MOTOR UNIT RECRUITMENT PATTERNS IN MULTIFUNCTIONAL MUSCLES

by

Stephan Riek

B.Sc. (Kinesiology), Simon Fraser University, 1990

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the School of Kinesiology

SIMON FRASER UNIVERSITY

July 1991

APPROVAL

Name: Stephan Riek

Degree: Master of Science

Title of thesis: Motor Unit Recruitment Patterns in Multifunctional Muscles

Examining Committee:

Chair: Dr. Igor Mekjavic

Dr. Parveen Bawa
Professor
Senior Supervisor

Dr. Arthur Chapman
Professor

Dr. Charles Krieger
External Examiner
Faculty of Medicine
University of British Columbia

Date Approved: July 26, 1991

Title of Thesis/Dissertation:

MOTOR UNIT RECRUITMENT PATTERNS IN MULTIFUNCTIONAL MUSCLES

Author:

(signature)

STEPHAN RIEK

(name)

Aug 7, 1991

(date)

ABSTRACT

During muscle contraction, motor units are proposed to be recruited in an orderly manner from small to large. This is known as the size principle of motor unit recruitment and has been observed during simple voluntary and reflex contractions. One muscle, however, generally contributes to more than one function and can contain more than one task group of motor units to perform each function.

This study examined motor unit recruitment of extensor carpi radialis muscle (ECR) during wrist extension and radial deviation and extensor digitorum communis muscle (EDC) during wrist extension and various finger extensions. Single motor unit potentials and force were recorded during voluntary contractions to determine twitch tension and recruitment threshold of each recorded unit. ECR units did not show separate task groups of motor units for wrist extension and radial deviation. Orderly recruitment of ECR units was observed for each of these contractions. During finger extensions, EDC units were divided into three main subpopulations: one contributing to middle finger extension, a second to ring finger extension and a third to both middle and ring finger extensions (common units). During extension of the middle finger, orderly recruitment was observed for the task group formed by the combination of middle finger and common units. Similarly, for ring finger extension, orderly recruitment was observed for the task group formed by ring finger

and common motor units. All motor units of EDC, comprising different task groups for fingers, form a composite task group for wrist extension. Orderly recruitment was also observed for this composite task group for wrist extension.

ACKNOWLEDGEMENTS

Special thanks go to Dr. Parveen Bawa for her continual support, encouragement and emphasis on high standards thoughout my tenure as a graduate student. I would also like to thank Dr. Arthur Chapman for his input into this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The control of movement can be studied from a number of perspectives using both animal and human models. Whatever the perspective, the expression of movement is through muscular contraction. This introduction deals with the organization of the neuromuscular system; a system which allows a seemingly endless repertoire of human movements.

Control of muscle contraction originates in the central nervous system and is expressed through the functional unit of muscle: the motor unit. A motor unit comprises a single alpha motoneuron and the muscle fibres which it innervates (referred to as its muscle unit). A variety of physiological and histochemical techniques indicate that the fibers within a single muscle unit are uniform in the cat medial gastrocnemius (MG) muscle (Burke et al., 1973), and the anterior tibialis muscle of the rat (Edstrom and Kugelberg, 1968). Perhaps the most extensively studied muscle in terms of motor unit populations is the MG muscle of the cat (Burke, 1968; Burke et al.,. 1971; Henneman and Olson, 1965; Stephens and Stuart, 1975). Burke et al. (1973), divided motor units of MG into 3 types: S, FR and FF. Type S units do not exhibit sag in tension output, and are highly resistant to fatigue (fatigue index ≥ 0.75). They also have long contraction times and generated small tetanic tensions. Type FF units are highly susceptible to fatigue (fatigue index ≤

0.25), show sag in tension, have short contraction times and generated high tetanic tensions. Type FR also have fast contraction times and show sag in tension, but are resistant to fatigue (fatigue index ≥ 0.75). Their tetanic tension tend to be between type S and type FF. This nomenclature for describing different motor units has also been used for motor unit populations of the cat tibialis anterior (Dum and Kennedy, 1980) and plantaris muscles (Zajac and Faden, 1985).

Peter et al., (1972) developed a classification scheme for muscle fibres based on their metabolic activity: SO (slow twitch, oxidative), FG (fast twitch, glycolytic) and FOG (fast twitch, oxidative-glycolytic). The histochemical profiles of fibers within a muscle unit match the above physiological profiles of the different motor units. Type S motor units have fibers which have high concentrations of oxidative enzymes (fiber type SO) . Type FF units, on the other hand, have low concentrations of oxidative enzymes but high concentrations of glycogen, glycolytic enzymes and myofibrillar ATPase (fiber type FG). Type FR units have muscle fibres with intermediate concentrations of glycolytic and oxidative enzymes (fiber type FOG). This nomanclature for classifying motor unit types has been successful for heterogeneous limb muscles of the cat (Burke et al., 1971; Burke et al., 1973; Collatos et al., 1977) guinea pig (Peter et al., 1972) and humans (Essen et al., 1975).

The differences in the alpha motoneurons which innervate the different unit types form a continuum. Those which innervate fast motor units are large, have low input resistance, and large axons giving them high axonal conduction velocities. Those innervating S type units tend to be small, have high input resistance and small axons, giving them slow axonal conduction velocities (Burke et al., 1982). The size of the alpha motoneuron is an important factor in determining the tension which a motor unit can produce. For one muscle, larger motoneurons with their large axons can innervate more muscle fibers than small motoneurons. This gives them a large innervation ratio and greater tension output (Henneman and Mendell, 1981). Innervation ratios tend to be high in large limb muscles and small in the intrisic muscles of the hand and eye where fine motor control is required (Burke, 1981).

The motoneurons innervating fibers of the same muscle make up a motoneuron pool. Constituents of a single pool are arranged in longitudinal columns within the ventral horn of the spinal cord. Motoneuron pools innervating axial musculature tend to be concentrated in the medial regions of the ventral horn (Rexed's lamina IX) while those innervating limb musculature are concentrated more laterally (Burke, 1981). The motoneuron pools of anatomically similar muscles can share the same longitudinal column as in the case of the medial gastrocnemius and soleus muscles of the cat (Burke et al., 1977).

I. Recruitment of Motor Units

The isometric force production of a muscle is determined by the number of active motoneurons within a pool and the rate at which they fire. This force can be increased by increasing the number of active motor units, referred to as "recruitment", and/or by increasing the rate at which the active units fire, referred to as "rate coding" (Stein, 1974). It has been shown that of all the motor units properties, size is of particular importance in the control of recruitment (Henneman et al., 1965).

a) Animal Studies

Many studies examining the recruitment pattern of motoneurons have been performed on decerebrate cat preparations. While recording from cut L7-S1 ventral roots, Henneman (1957) observed a progressive increase in the amplitude of newly recruited action potentials as the intensity of stimulation to the dorsal root was increased. Since the amplitude of a recorded discharge of an axon varies directly with the axon diameter (Clamann and Henneman, 1976) and axon diameter is related to cell size, then small amplitude discharges must originate from small motoneurons and large amplitude discharges must originate from large motoneurons. The order of motoneuron recruitment, therefore, is from small cells to large cells. This has been referred to as the "size principle" of motoneuron recruitment (Henneman et al., 1965).

The functional significance of this "size principle" is based on two observations: small motoneurons tend to innervate small tension producing muscle units (Henneman and Olson, 1965; Burke et al., 1982) and small motor units tend to be highly resistant to fatigue (Zajac and Faden, 1985). This allows small forces to be maintained for long periods of time. As tension demands increase, larger increments of force are added with recruitment of larger motor units, resulting in a smooth increase of force production.

Henneman and co-workers were the first to perform systematic studies providing a variety of both excitatory and inhibitory inputs to the spinal cord, and higher centres of decerebrate or anaethetized cats in an effort to determine whether the size related recruitment order is maintained for all inputs to the motoneuron pool (Henneman et al., 1965; Somjen et al., 1965). Upon stretch of the triceps surae muscles small amplitude action potentials, recorded from the L7 or S1 ventral roots, were observed first followed by larger amplitude spikes as the stretch was increased (Henneman et al., 1965). For crossed-extensor reflexes, extensor reflexes mediated by interneurons, flexor reflexes and monosynaptic reflexes (Henneman et al., 1965) as well as for inputs to the brainstem, cerebellum, basal ganglia, and motor cortex (Somjen et al., 1965) orderly recruitment of motoneurons according to the size principle was observed. These results suggest that the size of a motoneuron is strongly correlated, and varies inversely, with its susceptibility to discharge regardless of the source of excitatory stimulation.

Susceptibility to inhibition also seems to be a function of motoneuron size (Henneman et al., 1965). Weak stimulation of the ipsilateral peroneal nerve during a maintained stretch of the triceps surae in decerebrate cats resulted in inhibition of the largest motoneurons that had been recruited during the stretch (Henneman et al., 1965). As the intensity of this inhibition was progressively increased, smaller and smaller motoneurons were inhibited until only the smallest motoneuron remained during the strongest inhibition. Thus, susceptibility to inhibition varies directly, not inversely, with motoneuron size.

Throughout these early experiments, pairs of units were qualitatively compared and few exceptions to orderly recruitment were noted (Henneman et al., 1965). In an effort to quantify the order of recruitment of a pool of motoneurons, a technique was devised to rank order a given motoneuron as a percentage of the maximum monosynaptic output of the motoneuron pool (Clamann et al., 1974). The activity of a single motoneuron from the L7 ventral root was recorded simultaneously with the activity of the pool of motoneurons in the S1 ventral root in response to stimulation of the corresponding Ia afferents from the combined medial and lateral gastrocnemius and soleus nerves . As long as the post-tetanic response of the motoneuron pool exceeded a certain level, the given motoneuron recorded from the L7 ventral root discharged with every stimulus to the Ia afferents. When the population response fell below this level the single motoneuron ceased firing. The level of the pool's response corresponding to the discharge of the motoneuron was termed its critical firing level (CFL) and was expressed as a percentage of the maximum post-tetanic response of the pool during the monosynaptic reflex (Henneman et al., 1974). Using this technique, a number of motoneurons within a pool could be ranked in order of their CFLs (Henneman et al., 1974; Zajac and Faden, 1985).

CFL has also been related to axon size (Clamann and Henneman, 1976) and axonal conduction velocity (Clamann et al., 1983), suggesting that conduction velocity can be used as an indicator of cell size and recruitment order. Positive correlations between CFL and conduction velocity have been demonstrated in three cat hindlimb muscles (medial gastrocnemius, plantaris and tibialis anterior) in response to dorsal root stimulation (Clamann et al., 1983). Supporting these observations, recruitment order has been highly correlated with axonal conduction velocity in response to stretch reflex in medial gastrocnemius and soleus (Bawa et al., 1984) and in plantaris (Zajac and Faden, 1985) in decerebrate cats.

In addition to axonal conduction velocity, recruitment order has been correlated with the tetanic tension of the motor unit (Zajac and Faden, 1985). Tetanic tension was determined by stimulation of isolated motor axons at 100 pulses per second for up to 1 second. In each of 42 pairs of plantaris motor units of anesthetized cats, the units having the lower threshold for recruitment had the lower tetanic tension and in 30 of the 42 pairs the weaker units also had the slower axonal conduction velocity (Zajac and Faden, 1985).

Sypert and Munson (1982) suggested that motor units were recruited in order of type (S to FR to FF) rather than size and that recruitment order of motor units of the same type is random. The cat soleus is considered to be homogeneous with respect to fiber type (Henneman et al., 1965) yet recruitment of motor units in order of increasing conduction velocity has been observed (Bawa et al., 1984). The axonal conduction velocity of pairs of units were compared to their recruitment order. For differences in conduction velocity as little as 2 m/s, the slower conducting motoneuron was recruited first. According to the observations of Sypert and Munson, one would expect to see random recruitment order among motor units of the same type but different conduction velocities. Hence the majority of animal studies support orderly recruitment according to size.

b) Human Studies

The use of human subjects over animals has certain advantages for recruitment studies. Human subjects can voluntarily make graded contractions of different magnitude and speed or hold desired tensions at will. The movement repertoires for studying motor unit recruitment are therefore more extensive.

