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A QUANTITATIVE ANALYSIS OF THE DYNAMIC DISCHARGE PROPERTIES OF HUMAN FLEXOR CARPI RADIALIS MOTONEURONS

by

Louise C. Smith

B.Sc. (Kinesiology), Simon Fraser University, 1987

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ABSTRACT

Two sets of experiments were conducted with human subjects to investigate the dynamics of flexor carpi radialis motoneuron firing patterns.

Subjects traced ramp and hold isometric force trajectories, while surface, and intramuscular single motor unit, electromyographic activities were recorded. Conditions were controlled for background motoneuronal activity level, rate of rise and magnitude of isometric force. Average response histograms of single motor unit and surface electromyogram (EMG) activities associated with these contractions were constructed separately for each condition. These data were quantified in terms of the dynamic and steady-state phases of the force trajectories.

The range of motor unit firing patterns observed during the dynamic phase of the force trajectory were non-linearly related to the trajectory's rate of rise of force and the motoneuron's background excitation level. Lower and higher threshold motor units, recorded simultaneously, did not display any observable difference in their firing patterns during the dynamic phase of the trajectory. The dynamic phase of the motor unit population discharge (reflected in the surface EMG activity), during a small output of force, was linearly related to the rate of rise of force; however, during trajectories completed to greater magnitudes of force,

the dynamic phase of the EMG activity increased in a non-linear manner with respect to increases in rate of rise of force.

The range of single motor unit firing patterns during the steady-state phase of the force trajectory was not influenced by the trajectory's rate of rise of force, but was non-linearly related to the magnitude of force output and motoneuron's background excitation level. Simultaneously recorded lower and higher threshold units did not display any difference in their steady-state firing patterns if both units were active before the trajectory. The steady-state phase of the surface EMG activity was linearly related to the magnitude of the force output.

Although single motor units displayed non-linearity in their dynamic firing rate pattern, the linearity between the dynamic phase of surface EMG activity and rate of rise of force during low force outputs could be explained by the recruitment of additional motor units. The linearity between steady-state surface EMG activity and the magnitude of the force may be explained by the addition of units recruited during the trajectory since units active before the superimposed trajectory produced only small increments in steady-state firing rate.

DEDICATION

I would like to dedicate this thesis to Barry, my Mum and Dad, Peter and my friends, particularly Sophie and Shauna. Their continual support and encouragement will never be forgotten.

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No experience in my life to date equals in intensity or feeling of accomplishment the completion of this degree. The magnitude with which I have matured and developed new skills, scientific and otherwise, has been very satisfying. For this I must thank Dr. Parveen Bawa. Her constant availability and willingness to share her knowledge has not only given me considerable help with my thesis, but has also led to challenging discussions outside the realm of science.

I would also like to thank Dr. Eric Banister, Dr. Arthur Chapman, Dr. Tom Richardson and Dr. Igor Mekjavic for their time and assistance during my studies.

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GLOSSARY

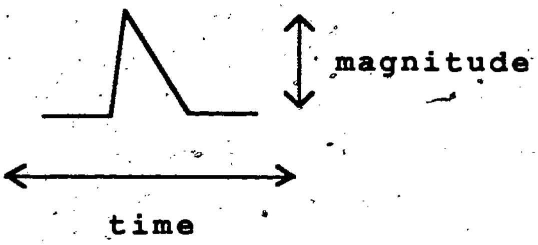
After-hyperpolarization (AHP) - a period of hyperpolarization in the soma following the generation of an action potential in the axon hillock.

Decerebrate preparation - an experimental surgical preparation performed on animal models where the brainstem is transected at the midbrain level.

Firing pattern - the serial pattern of action potentials generated by a motoneuron.

First order histogram - describes the distribution of interspike intervals between a series of action potentials.

Force impulses - a force trajectory describing very fast (ballistic) contractions completed to a target force level followed by relaxation.



Full-wave rectified surface EMG - all negative deflections in the raw EMG signal are inverted so that only positive values represent the EMG signal.

Homonymous muscle - the afferents from a homonymous muscle feedback onto the motoneuron pool of that muscle.

Ib muscle afferent - the afferent from the Golgi tendon organ which is sensitive to the rate of change and magnitude of tension.

Injected currents - controlled applicaton of current inputs to a neuron via an intracellular electrode.

Input resistance - the DC resistance to the flow of current applied across a motoneuron membrane.

Instantaneous firing rate - the inverse of the interspike interval.

Integrated EMG activity - the area calculated under the rectified surface EMG signal.

Interspike interval - the time interval between two successive action potentials.

Intracellular recording - recording completed by a micro - electrode inserted into a single cell.

Intramuscular recording - extracellular recording done with a micro-electrode inserted into a muscle.

Intrinsic neuronal factors - includes membrane properties such as membrane time constant and specific membrane resistivity.

Maximum voluntary contraction (MVC) - the maximum isometric force that a subject can generate from a given muscle or muscle group.

Motoneuron - includes the dendrites, soma, axon and end-plate terminals.

Motoneuron background excitation level - the steady-state firing rate of the motoneuron prior to, in these experiments, a superimposed force trajectory.

Motoneuron pool - a group of motoneurons which innervates a given muscle.

Motor unit - the motoneuron and the muscle unit it innervates.

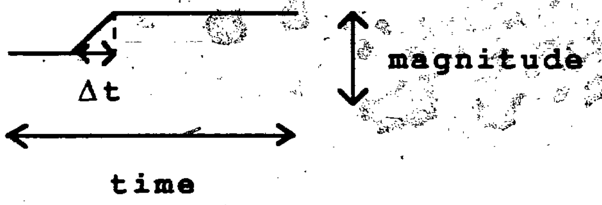
Muscle unit - all the muscle fibers within a muscle innervated by one motoneuron.

Phasic firing - a short burst of action potentials usually with very short interspike intervals.

Post-stimulus average response histogram - a method of averaging data over a given time period for a given condition. The ordinate of the histogram describes the number of occurrences of an "event" falling within a given sampling time. For instance, the average response histograms constructed for a motoneuron firing pattern in these experiments indicated the instantaneous firing rate of the motoneuron in relation to the trajectory completed.

Pulse-step model - a theoretical model developed to describe inputs to a motoneuron pool for the ramp-and-hold trajectories completed in these experiments.

Ramp-and-hold input/output - a quantifiable rate of rise of input or output taken to a steady-state level.



Rate - tension curve - relationship between experimentally generated stimulation rates and the tension generated in response by either muscle or muscle units.

Renshaw cell - an inhibitory interneuron which has monosynaptic connection with alpha motoneurons. It is excited by collaterals of motoneurons as well as segmental and supraspinal inputs.

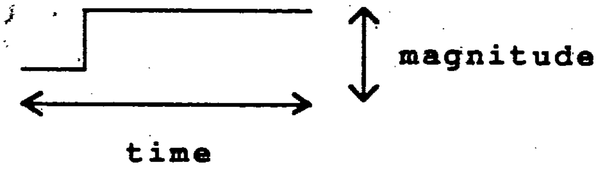
Root-mean-square of EMG amplitude - the rectified EMG signal is squared before integrating and then obtaining the root value.

S versus F type motor units - a classification of motor units based on physiological properties of both the motoneuron and the muscle unit. S type motor units have, for instance, slower conduction velocities and a greater resistance to fatigue than F type motor units.

Saturation non-linearity - in these experiments firing rate saturation non-linearity was observed when the increase in the motor unit's instantaneous firing rate was less during conditions of greater rate of rise of force or magnitude as well as when the background excitation level of the motor unit was high.

Spike - refers to a single action potential.

Step input - characterized by an infinite rate of rise to a maintained steady-state level.



Subthreshold depolarization - a level of depolarization which takes the membrane potential away from resting levels but does not bring it to threshold.

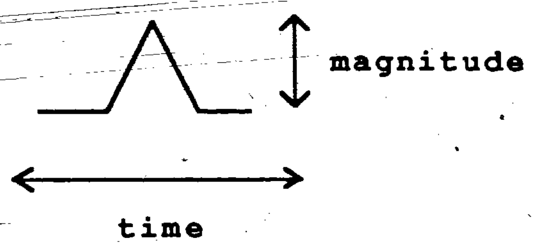
Surface electromyography (EMG) - a method of measuring the electrical activity of a motor unit population reflecting the number of motor units active as well as their firing patterns.

Synergist - a muscle which contributes to a function shared with other muscles (e.g. synergists of the flexor carpi radialis are flexor carpi ulnaris, flexor digitorum superficialis, palmaris longus, flexor digitorum profundus).

Tetanic tension - the maximal tension output of a muscle unit due to fusion of successive twitch tensions in response to a high firing rate.

Tonic firing - a continuous train of action potentials.

Triangular isometric force trajectories - a pattern of controlled force outputs where subjects increase force at a particular rate of rise and upon reaching a target level decrease force at the same rate.



Twitch contraction time - the time from initiation of the contraction to the attainment of maximum twitch tension.

INTRODUCTION

The firing pattern of a motoneuron governs the rate of rise and the magnitude of force produced by its muscle unit. The number of motor units recruited during a given input to a motoneuron pool as well as their firing patterns will determine the force output of the muscle. The holistic nature of surface electromyography (EMG) recordings can only provide partial information about the factors which influence the dynamics of motoneuron discharge; therefore, insight into the behaviour which underlies surface EMG activity can only be gained with recordings of a single motor unit firing pattern.

Single motoneuron firing patterns dictate the force production of its muscle unit and the sum of the outputs from the muscle units determines the total force output of a muscle. Therefore, single motoneuron firing properties described in the literature will be reviewed and then the comparative discharge patterns between small numbers of simultaneously recorded single motor units will be reviewed. The final section of the review will focus on surface EMG activity which reflects the combined discharge behaviour of a motor unit population.

