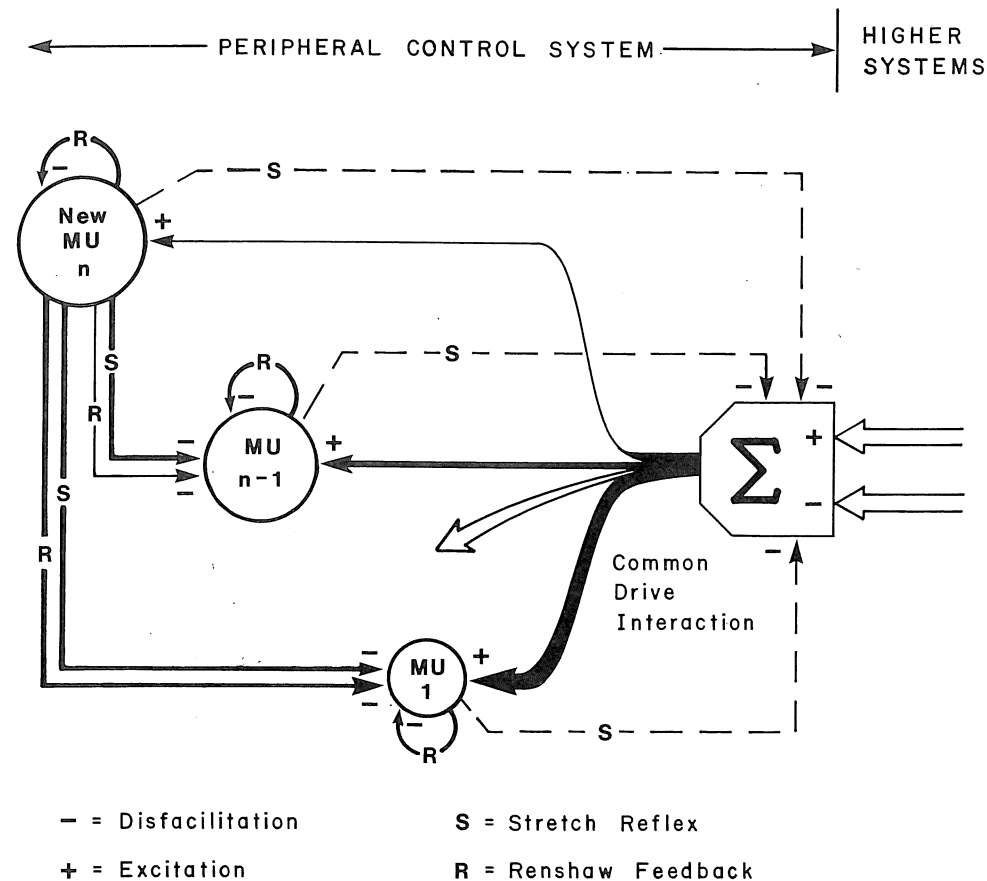
Figure 5.13. Schematic diagram describing the concept of the common drive and phenomenon of recruitment/firing rate interaction during a voluntary contraction. In this representation the excitatory and inhibitory inputs from sources other than the peripheral control system are shown to act on the motoneuron 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.

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 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 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.

The functional requirement of the muscle, coupled with the anatomical constraints of it, determine the firing rate-recruitment characteristics which the nervous system engages to achieve the required task. 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.

SUMMARY

The following description emerges from the information presented in this chapter.

1. The firing rates of motor units are muscle dependent. In small muscles, such as those in the hand, the firing rates begin firing at relatively lower values and reach relatively higher values than those in motor units of larger limb muscles. In larger muscles, the firing rates tend to plateau at 20 to 25 pps, whereas in small muscles the firing rates have a greater dynamic swing, reaching values of 60 pps.
2. During strenuous and high (>70% MVC) level contractions, the firing rate of high threshold motor units may display an abrupt and dramatic increase.
3. In abnormal (dysfunctioned) muscles, the firing rate of motor units appears to behave differently than that of healthy muscles.
4. During sustained contractions, the firing rate of motor units decreases as a function of time. This adaptation of the firing rate is complemented by an increase in the twitch tension of motor units. Data suggest that these two phenomena are more evident in fast-twitch fibers than in slow-twitch fibers.
5. A common drive exists which modulates the firing rates of all motoneurons of a homonymous pool. This indicates that the nervous system does not control the motor units individually.
6. Higher force-threshold motor units consistently have lower firing rates than the lower force-theshold motor units.
7. A muscle cannot generate a pure constant-force contraction in isometric conditions because the firing rates of the motor units are continuously perturbed.
8. Force reversals are accomplished by an ordered progression of firing rate decreases. The earlier recruited motor units decrease their firing rates before the latter recruited motor units.
9. Motor units are recruited and decruited in an orderly progression, possibly according to a size principle. The decruitment occurs in the opposite order of recruitment.
10. Modifications in the ordered progression of recruitment can be induced via electrical stimulation of sensory nerves.
11. The recruitment scheme varies among muscles. In smaller muscles, such as those in the hands, most of the motor units are recruited below 50% MVC, whereas in larger muscles in the limb, recruitment persists up to at least 90%, possibly 100% MVC.
12. The issue of motor unit time-dependent recruitment during constant-force isometric contractions is unsettled.
13. During force increasing contractions, newly recruited motor units have been observed to disfacilitate (decrease the firing rate of) previously activated motor units. This interaction may be explained by invoking the involvement of the stretch reflex and recurrent inhibition. This interaction provides a mechanism which enables the muscle to increase the smoothness of its force output.
14. Smaller muscles rely primarily on firing rate, larger muscles on recruitment to modulate their force. It is conceivable that the nervous system is configured to balance the contribution of the firing rate and recruitment control, so as to enhance the smoothness of the force output of the muscle.