Orderly recruitment of human motor units was first demonstrated by Stein and co-workers (Milner-Brown et al., 1973). In this study, single motor unit (SMU) action potentials and tension were recorded from the first dorsal interosseus (FDI) muscle during voluntary isometric contractions. Twitch tensions of individual motor units were determined using the spike triggered averaging (STA) technique (Stein et al., 1972) and plotted with respect to the force at which the unit was recruited (recruitment threshold). The resulting linear relationship suggested small motor units were recruited before large motor units. This confirmed that motor units in human FDI muscle were recruited in an orderly manner.

Similar techniques have been used to show orderly recruitment in the human masseter (Goldberg and Derfler, 1977; Yemm, 1977), temporalis (Yemm, 1977), abductor pollicis brevis (Thomas et al., 1987), flexor carpi radialis (Calancie and Bawa, 1985), extensor carpi radialis longus and brevis and extensor carpi ulnaris (Romaiguere, 1989) and extensor digitorum communis during middle finger extension (Monster and Chan, 1977).

The studies mentioned above required the subjects to perform slow isometric contractions. Recruitment at different rates of contraction have also been investigated. Desmedt and Godaux (1977), showed that the relative recruitment order of pairs of tibialis anterior motor units during slow ramp contractions was the same as for fast ballistic contractions.

c) Alternative Patterns of Recruitment

Although there is considerable evidence suggesting motor unit recruitment occurs according to the size of the motor unit in a variety of conditions, some investigators have presented different patterns of recruitment. It has been argued that motor units can be selectively activated if appropriate visual and auditory feedback is provided (Basmajian, 1963). It should be noted that selective control could only be demonstrated on the lowest threshold unit recorded and no evidence of conscious control of recruitment order of the entire pool has been presented.

In a study by Kanda et al. (1977), motor units from medial gastrocnemius were recruited in an orderly manner by stretch or vibration in decerebrate or anesthetized cats . However, when the skin innervated by the sural nerve was simultaneously stimulated, low threshold units were silenced while high threshold units were powerfully recruited. Garnett and Stephens (1981), investigated whether similar changes in recruitment threshold in response to cutaneous stimulation occured in humans performing grasping tasks. They found that the recruitment threshold of relatively high threshold units was reduced while recruitment threshold of low threshold units was increased. The functional significance of this altered pattern of recruitment may be to facilitate holding objects between the thumb and forefinger. The object would produce cutaneous input to the system and help reinforce the grip by promoting recruitment of larger, more powerful units (Garnett and Stephens, 1981). It was suggested that the input to the motoneuron pool for cutaneous afferents may be organized by motor unit type (Garnett and Stephens, 1980).

In a similar study, Kanda and Desmedt (1983) found a reduction in recruitment threshold of FDI motor units during a gripping manoeuvre following cutaneous stimulation by rubbing the thumb and index finger together. The reduction in recruitment threshold was seen in high threshold units such that reversals in recruitment were observed. It was concluded that cutaneous stimulation facilitates recruitment of high threshold units while leaving low threshold units unaffected.

II Task Groups in Multifunctional Muscles

Recent studies have demonstrated that some multifunctional muscle may be divided into task groups. A task group encompasses all the motor units which work in conjunction to perform a given task (Loeb, 1990). The order of motor unit recruitment within a multifunctional muscle has been suggested to depend on the function performed by the muscle (Desmedt and Godaux, 1981). Desmedt and Godaux, (1981) found that for the majority of unit pairs studied in FDI, the unit with the higher threshold for abduction also had the higher threshold for flexion. They also found a small population of units that showed a reversal in recruitment order between abduction and flexion. Thomas et al. (1985) studied recruitment order and twitch tension in the same muscle, FDI, during abduction and flexion of the index finger. The twitch tension of the SMUs showed similar time courses with each contraction, however, the greatest tension was developed when the muscle acted as a prime mover (abduction). Each motor unit contributed approximately the same proportion of tension during each contraction. Consistent linear relationships between motor unit twitch tensions and recruitment threshold during each contraction were found, suggesting that no alterations in motor unit recruitment occured in response to contraction in the different directions. It was felt, however, that there was sufficient scatter in the data to account for the small number of recruitment reversals noted earlier by Desmedt and Godaux (1981). An absence of task specific motor units was suggested for FDI since no units were activated more easily during one contraction than the other (Thomas et al., 1985).

Another multifunctional muscle, biceps brachii, has been studied by ter Haar Romeny et al. (1982, 1984). Single motor unit potentials from the long head of biceps brachii were recorded under three movement conditions; flexion/extension, supination/pronation, and exorotation/endorotation. Subjects were asked to maintain a level of force in one direction then increase the force in one of the other directions. Force in the third direction remained zero. For each combination, the order of recruitment between a pair of units recorded at different sites was determined. The critical firing level (CFL), in this case was defined as the combination of two forces at which the unit was recruited. This definition is different from that of Henneman et al. (1974; see page 7 of this INTRODUCTION). When plotting CFL for flexion versus supination, three types of graphs were evident. Units recruited only by flexion were found on the lateral side of the muscle. The CFL for these units was unaffected by the level of supination/pronation or exorotation/endorotation. Units that could be recruited by a combination of supination and exorotation, regardless of the level of flexion were found on the medial side of the muscle. Located centrally were units which responded to a combination of flexion and supination and their thresholds were linearly summated. Units silenced during pronation, regardless of the level of flexion or supination, were found medially. In an attempt to explain these results, ter Haar Romeny et al. (1984), developed a model of synaptic input to motoneurons of the long head of the biceps. They suggested an overlap of motoneuron pools of the biceps and supinator muscles. Flexion inputs extended only to the neurons innervating muscle units in the most lateral portion of the muscle. The summing units, found centrally, received both flexion and supination input, while the most medial units received only supination input. In addition to these excitatory inputs, inhibition from pronation affected the most medial units and a portion of the central units. This type of model would explain the location dependant motor unit activity that was observed (ter Haar Romeny et al., 1984) and suggests that some populations of motor units can be selectively recruited for specific tasks.

It appears that some multifunctional muscles contain different task groups while others do not. Task groups have also been shown to exist in the sartorius muscle of the cat during locomotion (Hoffer et al., 1987).

OBJECTIVES

In this project, the motor unit recruitment patterns in a single tendon, multifunctional muscle (extensor carpi radialis, ECR) and a multitendon, multifunctional muscle (extensor digitorum communis, EDC) were studied. ECR originates from the lateral epicondyle of the humerus, runs along the radial side of the forearm and inserts on the dorsum of the third metacarpal of the hand. It acts in synergy with extensor carpi ulnaris (ECU) to extend the wrist. It also acts in synergy with flexor carpi radialis (FCR) to radial deviate the hand (Goss, 1976). *Do separate subpopulations of motor units of ECR contribute to wrist extension and radial deviation and what is the recruitment order of motor units within each subpopulation?*

The extensor digitorum communis (EDC) muscle arises from the lateral epicondyle of the humerus and divides distally into four tendons. The tendons pass through a separate compartment of the extensor retinaculum and insert into the second and third phalanges of the fingers. On the back of the hand, the tendons of the middle, ring and little fingers are connected by oblique running bands. The main function of EDC is finger extension but it also participates in wrist extension (Goss, 1976). *Do separate subpopulations of motor units of EDC contribute to wrist extension and various finger extensions? What is the recruitment order within each* *subpopulation? Also, for the function of wrist extension, how does the contribution of EDC (mainly a finger extensor) compare with the contribution of ECR (a prime wrist extensor)?*

METHODS

Experiments were carried out on four healthy subjects (1 female and 3 males) with no history of neurological disease. All subjects signed informed consent forms before participating in the experiments. The study was approved by Simon Fraser University's Ethics Committee for Human Experiments. The experiments required extension of the wrist, radial deviation of the wrist and extension of the middle finger and ring finger in order to study the relationship between recruitment threshold and twitch tension for various contractions paradigms. The following physiological parameters were monitored during the experiments and data were analyzed offline.

I. Force Measurement

a) Wrist Extension

To measure tension during wrist extension, the subject's right arm rested on a horizontal pad such that the axis of rotation of the wrist was coaxial with a vertical shaft (figure 1A). A handle secured against the dorsum of the hand was connected to the vertical shaft by a horizontal bar equipped with strain gauges. The position of the vertical handle was adjusted for each subject's hand and the distance from the handle to the axis of wrist rotation was measured. Strain gauge output from the bridge amplifier (DC-1000Hz

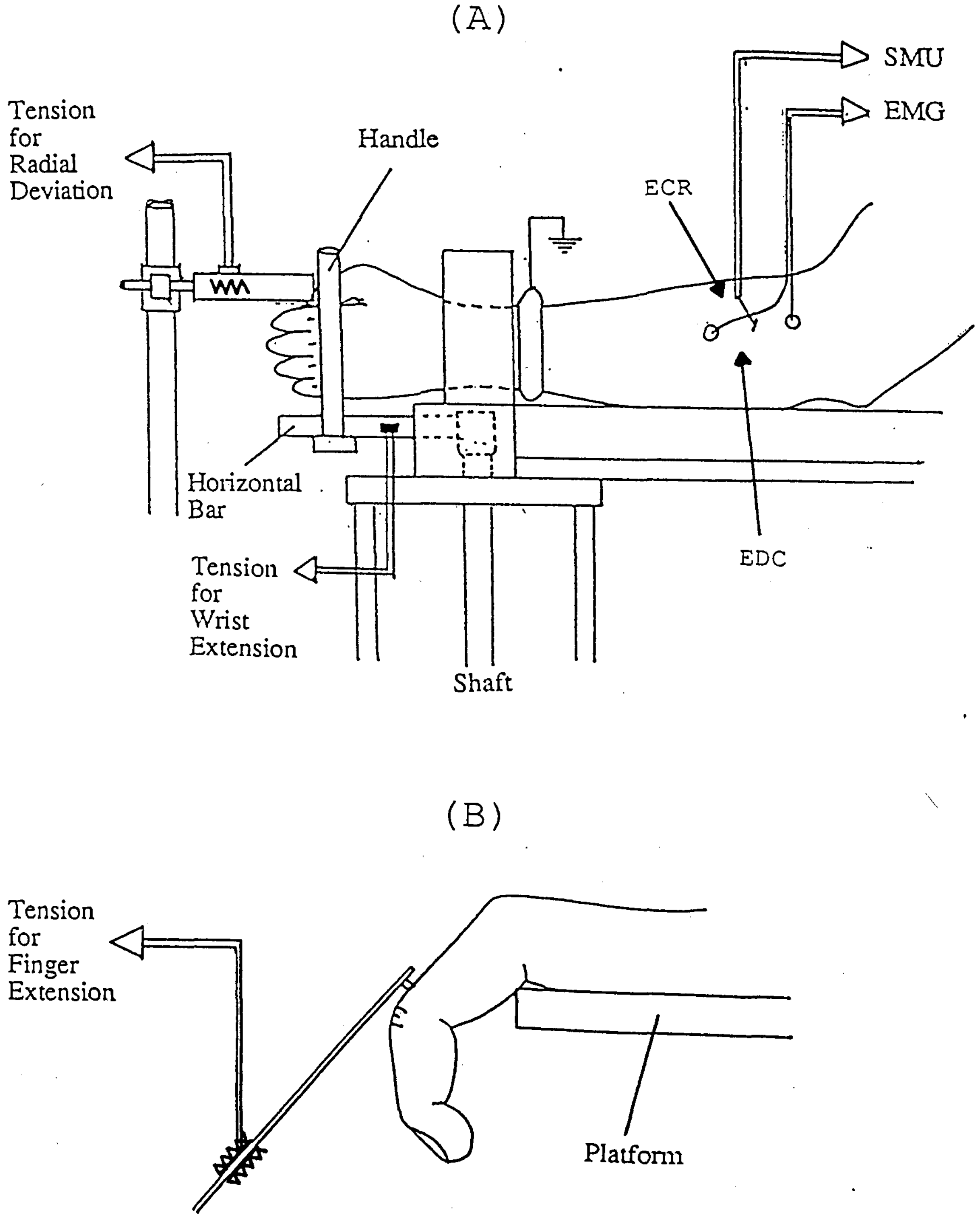

Figure 1. Experimental set-up. (A) The subject's hand was stablized on the horizontal platform. Force, surface EMG and SMU action potentials were recorded from ECR during wrist extension and radial deviation and from EDC during wrist extension. (B) Experimental set-up for recording tension during finger extension. See METHODS for further details.