Single Motoneuron Discharge Behaviour

Motoneuron repetitive firing patterns have been investigated using two different protocols. Investigators have either recorded single motoneuron firing patterns intracellularly from animals when the input to the motoneuron has been controlled, or, intramuscularly from animal and human subjects when force outputs have been controlled. The following review includes observations from both experimental designs.

Animal Studies: The current threshold for repetitive discharge, called the rhythmic threshold, for rat (Granit et al., 1963a) and cat (Granit et al., 1963; Mischelevich, 1969) motoneurons is approximately 1.3 - 1.4 times rheobase. Low and high threshold cat motoneurons (Kernell, 1965a; Kernell and Monster, 1982) are capable of repetitive firing.

Granit et al. (1963) observed that with the injection of a long-lasting step current, instantaneous firing rates, recorded intracellularly from rat and cat motoneurons, decreased from a maximum firing rate to a steady-state level of firing. This was called adaptation in firing rate. They also noted that the degree of adaptation increased with greater current intensities. Kernell (1965b) demonstrated that a plot of instantaneous firing rate (frequency (f)) against injected current intensity (I) completed for any interval could be fitted with two straight lines. A primary firing range was described by the slope of a line fitted to low firing rates generated from low intensity current inputs. The slope of this regression was less than the slope of a second line fitted to the higher firing rates generated during strong current inputs termed the secondary firing range. Kernell (1965b) investigated the influence of adaptation on the primary and secondary firing range. The slopes of the primary and secondary range were highest for the first interspike interval and lowest for intervals recorded 1.0 second after current onset. Therefore, current of a given intensity yielded a faster instantaneous firing rate from the first interspike interval than, for instance, the 10th interspike interval.

From the definition of adaptation in firing rate given by Granit et al. (1963) it is apparent that the firing pattern of a motoneuron may contain both a dynamic and steady-state component. The following will focus on factors suggested in the literature to influence the dynamic and steady-state phases of the motoneuron firing pattern.

Dynamic Phase

Animal Studies: A step current injected into an animal motoneuron yields an initial and a late phase of firing rate adaptation. Granit et al. (1963) and Kernell (1965b) observed an initial adaptation as a rapid decrease in the instantaneous discharge rate of the first 3 to 4 intervals (Kernell, 1965a) generated in response to the onset of a step current. Kernell (1965a) did not observe any relationship between degree of initial adaptation and the time course of after-hyperpolarization, a parameter which has been suggested to be inversely proportional to motoneuron size (Eccles et al., 1958). Late adaptation was defined as a slow decrease in instantaneous firing rate between the second and twenty-sixth seconds after a step current onset (Kernell and Monster, 1982). The most extensively investigated mechanisms under these conditions proposed for initial and late adaptation have focussed on intrinsic neuronal factors such as changes in potassium conductance. In particular, initial adaptation has been discussed in terms of after-hyperpolarization.

Initial adaptation has been ascribed by Kernell (1972) and Baldissera and Gustaffson (1974a) to the successive summation of after-hyperpolarization (AHP) from spikes occurring within an interval less than the duration of the motoneuron's AHP. Therefore, the first interspike interval displays the fastest instantaneous firing rate because there has, at that point, been no AHP summation, but the after-hyperpolarization conductance will sum in an approximately algebraic form as the third, fourth and fifth spikes are discharged (Baldissera and Gustaffson, 1971; 1974a; 1974b). This enhanced hyperpolarization will require a greater intensity of excitatory input to bring the membrane potential to threshold and generate another spike. Therefore, as more spikes are generated, the AHP increases such that the same intensity of excitatory input is less effective. The result is an increased time interval between successive spikes. For this reason, the instantaneous firing rate is markedly lower for those intervals following the first.

Late adaptation has been attributed to an accumulation of after effects resulting from a slowly activated increase in potassium permeability or a partial inactivation of the sodium pump (Kernell and Monster, 1982). Therefore, with a higher initial discharge rate there is greater accumulation of after effects and consequently, a more pronounced late adaptation (Kernell and Monster, 1982). Conversely, the proportion by which firing rate increases in response to a current applied during late adaptation is constant regardless of the current's intensity because the accumulation of after effects prior to the current application is the same. Late adaptation, however, is relatively small, and hence, it will be considered as part of the steady-state firing.

The dynamics of a firing rate pattern can not be investigated effectively with a current input restricted to a single rate of rise (e.g. the infinite rate of rise of the step current). Therefore, Baldissera et al. (1982;1987) injected into cat gastrocnemius motoneurons, ramp currents of different slopes, upto an intensity sufficient to yield maximal tetanic tension in the muscle unit, and concomitantly recorded the motoneuron firing pattern. This pattern of input will be referred to as ramp-and-hold. Baldissera et al.

showed that upon reaching rhythmic threshold a motoneuron increased its firing rate during the constant rate of rise of current and then adapted to a tonic level once current intensity reached steady-state. An overshoot best described the observed firing rate behaviour. The degree of overshoot was essentially proportional to the slope of the current ramp although the effect of increasing the current intensity during the ramp increase may have also been a factor (Baldissera et al., 1982). The dynamic firing pattern elicited from each motoneuron was quantified by calculating the instantaneous firing rate of the first interspike interval generated in response to the rate of rise of the injected current input. This form of quantification had been chosen earlier by this group for another set of experiments (Baldissera et al., 1982) to confirm that a component of the motoneuron firing pattern was related to the transient phase of the input. The slope from the linear portion of this relationship was taken as the index of dynamic sensitivity. The dynamic index value was used to ascertain differences in the dynamic firing behaviour between cat motoneurons. A weak relationship between dynamic sensitivity and the time course of after-hyperpolarization, coupled with a relatively strong inverse relationship between dynamic sensitivity and rheobase, suggested that small motoneurons displayed greater dynamic sensitivity than larger motoneurons.

A factor which influences the dynamics of the motoneuron firing pattern during ramp inputs is accommodation. Studies on rats and cats have suggested that the rheobase markedly increases with the application of a slow ramp current input (Bradley and Somjen, 1961; Burke and Nelson, 1971). This is called accommodation. Accommodation may alter the firing pattern of large motoneurons during a slow ramp input by delaying or hindering their discharge (Burke and Nelson, 1971). Based on studies by Hodgkin and Huxley, Bradley and Somjen (1961) suggested that accommodation maybe due to sodium channel inactivation produced by subthreshold depolarization.

Human Studies: The recruitment threshold for a human motor unit is defined by the amount of isometric force produced when a motor unit fires at its lowest rhythmic firing rate (Tanji and Kato, 1973; Milner-Brown et al., 1973; Freund et al., 1975). Lower and higher threshold human first dorsal interosseus motor units are capable of repetitive discharge during maintained force outputs (Freund et al., 1975). This is unlike the short toe extensor (Grimby and Hannerz, 1977) and tibialis anterior (Hannerz, 1974) muscles where low threshold motor units are capable of continuous repetitive firing, but high threshold units can only fire intermittently, with bursts.

Several studies have recorded the dynamic discharge patterns of motor units when force output was controlled rather than current input.

A number of human experiments have studied how motor unit inter-spike interval or instantaneous firing rate changes during triangular isometric force trajectories traced with different rates of rise. Person and Kudina (1972) and Milner-Brown et al. (1973) observed an increase in a motor unit instantaneous firing rate throughout the rising phase of the trajectory. Both groups also noted that the highest instantaneous firing rate occurred when the rate of rise of force was the highest and that the firing rate was markedly lower for a lower rate of change of force. This could possibly be due to accommodation. Grimby and Hannerz (1977) observed that short toe extensor motor units fired with the shortest inter-spike intervals during the fastest impulse trajectories. Desmedt and Godaux (1977) and Oishi et al. (1988) plotted instantaneous firing rate recorded during very slow to very fast rates of rise of traced force outputs. Both groups also observed increments in firing rate throughout the ramp slope when force was increased either quickly or slowly; however, during an extremely fast rate of rise of force (termed ballistic by both groups) the instantaneous firing rate of the first interval was the shortest and subsequent intervals were much longer, even though the rate of rise and the magnitude of the force trajectory was still increasing.

In addition to the relationship between instantaneous firing rate and the rate of rise of force, Grimby and Hannerz (1977) also demonstrated a relationship between maximum instantaneous firing rate and the unit's excitation level preceding the superimposed contraction. Interval lengths during the rate of rise of force were shortest when the background force level was low, although it is uncertain from their procedures whether a lower background force level corresponded to a lower background firing rate. Grimby and Hannerz only reported this behaviour for continuously firing motor units considered by them to be low threshold motor units.

The experiments reviewed above have shown that the single motoneuron instantaneous firing rate is related to the rate of rise of isometric force output generated by a given muscle or muscle group. Therefore, these studies have demonstrated that human motoneurons possess dynamic firing properties; however, the dynamic phase of the firing pattern was not quantified in the above experiments because of the force trajectories used. Triangular wave forms do not allow a clear distinction between the dynamic phase and adaptation necessary for quantification. The ramp and hold paradigm, already reviewed in terms of current inputs, may be better suited to study the dynamic and steady-state behaviour of motoneurons.