bandpass) was fed to two different conditioning amplifiers. From one channel, DC tension was recorded at low gain and was used to determine the unit's recruitment threshold. The second channel was highpass filtered at 0.1 Hz (AC tension) and recorded at high gain. The AC tension was used for spike triggered averaging to compute the twitch tension of each single motor unit. Both AC and DC tensions were recorded on VCR (Vetter PCM recorder).

b) Radial Deviation

During radial deviation, force was measured using a Grass FT10 or FT03 force transducer. With the subject in position for measuring extension force, the transducer was placed on the radial side of the hand, just proximal to the second metacarpophalageal joint. Both AC and DC tension were recorded in the same manner as during wrist extension.

c) Finger Extension

Recruitment order of extensor digitorum communis (EDC) motor units was examined during middle finger and ring finger extension in two subjects. In these experiments, the subject's hand was pronated and secured on a stable platform (figure 1B) with the fingers extending beyond the edge of the platform. With the fingers flexed, a strain gauge assembly was placed against the dorsal surface of the middle or ring finger just proximal to the first interphalangeal joint to measure force during extension. Both AC and DC tension were recorded as outlined above.

II. Single Motor Unit Recording

Single motor unit (SMU) potentials were recorded from EDC and extensor carpi radialis (ECR) using bipolar intramuscular electrodes. These electrodes consisted of two 75 or 50 micrometer stainless steel wires coated with HML or teflon. The wires were held, with epoxy, in the barrel of a 25 gauge needle for ease of insertion. The electrode was connected to a Grass P15 AC preamplifier (100Hz-10KHz) and recorded on a Vetter PCM recorder. The subject received both visual and auditory feedback to help control the firing rate of the motor unit.

III. Surface Electromyographic Recording

Surface electromyographic (EMG) activity was recorded from EDC and ECR using two circular Ag-AgCl electrodes placed over the muscle. The signal was fed to a Grass P15 AC preamplifier (30Hz - 3KHz) and recorded on a Vetter PCM recorder.

IV. Procedure

Before computing twitch profiles of voluntarily recruited single motor units, it was considered essential to estimate the time course of the twitch profiles of ECR and EDC. This would also ensure that the force recording set up was appropriate. Force in the wrist extension and radial deviation directions were recorded simultaneously during surface stimulation of ECR (approximately 80 - 110 volts at 400μs duration, 0.5 per second). Similarily, force in the wrist extension, middle finger extension and ring finger extension directions was recorded during surface stimulation of EDC (approximately 80 - 110 volts at 400μs duration, 0.5 per second).

During spike triggered averaging for wrist extension, radial deviation and finger extension contractions, subjects were asked to exert enough force to recruit a clearly identifiable motor unit and hold its firing rate at a constant and slow rate (less that 10 pulses per second) to minimize the fusion of twitches. The subject held this contraction for approximately 1-2 minutes. The procedure was repeated for as many motor units that could be clearly identified for each electrode position before the electrode was moved to a new position.

For EDC, motor units were tested to determine whether sub-populations existed for various finger extensions. This was done by isometric contraction of each finger against an extension load and noting which motor units were active. Units were divided into three populations: one contributing to middle finger (MF) extension, a second contributing to ring finger (RF) extension and a third contributing to both middle finger and ring finger (Common) extension. The index and little fingers were ignored since they receive a strong contribution from other muscle during extension. Similarly, for ECR each motor unit was identified as belonging to wrist extension, radial deviation, or both wrist extension and radial deviation populations.

V. Analysis

Data analysis was done offline on a Dell 310 microcomputer. The recruitment threshold of each motor unit was determined from the DC force replayed on a storage oscilloscope. For ECR, the threshold was defined as the force at which the unit began to fire tonically. However, once an EDC unit was recruited during wrist extension, two of the four subjects dramatically decreased the overall extension force to keep the unit firing at a slow rate needed for spike triggered averaging. For this reason, recruitment threshold for EDC units during wrist extension was defined as the mean of the force at which the unit began firing and the force 30 seconds after. In this way, both the initial and final force levels were incorporated into the recruitment threshold.

Next, SMU data were played back through a multilevel logic circuit with both voltage and time windows. Successful matching of the voltage and time criteria to the SMU action potential resulted in the output of a 5 volt TTL pulse. This pulse was fed to the computer and used to construct a first order interspike interval histogram. The histogram was used to determine the unit's mean firing rate and the accuracy of discrimination.

In order to ensure the reliability of the twitch tensions obtained during spike triggered averaging, two conditions are necessary: 1) the tension profile of the unit should not be fused and 2) the unit must fire asynchronously with respect to all other units. If either condition is not met, the resulting twitch tension obtained during spike triggered averaging may be distorted (Milner-Brown et al., 1973). To minimize the fusion of twitches, the rate at which the averager was triggered was limited to less that 10 per second.

Synchronization of motor unit activity was tested in two ways. One method was to construct a cross-correlation histogram between two simultaneously recorded spike trains. The spikes in one train were used to construct a histogram of the times to all spikes in the second train. For independent spike trains the resulting cross-correlation histogram is flat (Moore et al., 1966). Unit pairs that are synchronized will show a clear peak in the cross-correlation histogram.

The second method of determining synchronization is to compare the spike triggered average of the EMG potential with the average of the rectified EMG potential (Milner-Brown et al., 1973). When impulses from different motor units are synchronized, a period of increased activity in the average rectified EMG trace can be observed before or after the occurrence of activity in the averaged unrectified trace. Both EMG records were sampled at 50 KHz. Sampling at this rate results in a sufficiently high Nyquist frequency (25KHz) for sampling the EMG data. Units showing evidence of synchronization were discarded from the analysis.

The TTL pulse was then used as a trigger for spike triggered averaging of the AC tension record (sampled at 1 KHz) to determine twitch tension of the motor unit. The amplitude of the twitch tension was measured, in volts, from the lowest point at or near the time of the action potential to the highest point of the profile near the expected time to the peak tension determined from stimulation of the muscle. The voltage was proportional to the force exerted on the strain gauge assembly and was converted to units of force using a calibration curve. The force was converted to torque in Newton-meters (Nm) using the following equation

$$\text{Torque} = F \times s$$

where F is the force in Newtons (N) and s is the perpendicular distance from the axis of rotation of the wrist to the line of application of the force.

VI. Statistical Analysis

For each subject, a plot of motor unit twitch tension versus recruitment threshold was constructed using a software graphics package (Cricket Graph). A linear regression line was computed giving the slope (m), intercept (b) and correlation coefficient (r) of the best fit line. To test the significance of r the following t-distributed random variable, with n-2 degrees of freedom was used (Harnett and Murphy, 1980).

$$t_{(n-2)} = \frac{r\sqrt{(n-2)}}{\sqrt{(1-r^2)}},$$

where r is the correlation coefficent and n is the number of observations. The resulting t variable was compared to a t-distribution table to determine the level of significance (p value).

The slopes of the regression lines were compared using a test for parallelism (Kleinbaum and Kupper, 1978). In this test, a Z value was computed using the following equation to compare the slope of the ECR during wrist extension (WECR) to the slope of the EDC during wrist extension.

$$Z = \frac{m_{WECR} - m_{WEDC}}{\sqrt{S^2_{WECR} + S^2_{WEDC}}},$$

where m_{WECR} is the slope of the WECR graph, m_{WEDC} is the slope of the WEDC graph, S^2_{WECR} is the variance of the slope of the WECR graph, and S^2_{WEDC} is the variance of the slope of the WEDC graph.

The variance of the slope for the graphs is given by:

$$S^2 = \frac{S^2_{Y|X}}{(n-1)S^2_X},$$

where $S^2_{Y|X}$ is the mean square error of the data and S^2_X is the sample variance of the X values

The mean square error is given by:

$$S^2_{Y|X} = \frac{(n-1)}{(n-2)} (S^2_Y - m^2 S^2_X) ,$$

where S^2_Y is the sample variance of the observed Ys and S^2_X is the sample variance of the observed Xs

The variance of the observed X values is given by:

$$S^2_X = \frac{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}{n-1},$$

where n is the number of observations. The calculated Z value was compared to a table of standard normal cumulative probabilities to determine the level of significance (p value).

The correlation coefficients of the graphs were compared in a similar manner. The following test statistic for the test of equal correlations was calculated:

$$Z = \frac{\frac{1}{2} \ln \frac{1+r_{WECR}}{1-r_{WECR}} - \frac{1}{2} \ln \frac{1+r_{WEDC}}{1-r_{WEDC}}}{\sqrt{\frac{1}{n_{WECR}-3} + \frac{1}{n_{WEDC}-3}}}$$

where n_{WECR} is the number of ECR units and n_{WEDC} is the number of EDC units. The calculated Z value was compared to a table of standard normal cumulative probabilities to determine the level of significance (p value).

RESULTS

For motor units of extensor carpi radialis (ECR), the recruitment order for contraction in the wrist extension and radial deviation directions was determined. Also, for units of extensor digitorum communis (EDC) recruitment order for contraction in the wrist, middle finger and ring finger extension directions was determined. These results also compare the contribution of ECR to wrist extension with the contribution of EDC to wrist extension.

I. **Electrical Stimulation**

Electrical stimulation of extensor carpi radialis (ECR) and extensor digitorum communis (EDC) was found essential in determining the optimal set up for force recordings. Stimulation of ECR produced torque simultaneously in both the radial deviation and wrist extension directions. The peak torque in the wrist extension direction was consistently greater than in the radial deviation direction at the same stimulus amplitude (figure 2). Surface stimulation of EDC indicated that force could be recorded in the wrist extension direction only when the fingers were disengaged. The resulting twitch profile for wrist extension is shown in figure 3a. Surface stimulation of EDC also produced force in the middle finger (figure 3b) and ring finger (figure 3c) directions. These results indicate that the set up for force recording was appropriate.

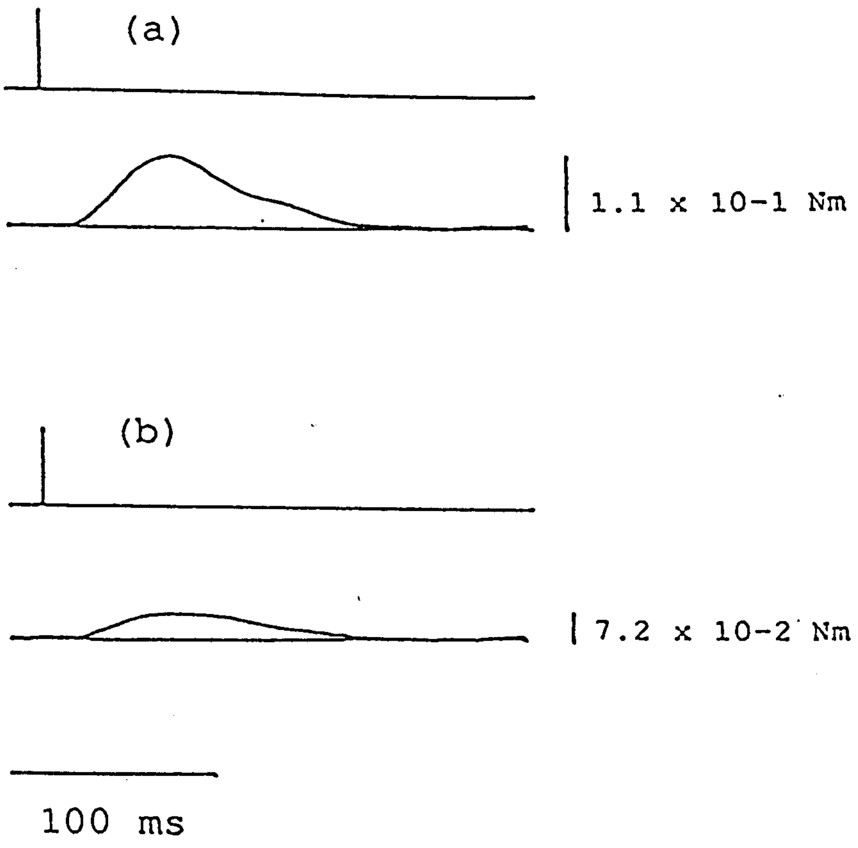

Figure 2. Twitch profiles obtained by surface stimulation of ECR while recording tension in the wrist extension (a) and radial deviation (b) direction.

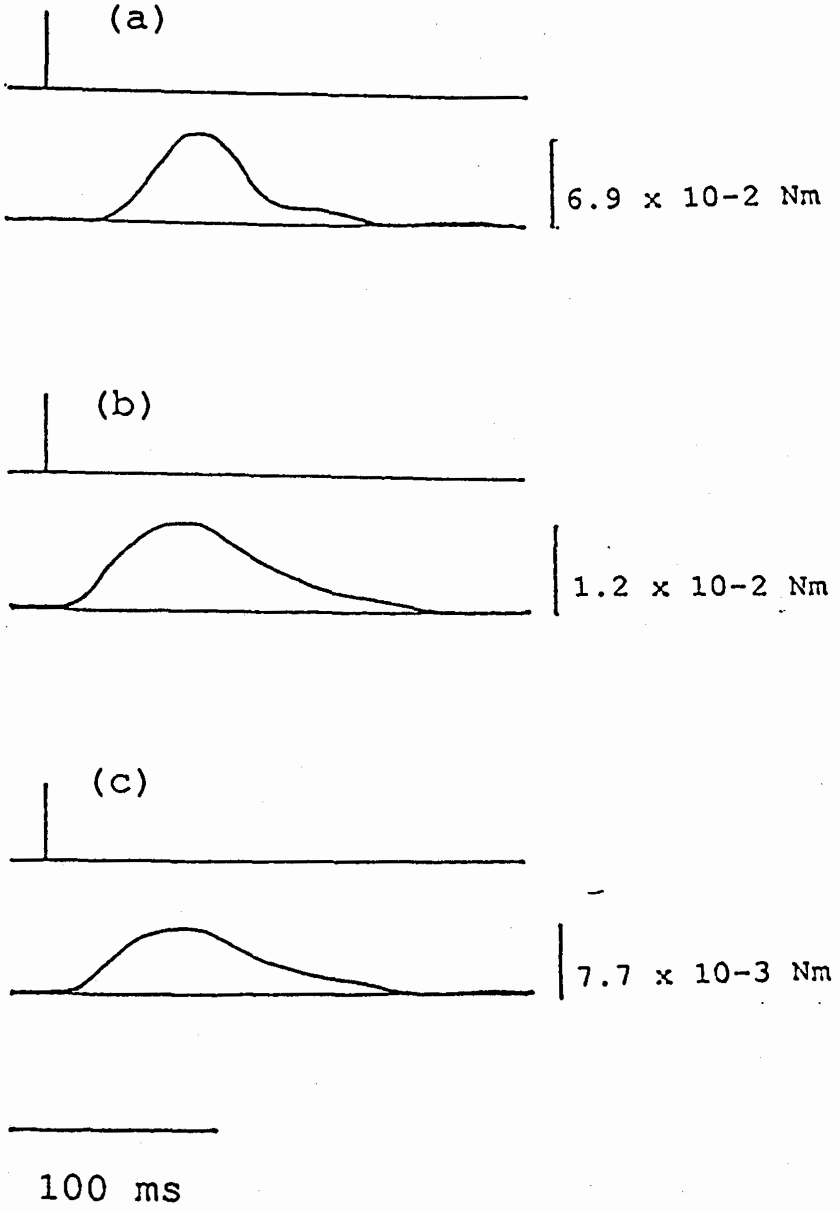

Figure 3. Twitch profiles obtained by surface stimulation of EDC while recording tension in the wrist extension direction when the fingers were not clamped (a), middle finger extension (b) and ring finger extension (c) directions.

II. Recruitment Order of Motor Units

Motor unit twitch tension versus recruitment threshold plots were constructed from at least 30 motor units from each subject recorded during each contraction (ECR during wrist extension and radial deviation and EDC during wrist extension). Figure 4 shows this plot for ECR during wrist extension. Results are given on a log-log plot to cover the wide range of values that were found although regression lines and correlation coefficients were computed from a linear plot. For each subject, motor units with lower recruitment thresholds gave a smaller twitch tension. The linear correlation coefficients (r) for this contraction were 0.88, 0.81, 0.73 and 0.96 ($p < 0.005$) for the four subjects. These results demonstrate orderly recruitment of motor units from small to large in ECR during wrist extension. Figure 5 shows similar results for ECR during radial deviation. The linear correlation coefficients were 0.87, 0.78, 0.53 and 0.92 ($p < .005$) for the four subjects, suggesting orderly recruitment of ECR motor units during radial deviation as well as for ECR during wrist extension. The correlation coefficients for these two lines were compared (see METHODS). No significant difference was found between r of the regression line for ECR during wrist extension and radial deviation ($p > 0.09$) for any of the four subjects (table 1).

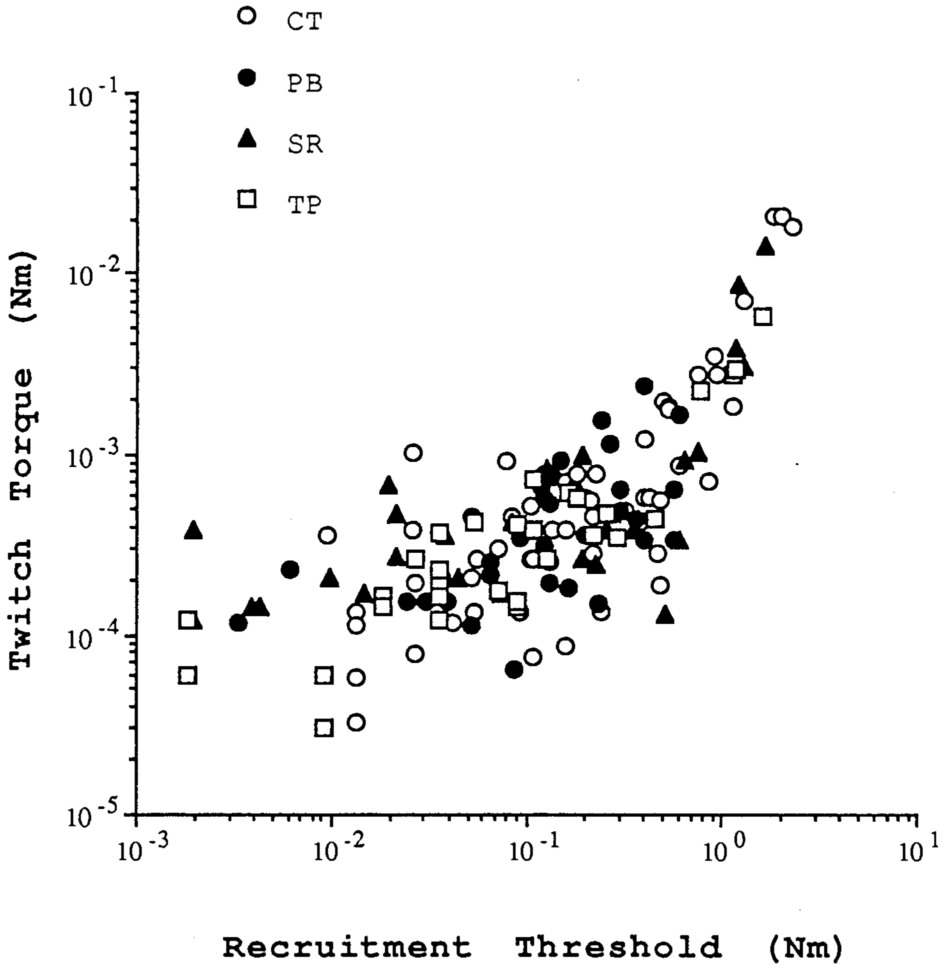

Figure 4. Log-log plot of twitch torque versus recruitment threshold for units from ECR during wrist extension contractions. Slope and correlation of the linear regression line for each subject is given in table 2.

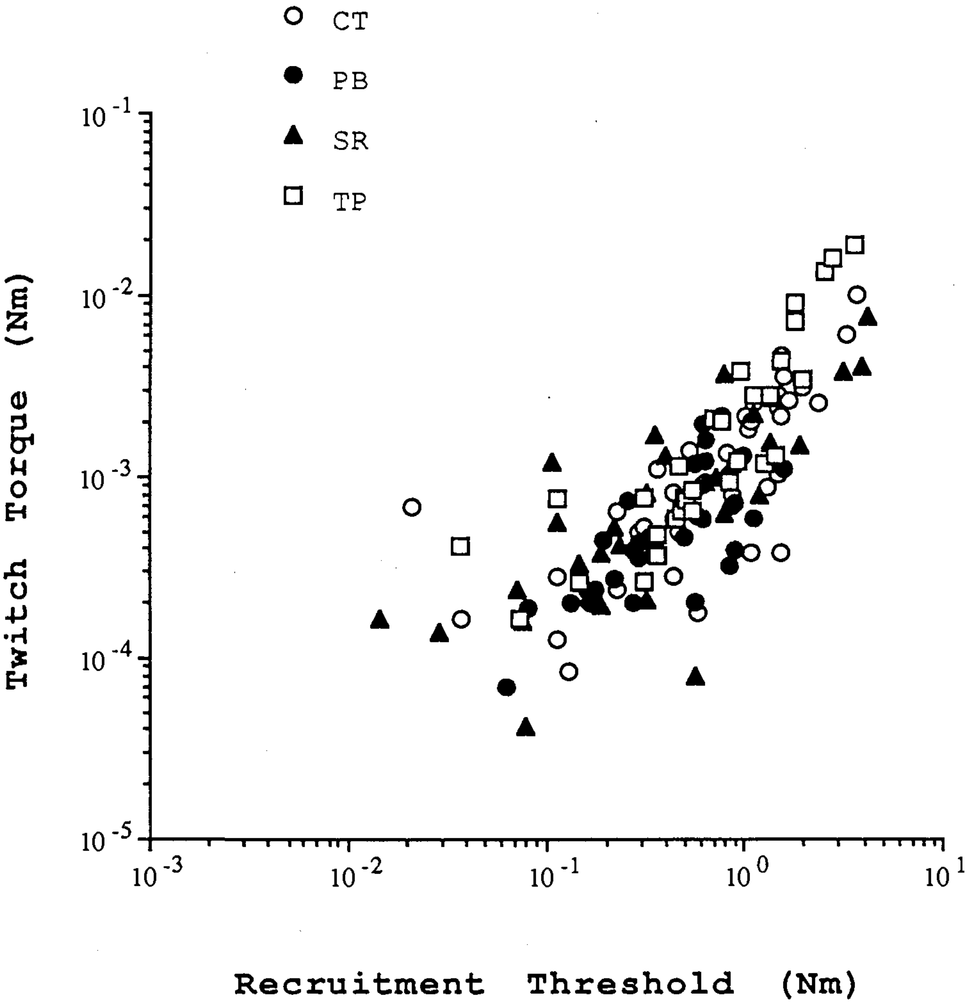

Figure 5. Log-log plot of twitch torque versus recruitment threshold for units from ECR during radial deviation. Slope and correlation of the linear regression lines for each subject are given in table 2.