Palmer and Fetz (1985) recorded single motor unit and surface electromyogram activity from rhesus macaque monkeys trained to perform ramp and hold isometric flexor and extensor wrist torques. Each unit was recorded during a trajectory of a single rate of rise and finally attained magnitude. The units were separated into different groups depending on their dynamic and steady-state discharge behaviours. Some units displayed an increase to a maximum instantaneous firing rate during the rate of rise of torque, decreasing their firing rate to zero during the hold portion of the trajectory. Other units displayed the same type of dynamic behaviour, but adapted from a maximum instantaneous firing rate to a static firing rate during the hold. Another group of units displayed only a steady-state firing pattern or a gradual decrease in firing rate not coincident with the completion of the ramp phase of the trajectory. From these results the authors suggested that there were four motor unit types distinguishable by their discharge pattern. Thresholds obtained from the extrapolation of firing rate versus torque level plots suggested that thresholds were lower for units firing with the steady-state patterns than for those units which generated the dynamic firing patterns. Palmer and Fetz also recorded several units during a number of trajectories differing in torque level. These results indicated that the discharge behaviour of the unit could change from a predominantly dynamic to an essentially steady-state pattern when the magnitude of the torque output was increased.

Tanji and Kato (1973) and Gillies (1972) investigated abductor digiti minimi motor unit firing properties during isometric ramp and hold force trajectories of varying rates of rise. Gillies varied the magnitude of the contraction whereas Tanji and Kato had subjects always contract to maximum. Both groups observed that a unit recorded during fast and slow rates of ramp trajectories fired its maximum instantaneous rate during the rate of rise of force and adapted to a steady-state firing rate during the "hold" period. The highest firing rate and maximal adaptation were observed during the fastest rate of rise of force, whereas during the slow rate of rise of force units were recruited much later, attained a much lower maximum instantaneous firing rates and displayed less adaptation in firing rate. Gillies also noted that a unit recruited during the ramp portion of the force trajectory only fired a short burst and then dropped out unless the steady-state force level was equal to, or greater than, the unit's recruitment threshold.

Although most studies have concentrated on observing the variety of dynamic discharge behaviours displayed by individual motor units, a few human motor unit investigations have also attempted to determine if dynamic firing rate properties are related to motoneuron recruitment threshold. Milner-Brown et al. (1973) did not observe any difference between low and high threshold first dorsal interosseus (FDI) motor units when increment in instantaneous firing rate per increment in force was compared. Person and Kudina (1972) investigated the firing behaviour of different rectus femoris units during linearly varying force trajectories. They noted that when discharge rate (taken as the mean inter-spike interval over each 0.5 seconds of the traced trajectory) was plotted against the increasing force level of the trajectory, the low threshold motor unit displayed a greater increment in firing rate than high threshold motor units. This was the case during both slow and fast rates of rise of force. However, the actual rise in firing rate per increment in force, as seen in their figure 1, did not seem to differ between motor units. Grimby and Hannerz (1977) observed that short toe extensor high threshold motor units, which fired intermittently, were capable of higher instantaneous discharge rates than low threshold motor units, which fired continuously.

Physiological Implications

The pattern of instantaneous firing rates observed during the dynamic phase, in response to the fastest rate of rise of current input or during the fastest rate of rise of isometric force of the ramp-and-hold paradigm, are very similar to experimentally generated stimulation patterns.

These are stimulation patterns assessed to be optimal for producing a large non-linear increase in the rate of rise and magnitude of force output. Gurfinkel and Levik (1973) showed that force production was enhanced when a very short interspike interval was added to a constant interval spike train during surface stimulation of human muscle. Subsequently, a number of studies demonstrated in the cat through stimulation of whole muscle (Stein and Parmiaggini, 1979), single motor units (Zajac and Young, 1980; Botterman et al., 1986) and with injections of depolarizing pulses into motoneurons (Burke et al., 1976), that optimal force outputs were not only reliant on short inter-spike intervals but also influenced by the sequence and length of the subsequent intervals. These animal studies also found that for an optimal force output, a fast muscle required shorter interspike intervals than a slow muscle. This has been explained as a compensation of the shorter contraction times for fast versus slow muscle units and muscle (Buller and Lewis, 1965).

Steady-state Phase

Animal Studies: Although late adaptation has been recognized to influence the motoneuron firing pattern, Kernell (1965b;1979) and Baldissera et al. (1987) have considered spikes generated 1.0 to 1.5 seconds after the onset of current application to be essentially, steady-state, or static, discharge (Kernell, 1965b;1979; Baldissera et al., 1987). The steady-state firing rate is proportional to injected current intensity in both the primary and secondary firing ranges; however, to achieve a secondary range steady-state firing rate, the current intensity must be considerably greater than a current intensity able to produce an equivalent secondary range firing rate during the first interspike interval (Kernell, 1965a; Baldissera and Gustaffson, 1974c; Baldissera et al., 1987). Baldissera et al. (1987) found no significant correlation between a motoneuron's dynamic and static sensitivity index (slope of the linear relation between static firing rate and current-step intensity). Therefore, the dynamic and steady-state phase of the motoneuron pattern may not be influenced by the same factors.

For motoneurons in the cat Kernell (1979) did not observe any correlation between the slope of the primary range for static firing rate versus current intensity (f-I curve) and twitch contraction time or tetanic force. This suggests that steady-state firing properties do not differ between different types of cat motor units.

Human Studies: The steady-state phase of human motor unit firing pattern has been investigated by having subjects voluntarily generate and maintain isometric increments in force while recording the contributing single motor unit activity. Tanji and Katc (1973) calculated static firing rate

1.0 second after the attainment of the desired force level, whereas neither Freund et al. (1975) nor Monster and Chan (1977) specified the point in the unit's discharge considered to be static. All three studies observed a non-linear relationship between mean static firing rate and magnitude of isometric force. That is, increments in steady-state firing rate were greatest during the smallest increment in force and became progressively less for a greater increment in force output.

It has been suggested that higher and lower threshold motor units differ in their ability to increase steady-state firing rate during a desired increment in force output. The literature indicates that different muscles possess different relationships between low and high threshold units. Tanji and Kato (1973) demonstrated that low threshold abductor digiti minimi motor units generated a greater range of static firing rates than high threshold units. If, however, for each unit, increment in static firing rate per increment in force is taken as the slope of the relationship plotted in their figure 6, no marked difference is apparent between low and high threshold units. In first dorsal interosseus, Freund et al. (1975) observed the greatest increase in static firing rate per increase in force from the low threshold motor units. On the other hand, in the extensor digitorum communis, high threshold units display greater increments in static firing rate per increase in static force than low threshold units (Monster and Chan, 1977).

Simultaneously Firing Motor Units

Many recruited motor units will contribute to the generation of any force output from a muscle; therefore, to provide another means of ascertaining differences between motoneuron discharge behaviour based on motoneuron recruitment threshold, it is important to compare single motor unit firing behaviour against other concurrently active motor units. This type of work has been done with human subjects.

Dynamic Phase: Tanji and Kato (1973) showed that between two units recruited during a slow, ramp and hold force trajectory, the higher threshold motor unit achieves its maximum instantaneous firing rate later than a concurrently active lower threshold unit. Person (1974) and Deluca et al. (1982) recorded multiple units during a ramp of two seconds to a final held force level of approximately 30-40% of maximum voluntary contraction. The rectus femoris units (Person, 1974) were recruited during the force trajectory, as was the case for all but the lowest threshold deltoid unit recorded by Deluca et al. In both studies, the lowest threshold motor unit reached a greater maximum instantaneous firing rate earlier than the higher threshold motor units.

Person and Kudina (1972) recorded six rectus femoris motor units during a triangular waveform with a rise time of 2 seconds. Of these six units, five fired tonically in the background before the superimposition of the force trajectory. The lowest background firing rate was generated by the highest threshold unit and the highest background firing rate by the lowest threshold unit. Due to differences in recruitment order the low threshold motor unit fired tonically in the background for 1.5 minutes, whereas the highest threshold unit fired for only 30 seconds before the superimposed contraction. All units during this condition displayed peak activity at the same time during the rate of rise of the force trajectory. Furthermore, the greatest increase in instantaneous firing rate was generated by the highest threshold unit compared to the lowest threshold unit. The discrepancy in the dynamic firing behaviour between low and higher threshold motor units, evident particularly between the studies of Person and Kudina (1972) and Person (1974), may indicate the influence of background excitation level, rather than recruitment threshold, on the unit's discharge pattern.

Only the following study has provided data on recorded motor units firing simultaneously during two different conditions. Freund et al. (1975) recorded from two FDI motor units during cyclic force trajectories of a slow (8.0 seconds to peak) and 'fast' (approximately 1.5 seconds to peak) rate of rise of isometric force. Both units fired tonically prior to each contraction with the higher threshold unit generating the lower background firing rate. During both force trajectories the lower threshold unit displayed the highest instantaneous firing rate with its maximum instantaneous firing rate occurring much earlier than the high threshold unit. This was particularly evident during the 'fast' condition. This study demonstrated that both low and high threshold motor units were capable of different dynamic firing patterns dependent on the rate of rise of force; however, it is uncertain whether the greater firing rate recorded from the low threshold unit were due to its presumably greater background excitation level or an intrinsic neuronal difference from the higher threshold unit.

Steady-state Phase: Tanji and Kato (1973) and Monster and Chan (1977) have presented data on the steady-state firing behaviour of concurrently recorded motor units. Although the results of Tanji and Kato (1973) showed that the lowest threshold unit recruited during the contraction, generated the highest mean static firing rate, their figure 6 also indicates that the increase in firing rate per increment in force was equivalent amongst units of all thresholds. Monster and Chan (1977) and Monster (1979) recorded pairs of extensor digitorum communis motor units and observed that the higher threshold unit always had a greater increase in steady-state firing rate than the lower threshold motor unit per increase in force output.