Table 1.

Subject	n	m	r		p value for m	p value for r
CT						
1.WECR	58	$7.89x10^{-3}$	0.88			
2.RD	40	$1.98x10^{-3}$	0.87	WECR*RD		> 0.40
3.WEDC	49	$3.00x10^{-3}$	0.81	WECR*WEDC	< 0.00001	> 0.10
SR						
1.WECR	36	$5.33x10^{-3}$	0.81			
2.RD	33	$1.42x10^{-3}$	0.78	WECR*RD		> 0.35
3.WEDC	32	$5.96x10^{-4}$	0.48	WECR*WEDC	< 0.00001	< 0.01
PB						
1.WECR	33	$1.57x10^{-3}$	0.51			
2.RD	32	$8.01x10^{-4}$	0.53	WECR*RD		> 0.45
3.WEDC	36	$1.17x10^{-3}$	0.81	WECR*WEDC	> 0.20	< 0.02
TP						
1.WECR	31	$2.86x10^{-3}$	0.96			
2.RD	31	$5.09x10^{-3}$	0.92	WECR*RD		> 0.09
3.WEDC	32	$7.91x10^{-3}$	0.78	WECR*WEDC	> 0.06	< 0.01

For each subject, the number of units analyzed (n), the slope (m) and linear correlation coefficient (r) of the regression lines are given for ECR during wrist extension (WECR), ECR during radial deviation, (RD) and EDC during wrist extension (WEDC). Also, the p values for comparison of slope between ECR during wrist extension and EDC during wrist extension (WECR*WEDC) and comparison of r for ECR and EDC during wrist extension (WECR*WEDC) and ECR during wrist extension and radial deviation are given.

In order to compare the relative recruitment thresholds and twitch torques of ECR units recorded during both wrist extension and radial deviation, recruitment threshold and twitch torques were plotted for units of ECR which would be identified for both contractions. Figure 6 shows that, in most cases, the recruitment threshold for radial deviation was higher than for wrist extension. The twitch torques were therefore normalized with respect to their recruitment thresholds. Figure 7 shows normalized twitch torque for radial deviation versus normalized twitch torque for wrist extension for the four subjects. The line represents unit slope (line of identity) and would be followed if units produced the same torque for contraction in both directions. The plot suggests units tend to have larger twitch torques for wrist extension than for radial deviation. This is shown by the fact that most points lie below the line of identity.

For EDC, several sub-populations of motor units were observed. These included a middle finger (MF) extension population, ring finger (RF) extension population and a population of units that were active for both ring and middle finger (Common) extension (table 2). All these units could be activated for wrist extension. Twitch torque versus recruitment threshold plots for EDC during wrist extension

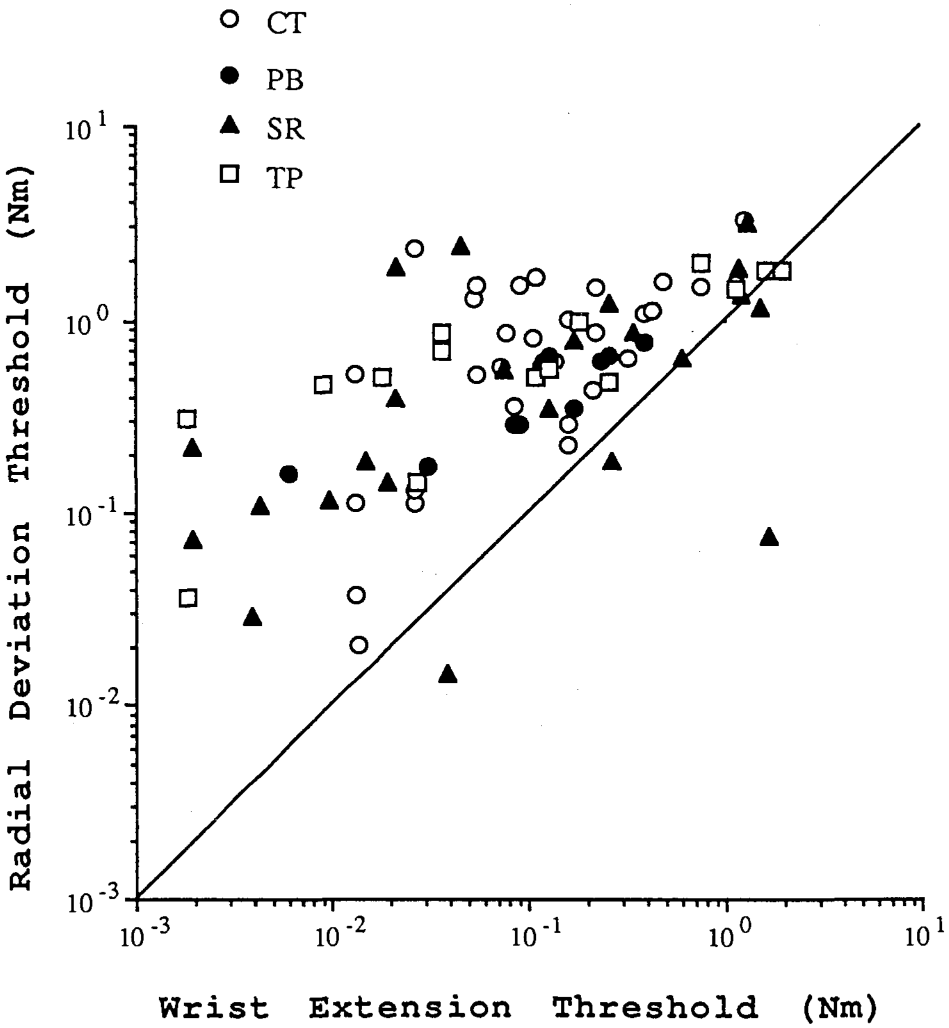

Figure 6. Threshold of motor units of ECR which could be identified for both wrist extension and radial deviation.

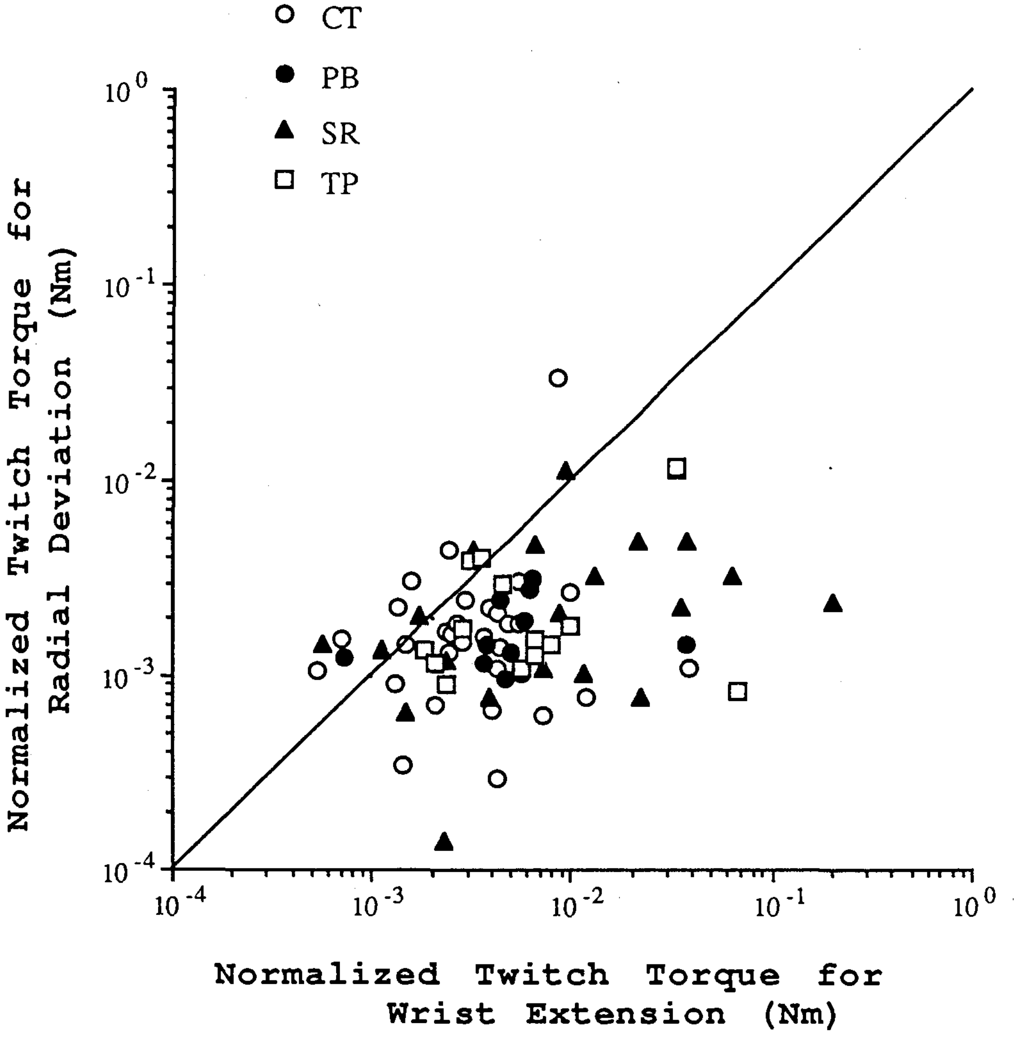

Figure 7. Relative twitch torque of motor units of ECR which could be identified for both wrist extension and radial deviation.

Table 2.

Subject	MF	RF	Common	Not Identified
CT	2	10	7	28
SR	7	12	5	8
PB	6	0	21	9
TP	7	15	2	9

This table shows the number of EDC motor units that were identified as belonging to the middle finger extension population (MF), ring finger extension population (RF), both ring finger and middle finger extension populations (Common).

are shown in figure 8. As in the previous examples, orderly recruitment of motor units was observed. The linear correlation coefficients were: 0.81, 0.48, 0.81 and 0.78 ($p < 0.005$).

In order to compare contributions of ECR to wrist extension and with the contibution of EDC to wrist extension, the slopes of the regression lines for these two plots were compared for each subject. The slope indicates the change in twitch torque with each change in recruitment threshold. A higher slope suggests that for the same increases in threshold, there are larger increases in torque. It is suggested that the relative contribution is greater for the muscle which demonstrates the higher slope. Slopes were compared using a test for parallelism (Kleinbaum and Kupper, 1978). In this test, a Z value was computed for the comparison of the two slopes (see METHODS). The null hypothesis (H_O) for this test was that the slope (m_{WECR}) for ECR during wrist extension was equal to the slope (m_{WEDC}) of EDC during wrist extension: H_O: $m_{WECR} = m_{WEDC}$. The critical Z value for the two tailed null hypothesis was 1.96 at the 95% confidence level. An alternate hypothesis (H_A) was that the slope of ECR during wrist extension was greater than EDC during wrist extension: H_A: $m_{WECR} > m_{WEDC}$ where the critical region was $Z \geq 1.645$. Similarly, H_A: $m_{WECR} < m_{WEDC}$. where the critical region was Z £ -1.645. These Z values were used to determine the significance of the comparison (table 1)

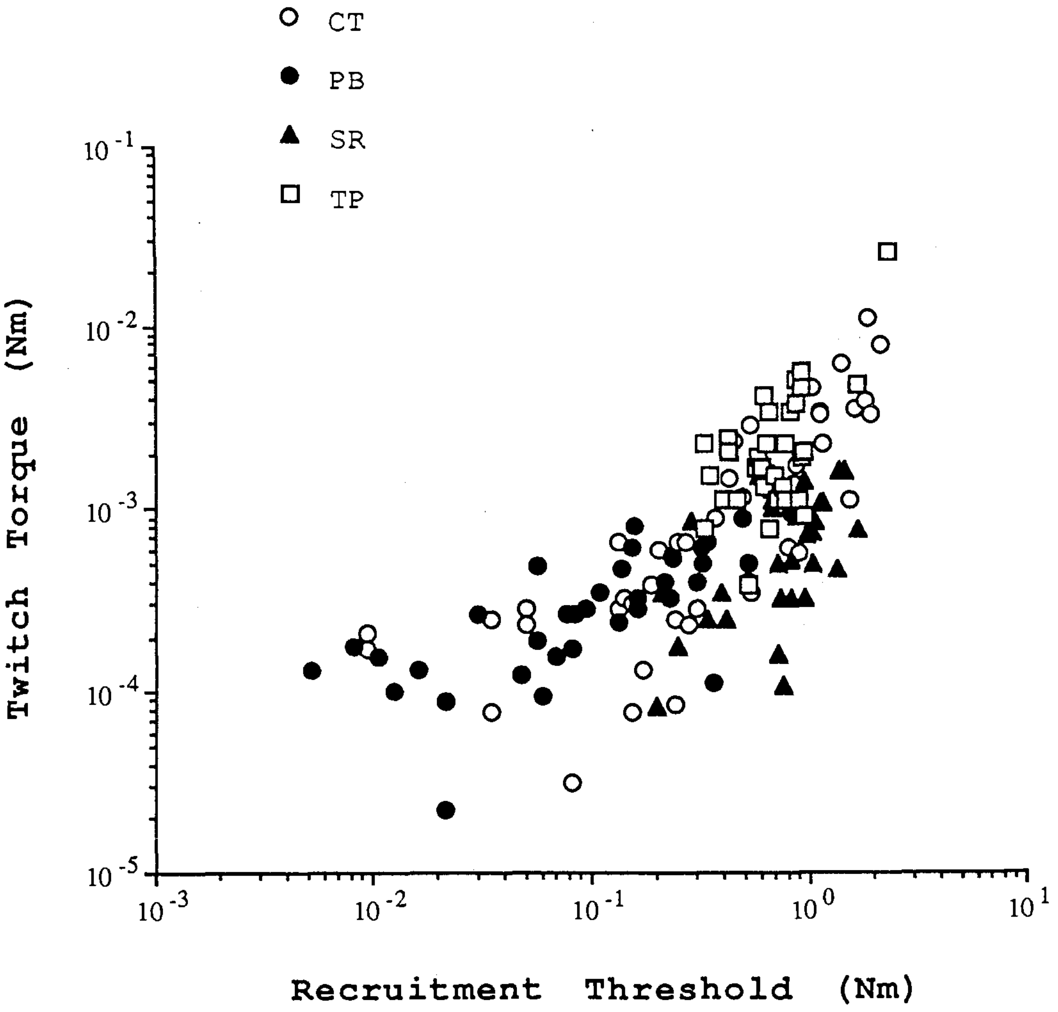

Figure 8. Log-log plot of twitch torque versus recruitment threshold for units from EDC during wrist extension. Slope and correlation of the linear regression lines for each subject are given in table 2.

For two subjects (CT and SR) the slope for ECR was significantly higher than the slope for EDC during wrist extension ($p < .00001$). For the other two subjects no significant difference was found. The correlation coefficient was significantly greater for ECR during wrist extension than for EDC during wrist extension for two subjects (SR and TP; $p < 0.01$). For a third subject, (CT) there was no difference in the correlation coefficient for ECR during wrist extension compared with EDC during wrist extension ($p > 0.10$). The fourth subject, (PB) showed a significantly greater correlation for EDC during wrist extension compared with ECR during wrist extension ($p < 0.02$).

Table 3 shows the mean twitch torque of ECR units during wrist extension was compared with the mean twitch torque of EDC units during wrist extension over the same threshold range. This is useful in comparing the contribution of the two muscle to wrist extension. For three of the four subjects (CT, PB and TP) the mean twitch torque from EDC was comparable to the mean twitch torque from ECR. For the fourth subject (SR), the twitch torque from ECR was approximately four fold greater than the twitch torque from EDC.

During finger extensions, a total of 57 units for middle finger extension (figure 9), 54 units for ring finger

Table 3

Subject	Threshold Range (Nm).	Mean ECR Twitch (Nm)	Mean EDC Twitch (Nm)
1.CT	0.03 to 1.0	7.04×10^{-4}	7.19×10^{-4}
2.PB	0.01 to 0.6	5.54×10^{-4}	3.39×10^{-4}
3.SR	0.2 to 1.6	2.65×10^{-3}	7.26×10^{-4}
4.TP	0.2 to 1.6	1.67×10^{-3}	2.24×10^{-3}

For each subject, the mean twitch torque from ECR during wrist extension and the mean twitch torque from EDC during wrist extension over the same threshold range are given.

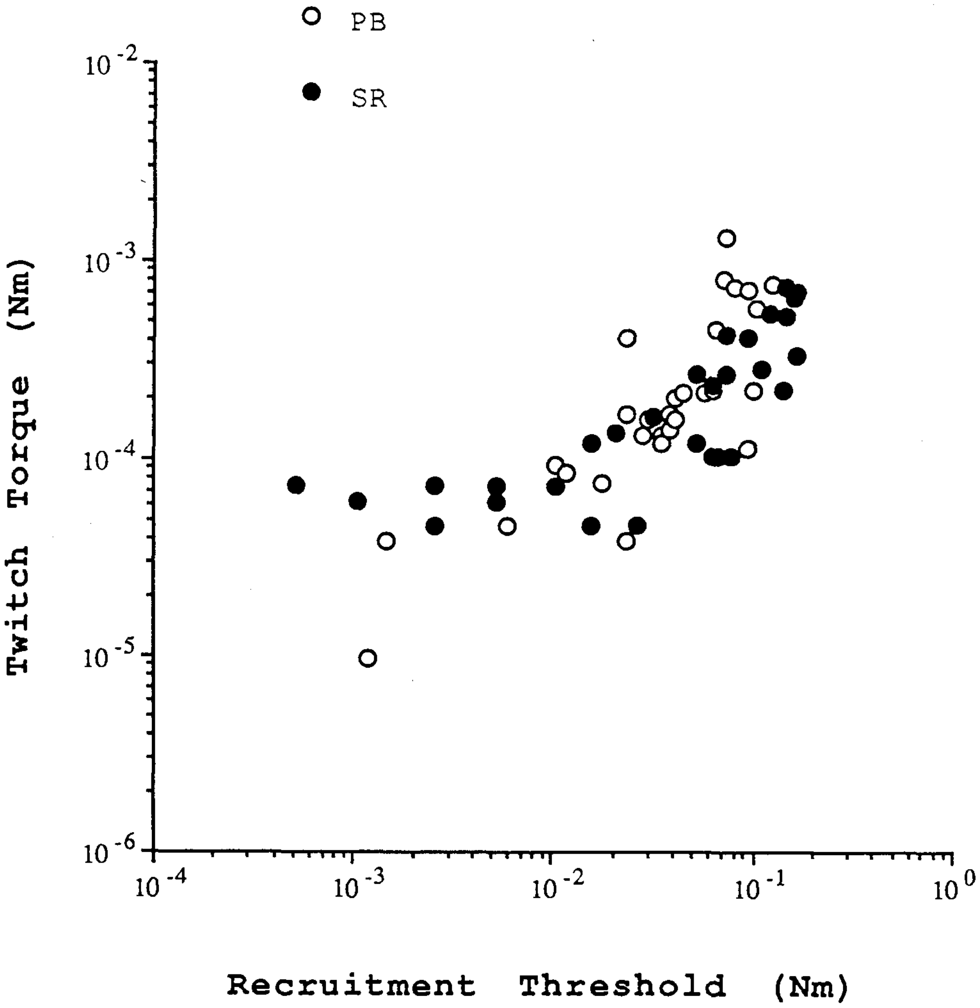

Figure 9. Log-log plot of twitch torque versus recruitment threshold for units from EDC during middle finger extension.

extension (figure 10) and 68 units for extension of both fingers together (figure 11) were recorded from two subjects (PB and SR). Twitch torque versus recruitment threshold plots showed orderly recruitment of motor units for each of these contractions. Linear correlation coefficients for the two subjects in these experiments were: subject PB: 0.74 for MF, 0.74 for RF and 0.49 for Both; subject SR: 0.85 for MF, 0.78 for RF and 0.60 for Both ($p < 0.005$). These results suggest orderly recruitment of motor units within each task group of EDC.

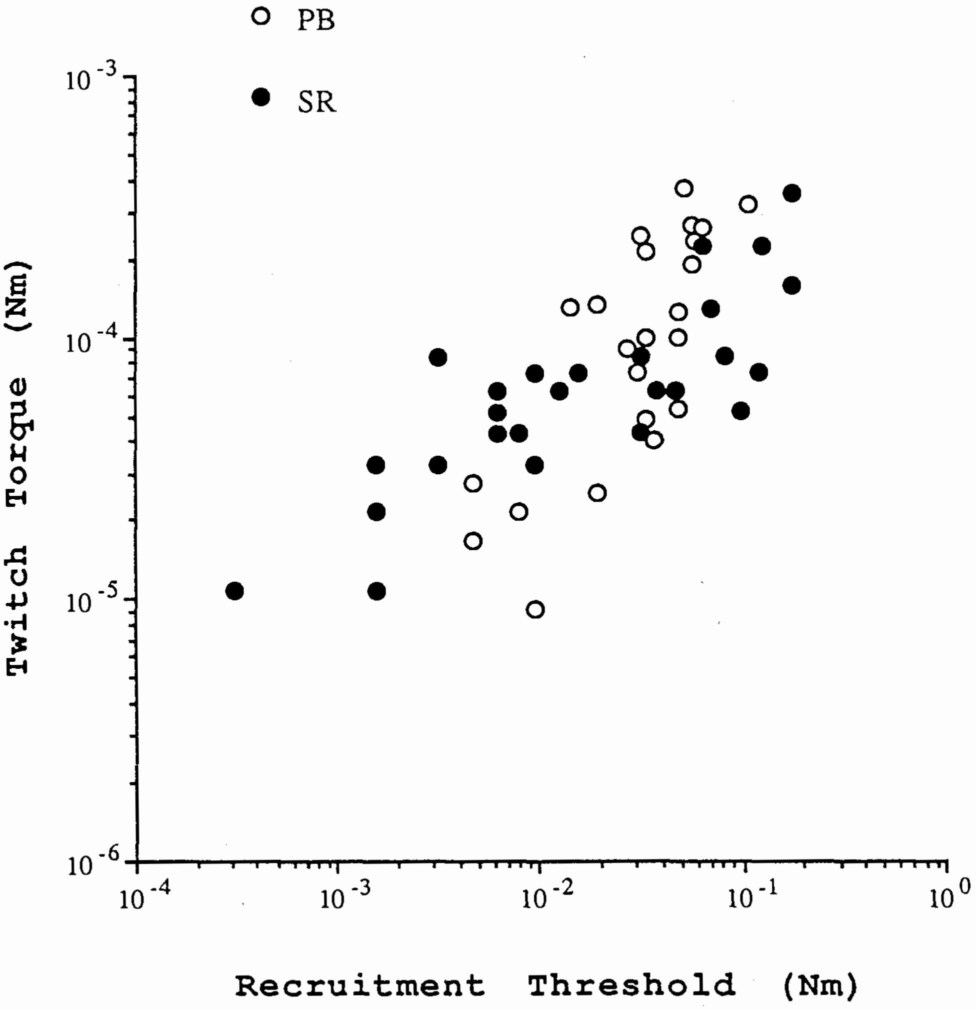

Figure 10. Log-log plot of twitch torque versus recruitment threshold for units from EDC during ring finger extension.