Surface Electromyogram Activity

Surface electromyography (EMG) is an effective method of measuring the population activity of motor units. The literature on single and multiple motor unit recordings have suggested that human motor units are capable of a variety of firing rate patterns dependent, most definitely, on the rate of rise of the desired force output (Milner-Brown et al., 1973; Person and Kudina, 1972; Grimby and Hannerz, 1977; Oishi et al., 1988; Tanji and Kato, 1973; Gillies, 1972) and, possibly, on the unit's excitation level preceding the contraction (Grimby and Hannerz, 1977; Person and Kudina, 1972). The following review indicates that surface EMG activity has been related to several controlled force and movement parameters; however, the link between single motor unit behaviour and surface EMG activity has not been shown in the literature. Although single motor unit studies are conducted primarily with isometric contractions, surface EMG data from non-isometric studies have been included to provide information regarding surface EMG activity under a number of different conditions. As was done for the single motor unit literature, the review will consider the dynamic and steady-state phases of surface EMG activity separately.

Dynamic Phase: Very few studies have investigated the dynamic phase of surface electromyograms when subjects trace isometric force trajectories. Ghez and Gordon (1987) had subjects produce isometric force impulses at the elbow joint "as fast as possible" to force levels ranging between 20% and 60% of maximum voluntary contraction. This type of trajectory has been referred to as a ballistic contraction. Freund and Budigen (1979) demonstrated that the rate of rise of force during a ballistic trajectory is constrained by the magnitude of the force impulse. This suggests that a very fast rate of rise of force can be placed on one end of a continuum of contraction speeds. The results of Gordon and Ghez suggested that the magnitude of the integrated biceps EMG burst was positively related to the magnitude of the force impulse.

Bigland and Lippold (1954a) demonstrated that integrated surface EMG recorded from calf muscles was linearly related to angular velocity and tension produced during isotonic movements. Mustard and Lee (1987) and Brown and Cooke (1981) showed that integrated surface EMG is linearly related to the angular velocity and the angular distance of the limb movement. In another type of isotonic paradigm Gielen et al. (1985) recorded elbow flexors during pointing movements at different rates and distances. They observed that flexor surface, and intramuscular, integrated electromyogram activity increased linearly with the velocity of the movement.

The isotonic study of Bigland and Lippold (1954a) also varied the load preceding the superimposed contraction. A subject produced a movement around the ankle joint varying in angular velocity and tension from four different levels of background surface EMG activity. Their results suggested that the linear relationship between magnitude of integrated EMG and force produced at different angular velocities was the same regardless of the background surface EMG activity.

As was the problem with the single motor unit studies, the dynamic phase of the surface EMG activity can not be quantified separate from the steady-state phase when the force trajectories do not contain a static component. Therefore, it is advantageous to use the ramp-and-hold force trajectory to investigate surface EMG activity. This has only been done by Lesteinne et al. (1981) for isotonic movements about the wrist and elbow joints. The ramp consisted of an angular movement at a particular velocity followed by a steady-state component when the attained angle was maintained. Although this group only quantified the surface EMG during the maintainence of the final limb position, their figures showed a peak in EMG activity coincident with the maximum angular velocity, followed by adaptation to a tonic activity level. Their data also suggested, qualitatively, that the dynamic phase of the surface EMG activity was greatest for the fastest angular velocity.

Steady-state Phase: The relationship between steady-state surface EMG activity and isometric force output has not been determined in a manner similar to single motor unit experiments; that is, maintainence of increments in isometric force for a period of time. The relationship between static EMG activity and force, therefore, must be approximated from the studies of Lawrence and Deluca (1983) and Milner-Brown and Stein (1975). These studies had a subject trace a slow isometric triangular waveform (2.0 and 10.0 seconds, respectively) and showed that a large muscle displayed a non-linear relationship between root-mean-square of EMG amplitude and increasing force (Lawrence and Deluca, 1983), whereas a small muscle showed a quasilinear relationship (Milner-Brown and Stein, 1975; Lawrence and Deluca, 1983).

Lesteinne et al. (1981) had subjects move either their elbow or wrist joint through an angle to a target where final angular position was maintained for several seconds. Steady-state integrated EMG activity was calculated over a 2.0 second period beginning approximately 1.0 second after the angular movement. A non-linear relationship between static surface EMG activity and maintained angle of elbow and wrist flexion was observed for both biceps and flexor carpi radialis.

Conclusions

Single Motoneuron Firing Patterns: A review of the literature has demonstrated that motoneurons are capable of a variety of firing patterns. With the exception of the cat work by Baldissera et al. (1987) and the monkey work of Palmer and Fetz (1985), most studies have investigated either the motoneuron's dynamic or steady-state firing rate behaviour, not both together. Intracellular recordings have shown that the dynamic phase of the cat motoneuron discharge pattern varies in relation to the rate of rise (Baldissera et al., 1982; 1987) and intensity (Granit et al., 1963; Kernell, 1965a; Baldissera et al., 1982) of the injected current input. In human studies, the force output has been controlled predominantly for the rate of rise of isometric force. These investigations have indicated that maximal instantaneous firing rate increases (Milner-Brown, 1973; Person and Kudina, 1972; Grimby and Hannerz, 1977; Desmedt and Godaux, 1977; Oishi et al., 1988) and that adaptation is greatest (Tanji and Kato, 1973; Gillies, 1972) during faster speeds of contraction.

The rate of steady-state discharge recorded from cat motoneurons is linearly related to the intensity of current input (Kernell, 1965a; 1979; Baldissera et al., 1987). The steady-state firing rate recorded from human subjects was shown, under conditions controlled for magnitude of force output, to saturate non-linearly in relation to the increment in force output (Tanji and Kato, 1973; Freund and Budigen, 1975; Monster and Chan, 1977).

The effect of a current input superimposed upon different levels of background excitation has not been investigated in terms of the observed motoneuron discharge pattern. Grimby and Hannerz (1977) demonstrated that the initial background activity level of the human motor unit controlled via the background force level, can influence the dynamic phase of the unit's discharge pattern. No other human study has controlled background excitation level while measuring the dynamic phase of the firing pattern, nor has anyone investigated its effect on the steady-state phase.

Several studies have attempted to discern differences in firing rate behaviours throughout a motoneuron pool. Baldissera et al. (1987) showed that small motoneurons in the cat recorded intracellularly displayed greater dynamic sensitivity than larger motoneurons in the cat in response to injected current inputs. In these studies all cells were injected with current when they were in a quiescent state. Experiments controlling force trajectories, completed by Palmer and Fetz (1985), indicated that low threshold primate motor units could only fire tonically and displayed very little dynamic behaviour compared with higher threshold motor units. Background activity level was not controlled in their study. Investigations where simultaneously firing units have been recorded have yielded conflicting results. Two separate studies showed that among units recruited during the force trajectory, the low threshold units displayed greater dynamic activity (Person, 1974; Deluca et al., 1982), whereas if the units were active before the contraction, the higher threshold units generated a greater increase in instantaneous firing rates (Person and Kudina, 1974). Therefore, it is difficult to ascertain from the literature whether dynamic firing patterns do differ between motoneurons of different size.

Surface electromyogram activity: Surface EMG activity reflects the discharge behaviour of a motor unit population. Many investigations have measured either the EMG activity during a dynamic force trajectory or just the steady-state phase of the EMG activity; no study has recorded EMG activity during a force trajectory which provides an opportunity to examine both the dynamic and steady-state phases. A review of existing work has suggested that during ballistic contractions, the dynamics of surface EMG activity are influenced by the magnitude of the isometric force output (Gordon and Ghez, 1987). During isotonic studies Gielen et al. (1985) demonstrated a linear relationship between velocity of arm movement and surface EMG activity, whereas Bigland and Lippold (1954a) found linear relationships between integrated EMG and tension as well as angular velocity of the movement around the ankle joint. Brown and

Cooke (1981) and Mustard and Lee (1987) suggested that the first agonist surface EMG burst was related to the angular velocity and the angular distance of the limb movement.

The steady-state phase of EMG activity has not been investigated during truly static force outputs. The paradigms used, however, have suggested that steady-state EMG activity is linearly or non-linearly related to isometric force output dependent on whether the muscle investigated is large or small (Deluca et al., 1982; Milner-Brown and Stein, 1975). Therefore, since the EMG burst has also been related to magnitude of isometric force (Gordon and Ghez, 1987), separation of the dynamic and static phase of EMG activity recorded under the same condition would indicate whether each phase is related to the same or different parameters.

Only a study by Bigland and Lippold (1954a) varied the excitation level of the motor unit population before the completion of an isotonic contraction. They did not observe any difference between EMG and tension completed during ankle movements of different angular velocities. The effect of background EMG activity on the steady-state phase of EMG activity has not been investigated.

A review of the literature suggests that several studies have recorded single motor unit activity in parallel with surface EMG activity (Palmer and Fetz, 1985; Monster and

Chan, 1979); however, none have linked the two activities together.

Freund and Budigen (1979) demonstrated a constrainment of maximum speed of contraction by the magnitude of the isometric force produced; a relationship between two output parameters. On the other hand, Fitts Law (Fitts, 1954) established that the shortest possible movement time was inversely related to the width of the target such that thinner target widths resulted in longer movement times. This suggests that perceptual factors can also constrain the force output (Warren, 1988). It maybe possible that other visual cues constrain the maximum speed of contraction.

Objectives

To investigate the factors which influence the dynamic and steady-state phases of the single motoneuron firing pattern, single motor unit activity will be recorded during isometric ramp and hold force trajectories controlled for rate of rise and steady-state magnitude. In addition, motoneuronal background firing rate will also be controlled.

To assess whether dynamic and steady-state phases of the motoneuronal firing pattern are different for motor units of different recruitment threshold, motor units, firing simultaneously, will be recorded during ramp and hold isometric force trajectories. The background firing rate of each concurrently active motor unit will also be controlled.

To separate surface EMG activity into a dynamic and steady-state phase and to investigate the factors which influence these components, surface EMG activity will be recorded during ramp and hold isometric force trajectories completed to low percentages of maximum voluntary contraction. These trajectories will be controlled for rate of rise and magnitude of force output as well as for background force level.

A qualititative interpretation to link the observed single motor unit firing pattern to the surface EMG activity will also be attempted.

To investigate whether maximum speed of contraction can be constrained by visual cues altered in the time domain, subjects will trace the same force trajectory "as fast as possible" at different timebase settings of a storage oscilloscope.

METHODS

Three sets of experiments, all requiring subjects to trace isometric ramp and hold force trajectories, were conducted. In one set of experiments single motor unit and surface electromyograms (EMGs) from the wrist flexors were recorded simultaneously from the flexor carpi radialis. In another set of experiments only surface EMG from the wrist flexors was recorded. A small number of experiments was also designed to assess the influence of visual cues on maximum rate of rise of isometric force.

The same experimental arrangement was used for all three experimental designs.

Experimental Arrangement

The subject sat comfortably in a chair facing a storage oscilloscope with his right forearm resting on a padded, horizontal platform (figure 1). The subject's metacarpal-phalangeal joints were taped against a rigid vertical handle to ensure there was no wrist adduction or abduction. With fingers relaxed, the subject exerted isometric force against the handle with the wrist flexors. The position of the vertical handle was adjusted for each subject's hand and the distance from vertical handle to the axis of wrist rotation was measured. The axis of wrist rotation was positioned to be coaxial with the central shaft of the apparatus and adjustable padded stops were secured to minimize lateral

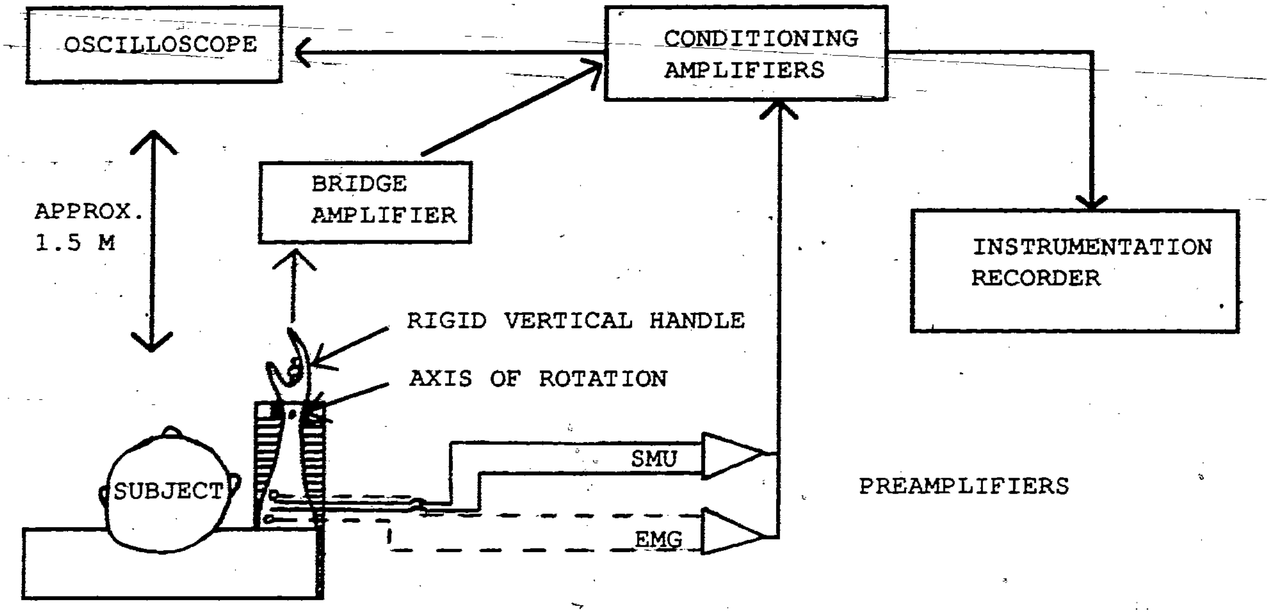


Figure 1 Experimental arrangement used for single motor unit, surface EMG and maximum speed of contraction experiments. Subject faced a storage oscilloscope with right forearm resting on a padded, horizontal platform. With fingers relaxed, the subject exerted isometric force with the wrist flexors to trace different trajectories. Surface EMG and single motor unit activity were recorded from the flexor carpi radialis.

movement of the wrist. Through all conditions the experimenter ensured that there was no lateral movement of the forearm and minimal activity in the upper arm muscles by visually monitoring the subject's posture. A horizontal bar connecting the vertical handle to the central shaft was equipped with strain gauges to measure force. The output of the strain gauges was fed to a bridge amplifier (Vishay Instruments) set from DC to 1KHz band pass filter. Before display on the storage oscilloscope, on which the subject traced the force trajectories, further amplification was provided by a conditioning amplifier.

Subjects

Single Motor Unit Experiments: Thirty-seven experiments with eight healthy subjects 22-44 years of age were completed (three females, five males). All subjects signed informed consent forms before experiments proceeded. The amount of data collected during any experiment was dependent on the subject's comfort and the clarity of the record.

Surface Electromyogram Experiments: Twenty-two successful experiments were completed involving sixteen subjects in the age range of 22-44 years (five females and eleven males). Eleven experiments required a maximum force output of approximately fifteen percent of a subject's maximum voluntary contraction (MVC), whereas eleven experiments were completed with a force output of approximately thirty percent of MVC. Subjects completed at least three isometric force trajectory conditions during each experiment. Six of these subjects also participated in the single motor unit experiments.

Maximum Rate of Rise of Force Experiments: Eleven experiments involving seven subjects ages 22-44 years (two females, seven males) were completed. In addition to this set of experiments, six of these subjects also participated in the surface EMG or single motor unit experiments.

Recording

Surface flexor EMG was recorded with two Ag-AgCl, 0.8 mm diameter surface electrodes located over the belly of the flexor carpi radialis. The electrodes were connected to a Grass P15 AC preamplifier (30Hz - 3KHz bandpass).

Single motor unit activity was recorded midway between two surface electrodes with a bipolar needle electrode. The micro-electrodes were composed of two teflon coated stainless steel wires of 75 µm diameter embedded in epoxy within the shaft of a 25 gauge needle (Calancie and Bawa, 1985). An AC Grass P15 preamplifier set predominantly with a bandpass of 100Hz to 10KHz was used for the first stage filtering of single motor unit activity. High pass filtering with a Wavetek Rockland filter was used to further enhance the single unit record. Single motor unit activity was displayed on an oscilloscope for visual feedback and fed to an audio amplifier for audio feedback.

Force, surface EMG and single motor unit activities were further amplified by conditioning amplifiers and recorded on an FM tape recorder (Hewlett Packard 3968A). The majority of experiments were recorded at a tape speed of $3^3/_4$ inches per second (ips); however, to improve clarity of the single motor unit record, higher tape speeds of $7^1/_2$ ips and 15 ips were used.

Procedure

Single Motor Unit Experiments: A period of practice in recruiting and maintaining individual motor units distinct from the background activity and at different levels of isometric force was provided to each subject. Recording began once the subject was comfortable with the procedure of controlling tonic motor unit activity. At the beginning of a set of conditions each motor unit was identified by establishing its recruitment threshold through slow ramp contractions.

Each trajectory completed by the subject was controlled for the rate of rise and magnitude of the isometric force trajectory (figure 2A) as well as the background firing rate of the motor unit. Single motor unit activity was recorded during three conditions involving different speeds