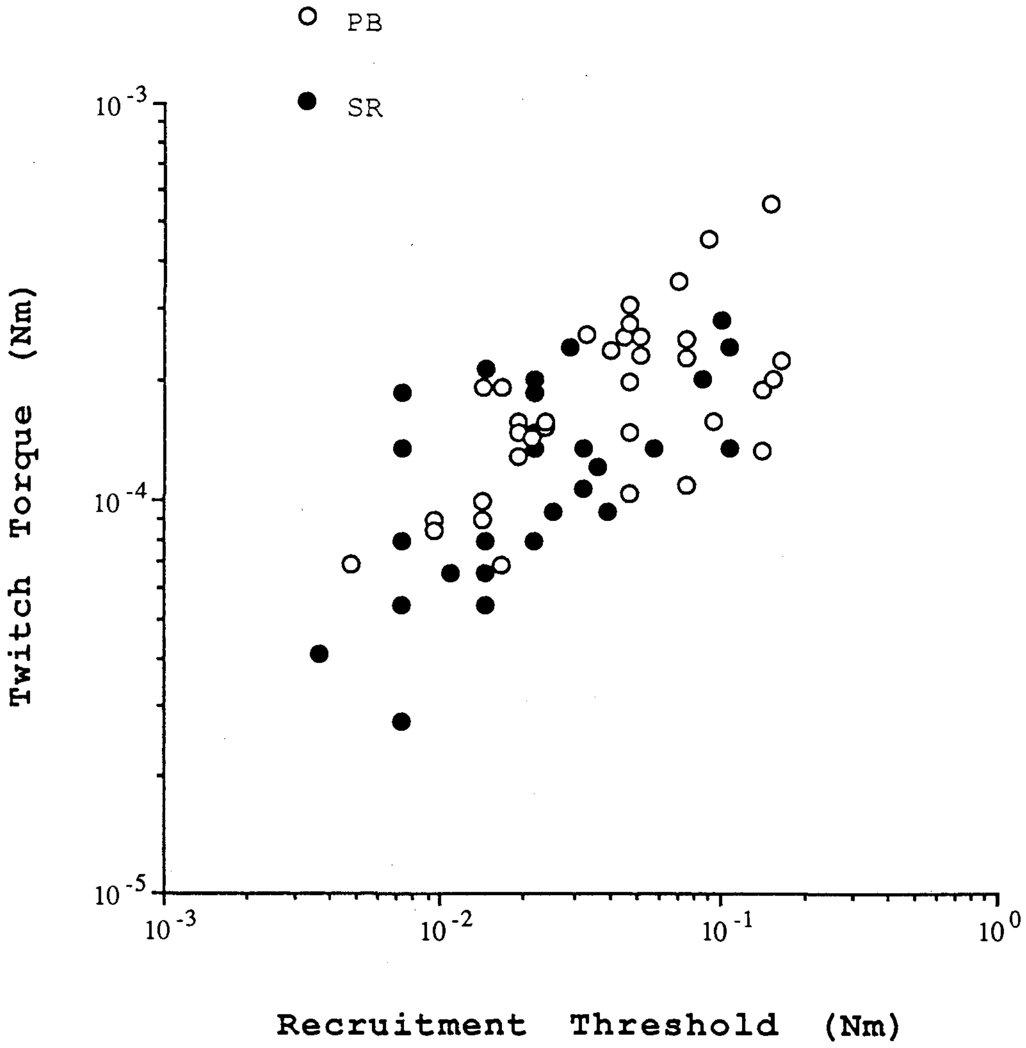

Figure 11. Log-log plot of twitch torque versus recruitment threshold for units of EDC during extension of both the middle and ring fingers together.

DISCUSSION

The twitch tensions of single motor units in extensor carpi radialis (ECR) and extensor digitorum communis (EDC) were compared to their recruitment threshold for various contraction paradigms. In each contraction, a strong correlation between twitch torque and recruitment threshold was observed suggesting orderly recruitment of motor units.

The amplitude of the twitch torque obtained can not be considered to be the "true" amplitude because of the techniques used to compute the motor unit's twitch. The tonic firing of motor units leads to partial fusion of twitches, resulting in a decrease in twitch amplitude, even at stimulus rates as low as 2 per second (Calancie and Bawa, 1986). This is lower than the rates used in this study which tended to be near 10 per second. Although the twitch amplitudes obtained in this study were probably distorted, the relation between twitch torque and recruitment threshold is unaffected.

I. Task Groups

A task groups consists of a group of motoneurons acting together to perform a given function. One task groups was found for ECR comprising the entire motoneuron pool. That is, all units that were active during wrist extension were also active during radial deviation. If separate task groups existed, one would expect to find large numbers of units that were more easily activated for contraction in one direction than the other. Similar results have been shown in FDI for contractions in three directions (Thomas et al., 1985). This implies that although these are multifunctional muscles, they do not show separate task groups for each function.

During contractions of EDC, separate motor unit task groups were observed for various finger contractions. Units were divided into three subpopulations for finger extensions: one for extension of the middle finger (MF), one for extension of the ring finger (RF), one for extension of both middle and ring fingers (Common). Although subpopulations of EDC exist for finger extensions, each unit was also active during wrist extension. Therefore, all motor units of EDC motor units form a composite task group for wrist extension. Separate motor unit populations for different functions of the same muscle have also been shown in human biceps muscle (ter Haar Romeny et al., 1984) and in sartorius muscle of the cat (Hoffer et al., 1987)

II. Recruitment Order

The recruitment order of motor units in each of these task groups was determined by plotting twitch torque versus recruitment threshold of each unit. For each task group, small torque producing units were recruited before large torque producing units. This is shown by the positive relation between twitch torque and recruitment threshold This suggests orderly recruitment of motor units within each task group of a muscle. Orderly recruitment has been demonstrated in this manner in a number of other muscle including; first dorsal interosseus (Milner-Brown et al., 1973; Stephens and Usherwood, 1977; Thomas et al., 1985), extensor digitorum communis during middle finger extension (Monster and Chan, 1977), masseter (Goldberg and Derfler, 1977; Yemm, 1977), temporalis (Yemm, 1977), flexor carpi radialis (Calancie and Bawa, 1985) and extensor carpi radialis (Romaiguere et al., 1989).

For each graph, a linear regression line was fitted to the data points. The underlying assumption for this procedure is one of linearity between twitch torque and recruitment threshold. This assumption has been used in many other studies (Milner-Brown et al., 1973; Thomas et al., 1985; Yemm, 1977; Calancie and Bawa, 1985; Romaiguere et al., 1989). The correlation coefficient r, indicates the strength of the linear relation between twitch torque and recruitment threshold. Data showing more scatter would result in a smaller r value. The high linear correlations between twitch torque and recruitment threshold for ECR motor units confirms orderly recruitment for both wrist extension and radial deviation contractions. The correlations for wrist extension were higher than in a study by Romaiguere et al. (1989), who reported r = 0.39 compared to the lowest correlation in this study of 0.51. This indicates that the strength of the relation in this study was much greater. The correlations found in this study, with the exception of one subject, are more similar to those found for first dorsal interosseus (FDI) muscle in man by Milner-Brown et al. (1973) who reported correlations above 0.81.

The comparison of relative twitch torque of units during wrist extension and during radial deviation, showed that the twitch tensions of motor units were generally higher for wrist extension than for radial deviation contractions. This suggests that wrist extension is a slightly more effective contraction for ECR and is supported by the data obtained by surface stimulation. The biomechanical arrangement of the muscle fibres may allow the most effective generation of force during wrist extension. Similar results have been noted for contraction of FDI in different directions (Thomas et al., 1985). The most effective contraction for FDI was abduction (its prime function) as opposed to flexion of the finger.

The correlation coefficients between the two directions of contraction of ECR were also compared. Differences in r may indicate that the linear approximation is appropriate for contraction in one direction but not the other. For contraction in both directions, ECR units showed similar high correlations suggesting the linear approximation was appropriate for this muscle in both directions of contraction. This was expected since the same units were recruited with no reversals between the two contractions. Even though, twitch tensions tended to be lower for radial deviation contractions, the torque during radial deviation may be proportional to the torque during wrist extension resulting in equal scatter about the linear regression line for radial deviation compared with wrist extension.

For EDC, contraction of each finger separately showed equally strong correlations for both subjects. The amount of scatter in the data may be attributed to the mechanical arrangement of the muscle tendon complex. As the tendon of EDC travels toward the wrist it splits to send a tendon to each of the fingers. On the dorsum of the hand, these tendons are connected by oblique running bands (Goss, 1976). This means that each unit, regardless of which subpopulation it belongs to, contributes to extension of each finger by varying amounts. For example a middle finger unit would primarily contribute to middle finger extension, but because the tendons are connected, would also contribute to ring finger extension. Therefore, during extension of the fingers separately, only a portion of the torque produced by a given unit would be recorded. During extension of both fingers together one would expect to record the optimum twitch torque from each unit, since torque was recorded from both the middle and ring fingers and find less scatter in data points.

This, however, was not the case. The correlation coefficient for extension of both fingers together was less than for each finger separately. The larger scatter during extension of both fingers together may be due to preferential extension of one finger over the other. For example, preferential extension of the middle finger while recording from a low threshold ring finger unit would result in an artificially high recruitment threshold for this unit. This would result in a larger scatter in data points than when extending each finger separately.

Comparing the slopes of the twitch torque versus recruitment threshold plots allows one to compare the relative contribution of two muscles during the same contraction. Since the line of best fit must theoretically pass through the origin, a larger slope indicates a greater contribution to the contraction. That is, for each increase in threshold force, there are greater increases in torque. Comparing slopes in this manner showed that the contribution of ECR to wrist extension was greater than the contribution of EDC to wrist extension for two subjects (SR and CT). This, in itself, does not indicate that ECR is more important for wrist extension. When the mean twitch torque of EDC units were compared to the mean twitch torque of ECR units over the same threshold range, three of the four subjects (CT, PB and TP) showed similar values between the two muscles, however, only subjects CT and PB recruited units from both muscles over a wide range of forces. This would indicate that EDC is an important wrist extensor for these three subjects. For the fourth subject (SR), mean twitches were approximately four fold greater for ECR than for EDC over the same threshold range. For this subject (as well as TP), EDC units were only recruited at high thresholds compared with ECR units. This indicates that EDC is not a prime mover during wrist extension for this subject (SR). During normal function, prime movers are the first muscles active. As tension increases, synergist muscles become active for fixation and stabilization of joints through co-activation (Smith, 1981). For the other three subjects, EDC is an important wrist extensor as well as finger extensor.

As mentioned previously, two subjects (SR and TP) were forced to decrease dramatically, the overall wrist extension force in order to keep EDC units firing at a low rate needed for STA. It would appear that the central nervous system can focus segmental and descending input onto EDC motoneurons once they have been recruited.