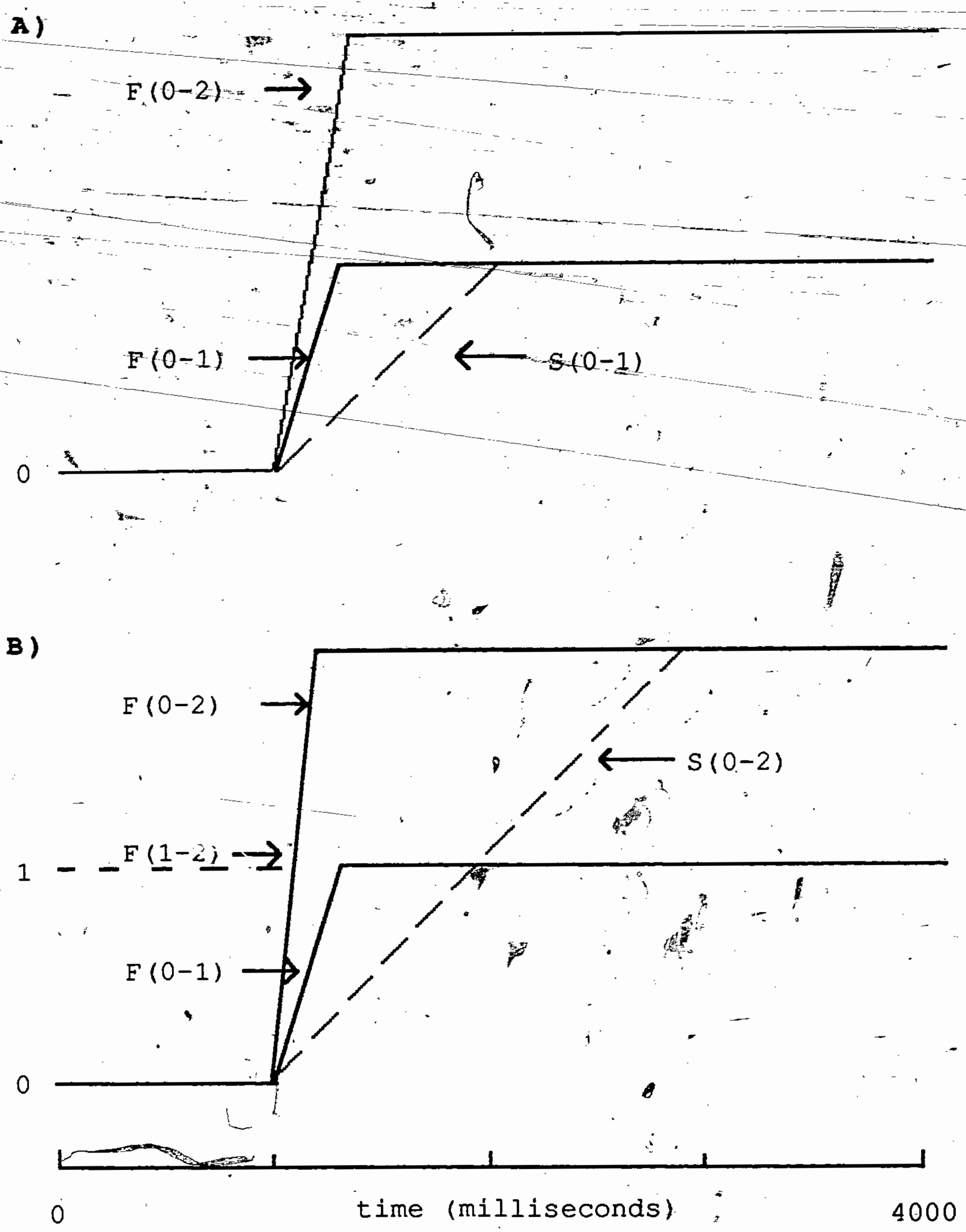


Figure 2 Isometric torque trajectories which differed in the speed of contraction or magnitude. **A)** trajectories traced during single motor unit experiments. Background firing rate of unit was also controlled; **B)** trajectories traced during surface EMG experiments. Background torque was also controlled at either the "1" or "0" level.

of contraction. The instruction for the two fast conditions was to trace "as fast as possible" a step indicated by a vertical line on the oscilloscope (timebase set at 0.5 seconds/division). For the slow ramps, S(0-1), the subject traced, in one second, one diagonal division of the oscilloscope with the timebase set at 1.0 second/division. Conditions also varied in the magnitude of the force output. The magnitude of the F(0-2) condition was established as the maximum force level possible with ensured clarity of the motor unit, whereas the magnitude of the F(0-1) condition was one-half of F(0-2). Each trajectory lasted approximately 3-4 seconds. In addition to controlling the force trajectories, the background firing rate(s) of the motor unit(s) was also controlled. The background firing rate of the unit was either zero, just above recruitment threshold, or well above recruitment threshold.

Subjects completed conditions which either involved examining the firing rate behaviour of one unit across a number of conditions, or recording two simultaneously firing units during one or more conditions. At least thirty trials of each condition were completed. Each trial began with a visual cue displayed as the initiation of a sweep on the storage oscilloscope. The oscilloscope was triggered by a Schmitt trigger which received input from a pulse generator. The Schmitt trigger was controlled by the experimenter who, therefore, controlled the inter trial time.

Within a given experiment attempts to investigate different motor units were made by moving the position of the electrode in the muscle.

Surface Electromyogram Experiments: The four possible isometric force trajectories traced during the surface EMG experiments varied in background, rate of rise and magnitude of isometric force (figure 2B). For all experiments a subject was completely relaxed at the "0" level. Level "2" for eleven experiments corresponded to a comfortable contraction that the subject could repeatedly hold without fatigue (approximately 15% of maximum voluntary contraction (MVC), whereas for eleven experiments level "2" corresponded to a force level approximately 30% of MVC. Force level "1" was halfway between levels "0" and "2". In an attempt to compare the effect of background excitation level of the motor unit population on the surface EMG activity the F(0-1), F(0-2) and S(0-2) conditions began from "zero" (rest) whereas the F(1-2) trajectory began from a force level equal in magnitude to F(0-1). Rate of rise of force was varied in the manner described for the single motor unit experiments. The beginning of each trial was controlled by the experimenter as was previously described.

The subject carried out 30 trials for each of the four possible trajectories i.e. fast (0-1), (0-2) and 1-2) and slow (0-2). In the initial experiments, subjects also completed slow (0-1) and (1-2) conditions, but since they only added fatigue to the experiment and not much information to the results, they were not included in the remainder of the experiments. Since most of the information on surface EMG activity was obtained from the fast trajectories these were the only conditions completed to 30% of MVC.

Maximum Rate of Rise of Force Experiments: At least five conditions, of twenty trials each, were completed during each experiment. The F(0-2) condition was completed under three different oscilloscope sweep speeds: 0.5 sec/div., 0.2 sec/div. and 0.1 sec/div. The F(0-1) condition was completed with only the first two oscilloscope sweep speeds. The maximum force output for the F(0-2) condition was kept to approximately fifteen percent of MVC for seven of the experiments and about thirty percent of MVC for an additional four experiments. The sequence of conditions was varied between subjects to minimize an order effect in the results.

Analysis

Stimulus, force, surface EMG and single motor unit recordings were all taken from the HP 3968A instrumentation tape recorder and passed through conditioning amplifiers before digitization.

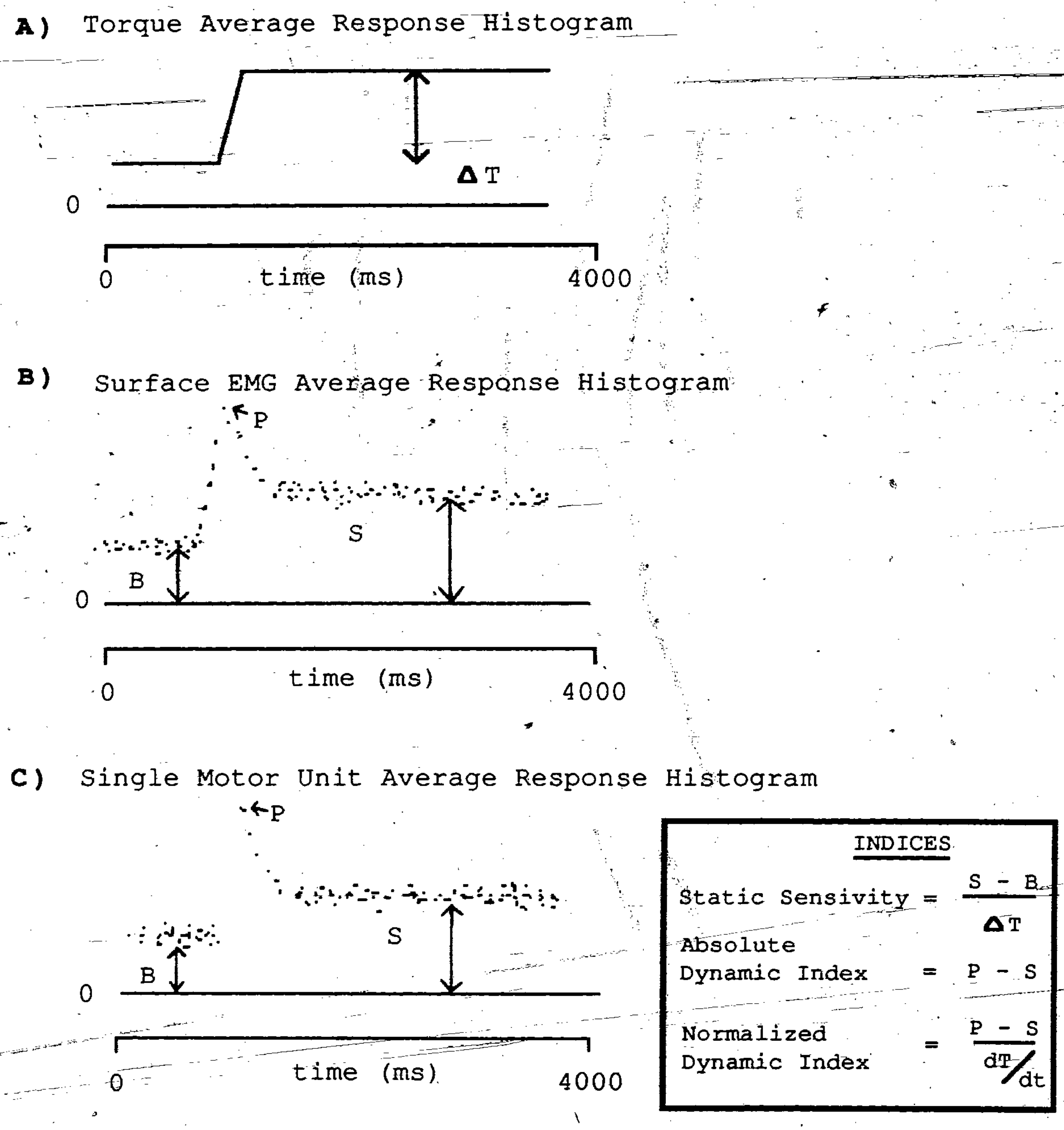
The single motor unit compound action potential was discriminated from other simultaneously recorded motor unit activity by a time-window discriminator. Accurate discrimination of a motor unit was confirmed by constructing first order histograms.

Force, full-wave rectified surface EMG, and single motor unit, post-stimulus average response histograms (ARHs) were constructed on an LSI-II/03 minicomputer, with averaging programs, at a sampling rate of 40Hz. A defined level on the rate of rise of the force trace was used to trigger the computer to average force, surface EMG and single motor unit activity.

Motor units were active before the corresponding trigger level on the force output was attained, and therefore, force, EMG and single motor unit activity were delayed before averaging. Force and surface EMG recorded during force outputs of approximately 15% of MVC were delayed by 130 milliseconds by two in-series Bak analog delay lines, whereas force and surface EMG recorded concurrently with the single motor unit activity as well as during force trajectories to thirty percent of MVC were delayed 682 milliseconds with an Alesis Microverb II digital delay line before being sent to the computer. The 5V square pulse emitted from the logic circuit during motor unit discrimination was delayed 1325 milliseconds with two in-series Alesis Microverb II delay lines.

Diagrammatic average response histograms typical in form to those constructed for force, rectified surface EMG and single motor unit activity is shown in figure 3. Mean background activity per msec, B, peak activity per msec, P, and mean static activity per msec, S were calculated from values obtained from the single motor unit and surface EMG average response histograms with a subprogram on the LSI-II/03 mini-computer. Mean background activity per millisecond was calculated from the initial 200 milliseconds of the surface EMG histogram and the initial 600 milliseconds of the single motor unit average response histogram. Peak activity was ascertained by visual estimate. Adaptation of surface EMG and single motor unit activity was complete within 1000 milliseconds after peak activity (Tanji and Kato, 1973; Lesteinne et al., 1981); therefore, static activity was computed by averaging the activity between 1400 and 2900 milliseconds after the peak. Several of the trajectories, completed to 30% of MVC during the surface EMG experiments, were of duration shorter than 3-4 seconds (see figure 18). In these circumstances steady-state activity was averaged over 1000 msec.

Background and maximum force levels for each condition were also obtained from the minicomputer and converted into torques by accounting for the distance from the axis of wrist rotation to the rigid vertical handle. These values were expressed as Newton-metres (N-m). Trajectories were also


A) Torque Average Response Histogram

B) Surface EMG Average Response Histogram

C) Single Motor Unit Average Response Histogram

Figure 3 Diagrammatic average response histograms for **A)** isometric torque **B)** surface EMG activity and **C)** single motor unit activity. The dynamic and static phases of the surface EMG and single motor unit average response histograms were quantified with three indices: absolute dynamic, normalized dynamic and static sensitivity. The latter two indice were calculated in terms of the torque trajectory. B = mean background activity per msec; P = peak activity per msec; S = mean static activity taken 1400 msec after peak.

differentiated to obtain maximum speed of contraction (dT/dt).

Two indices were calculated from the obtained values to quantify the dynamic component of the average response histograms:

$$\text{absolute dynamic index} = P - S,$$
$$\text{normalized dynamic index} = (P - S)/(dT/dt)$$

The steady-state component of the surface EMG and the single motor unit activity was quantified as follows:

$$\text{static sensitivity index} = (S - B)/\Delta T$$

where ΔT was the change in the step or ramp torque. The static single motor unit firing pattern was also quantified with respect to the absolute static firing rate particularly for those conditions where the motor unit was recruited during the trajectory since background excitation level could not be quantitatively described.

Statistical Analysis

All statistical analyses were completed on the software package Statsview 512+ for the MacIntosh microcomputer system.

Single Motor Unit Experiments: Data were grouped from all subjects and dependent t-tests were used to compare single motor unit behaviour across pairs of conditions or to compare the behaviour of two units recorded simultaneously under the same condition. Mean values were considered significantly different at $p \leq 0.05$. Standard error was used as an indicator of the variance as it accounted for the sample size of the grouped data. This was important because the sample size varied between each set of conditions completed in these experiments.

Surface Electromyogram Experiments: During a given experiment subjects completed all the force trajectories required (i.e. F(0-1), F(0-2), F(1-2), and sometimes S(0-2)). Therefore, statistically significant differences between each condition for a particular index value were determined using one-way, repeated measures analyses of variance. If the ANOVA indicated a significant difference between the mean index values of the different trajectories, specific statistical differences between conditions were investigated with Scheffe multiple comparison tests (at $p \leq 0.05$).

Maximum Rate of Rise of Force Experiments: One-way, repeated measures analyses of variance tests followed by Scheffe multiple comparison tests (at $p \leq 0.05$) were used to determine significant differences in the maximum rate of rise of the F(0-2) trajectory completed at three different settings of the oscilloscope timebase.

RESULTS

The dynamic and steady-state phases of motor unit firing patterns were studied under a number of conditions. Thirty-seven experiments with eight subjects were carried out to investigate the firing behaviour of a single motor unit as well as to compare simultaneously firing units. Twenty-two experiments with sixteen subjects were completed to investigate dynamic and steady-state surface EMG activities during two different ranges of force output.

Single Motor Unit Discharge Behaviour

The maximum step increment in torque during the single motor unit experiments was no greater than 10% of maximum voluntary contraction (MVC). [This is an approximation for six of the eight subjects since MVC was only obtained from two subjects. This was due to limitations of the force transducer in terms of the maximum force measurable. Therefore, the ninety-one units recorded during these low increments in force have been considered as low-threshold motor units.

Dynamic Phase: From the raw data, maximum instantaneous firing rates observable during the dynamic phase were usually less than 40 pps although it was possible to periodically observe firing rates of 70 - 80 pps.

The relationship between the dynamic phase of the single motor unit firing pattern and the rate of rise of isometric force was investigated by recording the same motor unit firing during the F(0-1) and the S(0-1) conditions and/or during the F(0-1) and F(0-2) conditions. Subjects were instructed to keep background firing rate constant between the pairs of conditions.

Twenty-nine motor units were recorded from six subjects during the F(0-1) and S(0-1) conditions. Typical average response histograms constructed from the firing activity of the same motor unit during the F(0-1) and S(0-1) conditions are shown in figure 4. Qualitatively, it is evident from these histograms that there was greater overshoot in the motor unit's firing pattern during the F(0-1) versus the S(0-1) condition. This behaviour was typical of twenty-six of the twenty-nine motor units recorded.

The absolute dynamic index reflected the qualitative observations made from figure 4. It was significantly greater for the F(0-1) condition than for the S(0-1) condition ($p \leq .0002$) (figure 5); however, when this index was normalized to the rate of rise of isometric force, it was markedly less for the fast condition than for the slow condition ($p \leq .0001$) (figure 6). The absolute dynamic index and the normalized dynamic index values showed the same trend when the unit was recruited during the contraction. The

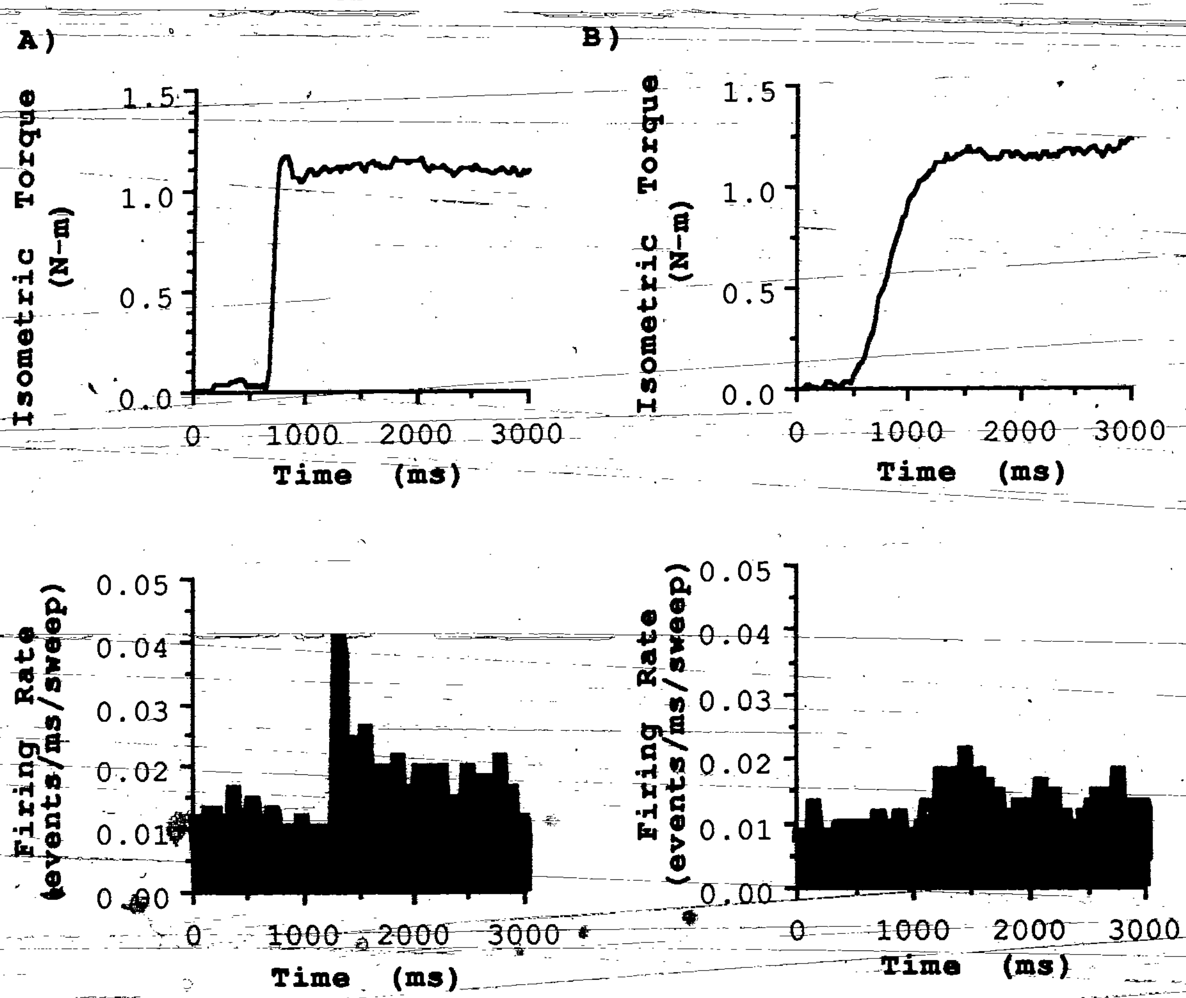


Figure 4 Typical average response histograms for isometric torque (on top) and single motor unit activity (on bottom) for **A)** F(0-1) and **B)** S(0-1) conditions. Number of sweeps=25.

relatively low increment in firing rate during the F(0-1) condition was also evident at even faster speeds of contraction. Thirteen units were recorded from five subjects during the F(0-1) and F(0-2) conditions completed from a tonic background firing rate. The speed of contraction of the F(0-2) force trajectory was much greater than the speed of the F(0-1) condition when the "as fast as possible" instruction was given for both conditions (Freund and Budigen, 1979). Therefore, although the absolute dynamic indices did not differ between the F(0-1) and F(0-2) conditions (figure 5, p≤.56), the normalized dynamic index was significantly greater for the F(0-1) condition than for the F(0-2) condition (p≤.023)(figure 6). These results support the observations between the F(0-1) and S(0-1) trajectories implying that the relative increment in the dynamic activity decreases, in a non-linear manner, with faster speeds of contraction.