Descending and segmental input can influence spinal cord circuitry at a number of sites. Specifically, Renshaw cells, Ib interneurons and the motoneurons itself are all possible sites. Renshaw cells receive input from motoneuron collaterals as well as from a variety of descending pathways. Their output is extensive, providing recurrent inhibition to synergistic motoneurons as well as Ia inhibitory interneurons and other Renshaw cells in the same motor nucleus (Baldiserra et al., 1981). Recurrent inhibition by Renshaw cells is strongest amongst motoneurons of the same motor nucleus and those closest in distance. These descending inputs may adjust Renshaw cell activity to provide greater inhibition to ECR and extensor carpi ulnaris (ECU) motoneuron pools than to EDC resulting in focussing on the active EDC motoneurons. Once the EDC motoneuron has been recruited, the other wrist extensors relax while the firing rate of the EDC motoneuron is maintained.

Inhibition by Ib interneurons can also provide focussing on the EDC motoneurons. Ib interneurons receive input from Ia, Ib, cutaneous and joint afferents as well as descending pathways and provide inhibition to synergist motoneurons as well as excitation to antagonist motoneurons (Baldiserra et al., 1981). The descending inputs may focus inhibition onto ECR and ECU allowing EDC motoneurons to remain active as extension force falls. In general, the convergence of descending and segmental inputs allow these pathways to be modified. The more synapses present in a pathway the more potential for flexibility of its output.

CONCLUSIONS

This study shows that some multifunctional muscles (EDC) may show separate task groups for each function while others (ECR) do not. The conclusion of orderly recruitment of motor units confirms the observation originally made by Henneman and co-workers (1965). However, the original formation of the 'size principle' suggested orderly recruitment within a pool of motoneurons. In light of this study, the 'size principle' should be modified to suggest orderly recruitment of motor units within each task groups of a muscle.

REFERENCES

Basmajian JV. Control and training of individual motor units. Science 141, 440-441, 1963.

Baldissera F, Hultborn H, Illert M. Integration in spinal neuronal systems. in VB Brooks (ed) Handbook of Physiology, Section 1: The Nervous System, Vol 2 Motor Control, Bethesda, American Physiological Society, pp509-595, 1981.

Bawa P, Binder MD, Ruenzel P, Henneman E. Recruitment order of motoneurons in stretch reflexes is highly correlated with their axonal conduction velocity. Journal of Neurophysiology. 52, 410-420, 1984.

Bizzi E, Abend W. Posture contol and trajectory formation in single and multi-joint arm movements. In JE Desmedt (ed) Motor Control Mechanisms in Health and Disease. New York, Raven Press, pp31-45, 1983.

Burke RE, Dum RP Fleshman JW, Glenn LL, Lev-Tov A, O'Donovan MJ and Pinter MJ. An HRP study of the relation between cell size and motor unit type in cat ankle extensor motoneurons. Journal of Comparative Neurology 209, 17-28, 1982

Burke RE, Levine DN, Tsairis P and Zajac FE. Physiological types and histochemical profiles in motor units of the cat gastrocnemius. Journal of Physiology 234, 723-748, 1973.

Burke RE, Levine DN, Zajac FE, Tsairis P and Engel WK. Mammalian motor units: physiological-histochemical correlation in three types in cat gastrocnemius. Science 174, 709-712, 1971.

Burke RE, Motor units: anatomy, physiology and functional organization. in Handbook of Physiology. Vol II, Sect 1, Part 1: The Nervous System. Motor Control. American Physiological Society, Bethesda, Md., pp345-422. 1981.

Burke RE, Strick PL, Kanda K, Kim CC and Walmsley B.

Anatomy of medial gastrocnemius and soleus motor nuclei in cat spinal cord. Journal of Neurophysiology 40, 667-680, 1977.

Burke RE. Firing patterns of gastrocnemius motor units in the decerebrate cat. Journal of Physiology 196, 631-654, 1968.

Calancie B, and Bawa P. Voluntary and reflexive recruitment of flexor carpi radialis motor units in humans. Journal of Neurophysiology, 53, 1194-1200, 1985.

Calancie B and Bawa P. Limitations of the spike triggered averaging technique. Muscle and Nerve 9, 78-83, 1986.

Carew TJ, Ghez C. Muscles and muscle receptors. in ER Kandel and JH Shwartz (eds) Principles of Neural Science, New York, Elsevier, pp443-456, 1985.

Clamann, H.P., Gillies, J.D., Skinner, R.D. and Henneman, E., Quantitative measures of output of a motoneuron pool during monosynaptic reflexes. Journal of Neurophysiology, 37, 1328-1337, 1974.

Clamann, HP, Gillis JD and Henneman E., Effects of inhibitory inputs on critical firing level and rank order of motoneurons. Journal of Neurophysiology 37, 1350-1360, 1974.

Clamann, HP and Henneman E, Electrical measurements of axon diameter and its use in relating motoneuron size to critical firing level. Journal of Neurophysiology, 39, 844-851, 1976.

Collatos TC, Edgerton VR, Smith JL and Botterman BR. Contractile properties and fiber type compositions of flexors and extensors of elbow joint in cat: implications for motor control. Journal of Neurophysiology 40, 1292-1300, 1977.

Desmedt JE and Godaux E, Spinal motoneuron recruitment in man: rank deordering with direction but not with speed in voluntary movement, Science 214, 933-936, 1981.

Desmedt JE and Godaux E. Fast motor units are not preferentially activated in rapid voluntary contractions in man. Nature, 267, 1977.

Dum RP and Kennedy TT. Physiological and histochemical characteristics of motor units in cat tibialis anterior and extensor digitorum longus muscles. Journal of Neurophysiology 43, 1615-1630, 1980.

Edstrom L and Kugelberg E. Histochemical composition, distribution of fibres and fatiguability of single motor units. Anterior tibial muscle of the rat. Journal of Neurology, Neurosurgery and Psychiatry 31, 424-433, 1968.

Essen B, Jansson E, Henriksson J, Taylor AW and Saltin B. Metabolic characteristics of fibre types in human skeletal muscle. Acta Physiologica Scandinavica 95, 153-165, 1975.

Garnett R and Stephens JA. The reflex responses of single motor units in human first dorsal interosseous muscle following cutaneous afferent stimulation. Journal of Physiology 303, 351-364, 1980.

Garnett R and Stephens JA, Changes in the recruitment of motor units produced by cutaneous stimulation in man. Journal of Physiology 311, 463-473, 1981.

Goldberg LJ and Derfler B. Relationship among recruitment order, spike amplitude, and twitch tension of single motor units in human masseter muscle. Journal of Neurophysiology 40, 879-890, 1977.

Goss CM. Gray's Anatomy. 29th Edition. Lea and Febiger, Philadelphia, Chapter 6, pp 371-520, 1976.

Harnett DL and Murphy JL. Introductory Statistical Analysis. 2nd Ed. Addison-Wesley Publishing Co. Ontario, Canada, Chapter 11 pp 484-485, 1980.

Henneman E and Mendell LM. Functional organization of motoneuron pool and its inputs. in Handbook of Physiology. Vol II, Sect 1, Part 1: The Nervous System, Motor Control. American Physiological Society, Bethesda Md., pp 423 - 507. 1981.

Henneman E and Olson CB. Relations between structure and function in the design of skeletal muscles. Journal of Neurophysiology 28, 581-589 1965.

Henneman, E . Relation between size of neurons and their susceptibility to discharge. Science 126, 1345-1347, 1957.

Henneman, E, Clamann, HP, Gillies, JD and Skinner, RD, Rank order of motoneurons within a pool: Law of combination. Journal of Neurophysiology, 37, 1338-1349, 1974.

Henneman, E, Somjen, G and Carpenter, DO, Excitibility and inhibitibility of motoneurons of different sizes. Journal of Neurophysiology, 28, 599-620, 1965.

Henneman, E, Somjen, G, Carpenter, DO, Functional significance of cell size in spinal motoneurons. Journal of Neurophysiology 28, 560-580, 1965.

Hoffer JA, Loeb GE, Sugano N, Marks WB O'Donovan MJ and Pratt CA. Cat hindlimb motoneurons during locomotion. III. Functional segregation in sartorius. Journal of Neurophysiology, 57, 554-562, 1987.

Kanda K and Desmedt JE. Cutaneous facilitation of large motor units and motor control of human fingers in precision grip. in Advances in Neurology. Motor Control Mechanisms in Health and Disease. JE Desmedt (ed). Raven Press New York, pp253-261, 1983.

Kanda K, Burke RE and Walmsley B, Differential control of fast and slow twitch motor units in the decerebrate cat. Experimental Brian Research 29, 57-74, 1977.

Kleinbaum DG and Kupper LL. Applied Regression Analysis and Other Multivariable Methods. Duxbury Press, Massachusetts, Chapter 6, pp71-78, 1978.

Loeb GE, The functional organization of muscles, motor units, and tasks. in Segmental Motor Control Binder MD and Mendell LM eds. Oxford Press, pp 23-35, 1990.

Milner-Brown HS, Stein RB and Yemm R. The orderly recruitment of human motor units during voluntary isometric contractions. Journal of Physiology 230, 359-370, 1973.

Monster AW and Chan H. Isometric force production by motor units of extensor digitorum communis muscle in man. Journal of Neurophysiology. 40, 1432-1443, 1977.

Moore GP, Perkel DH, Segundo JP. Statistical analysis and functional interpretation of neuronal spike data. Annual Review of Physiology, 28, 493-522, 1966.

Peter JB, Barnard RJ, Edgerton VR, Gillespie CA and Stempel KE. Metabolic profiles of three fiber types of skeletal muscle in guinea pigs and rabbits. Biochemistry 11, 2627-2633, 1972.

Romaiguere P, Vedel J-P, Pagni S and Zenatti A. Phyiological properties of the motor units of the wrist extensor muscles in man. Experimental Brain Research, 78, 51-61, 1989.

Smith AM. The coactivation of antagonist muscles. Canadian Journal of Physiology and Pharmacology 59, 733-747, 1981.

Somjen G, Carpenter DO and Henneman E. Responses of motoneurons of different sizes to graded stimulation of supraspinal centers of the brain. Journal of Neurophysiology. 28, 958-965, 1965.

Stein RB. Peripheral control of movement. Physiological Reviews, 54, 215-243, 1974.

Stein RB, French AS, Mannard A and Yemm R. New methods for analysing motor function in man and animals. Brain Research 40, 187-192, 1972.

Stephens JA and Stuart DG. The motor units of cat medial gastrocnemius. Twitch potentiation and twitch-tetanus ratio. Pfluegers Archives 356, 359-372, 1975.

Sypert GW and Munson JB. Basis of segmental motor control: motoneuron size or motor unit type? Neurosurgery 8, 608-621, 1982.

ter Haar Romeny BM, Denier van der Gon JJ and Gielen CCAM. Changes in recruitment order of motor units in the human biceps muscle. Experimental Neurology 78, 360-368, 1982.

ter Haar Romeny BM, Denier van der Gon JJ and Gielen CCAM. Relation between location of a motor unit in the human biceps brachii and its critical firing levels for different tasks. Experimental Neurology, 85, 631-650, 1984.

Thomas CK, Ross BH and Calancie B. Human motor-unit recruitment during isometric contractions and repeated dynamic movements. Journal of Neurophysiology, 57, 311-324, 1987.

Thomas CK, Ross BH and Stein RB, Motor unit recruitment in human first dorsal interosseous muscle for static contraction in three different directions. Journal of Neurophysiology, 55, 1017-1029, 1985.

Yemm R. The orderly recruitment of motor units of the masseter and temporal muscles during voluntary isometric contraction in man. Journal of Physiology 265, 163-174, 1977.

Zajac FE and Faden JS. Relationship among recruitment order, axonal conduction velocity and muscle unit properties of type identified motor units in cat plantaris muscle. Journal of Neurophysiology 53, 1303-1322, 1985.