The relationship between the background excitation level of the motor unit and the dynamic phase of its firing pattern was also investigated. This was accomplished by controlling the unit's background excitation level between pairs of conditions. In one set of conditions the F(0-1) trajectory was completed once when the unit was recruited during the trajectory and again when it began from a minimal, tonic firing rate. Nineteen motor units from seven subjects completed these conditions. In another set of conditions, 11

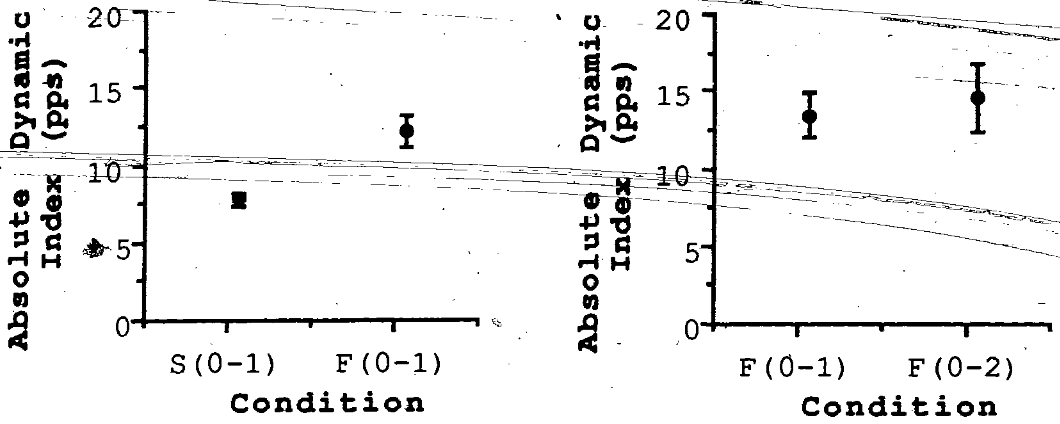


Figure 5 The mean and standard error of absolute dynamic index for the F(0-1) and S(0-1) conditions ($p \leq 0.0002$) and F(0-1) and F(0-2) conditions ($p \leq 0.16$) when background firing of the single motor unit was a low tonic rate. Number of subjects, $n_s=6$, number of motor units, $n_u=29$ for F(0-1) and S(0-1). Number of subjects, $n_s=5$, number of motor units, $n_u=13$ for F(0-1) and F(0-2) trajectories.

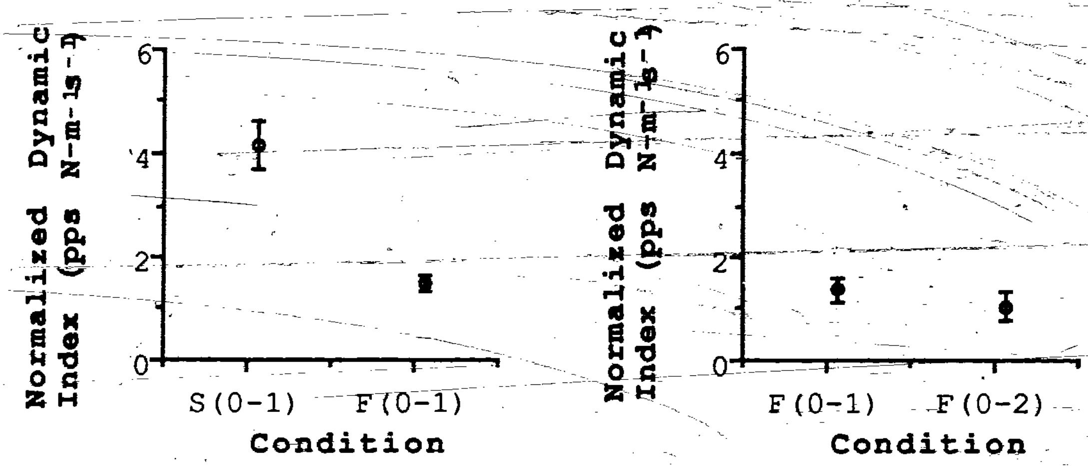


Figure 6 Mean and standard error of normalized dynamic index for the F(0-1) and S(0-1) conditions ($p \leq 0.0001$) and the F(0-1) and F(0-2) conditions ($p \leq 0.023$) when background firing of single motor unit was a low tonic rate. Number of subjects, $n_s=6$, number of motor units, $n_u=29$ for F(0-1) and S(0-1). Number of subjects, $n_s=5$, number of motor units, $n_u=13$ for F(0-1) and F(0-2) trajectories.

motor units were recorded from six subjects who completed the F(0-1) condition where the unit began from a minimal firing rate and then from a considerably faster tonic background firing rate. The effect of the background excitation level on the dynamic phase of the firing patterns was determined with the normalized dynamic index because it accounted for differences in the rates of rise of the completed force trajectories which, theoretically, were constrained to be similar under both conditions. The normalized dynamic index value obtained when the unit began from a minimal rhythmic firing rate or when it was recruited during the trajectory did not differ significantly. In an attempt to determine if there was a relationship between the amount of change in background firing rate and the unit's dynamic firing pattern, the difference in background firing rate was plotted against the difference in normalized dynamic index values and represented by the filled circles in figure 7. The lower background firing rates and the corresponding normalized dynamic index values were always subtracted from the values obtained when the unit began from a higher background firing rate. The trend of this plot suggests that at a higher, tonic background firing rate the normalized dynamic index was less than the normalized dynamic index value when the unit began from "zero". The scatter in this plot maybe due to the indefinable "zero" background activity as it could represent an excitation level anywhere from well below rheobase to just sub-recruitment threshold. When the unit began from a high versus a low tonic background firing rate the normalized dynamic index value was significantly less ($p \leq 0.039$). This non-linear behaviour may suggest a saturation phenomenon in the motoneuron's dynamic firing pattern. The open circles in figure 7 represent the difference in tonic background against the difference in normalized dynamic index between these two conditions. The observable linear trend in this plot is difficult to explain physiologically and therefore, will not be interpreted.

Steady-state Phase: Firing rates during the steady-state phase ranged from approximately 7 - 18 pps, but the majority of static firing rates were consistently between 9 - 13 pps.

The static phase of the motor unit firing pattern was analysed both in terms of the absolute static firing rate and the static sensitivity index. Although the definition of the static sensitivity index required definable background firing activity, in order to ensure consistency in comparisons across all conditions, it was also calculated for conditions when the unit was recruited during the trajectory and therefore, had "zero" background activity.

The rate of rise of isometric force does not influence the static firing behaviour of the unit since neither the static firing rates nor the static sensitivity values

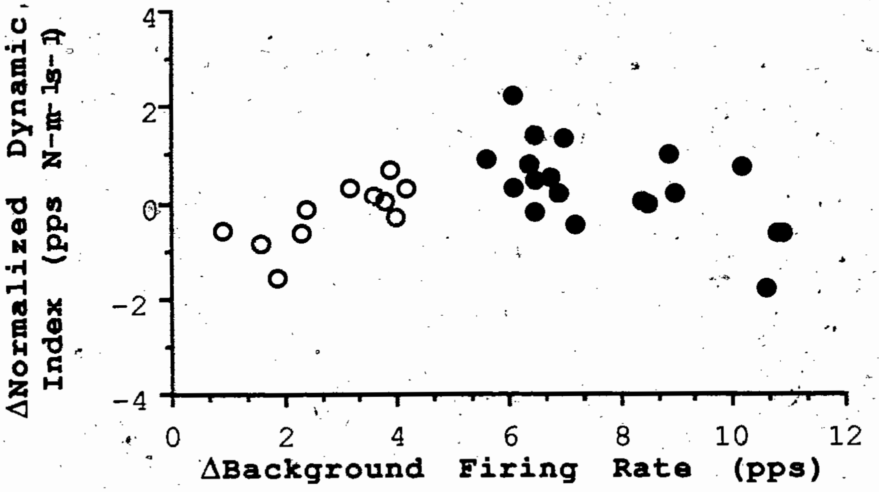


Figure 7 Each point represents the difference in background firing rate versus the difference in normalized dynamic index for single motor units recorded during the F(0-1) condition. Unfilled circles (*o*) are differences between a high and low, tonic background firing rate, whereas the filled circles (●) represent differences between a zero and a low, tonic background firing rate. Values obtained at the lower firing rate were always subtracted from values obtained when the unit fired at the higher background firing rate. Unfilled circles, number or subjects n_s=6, number of motor units, n_u=11. Filled circles, number or subjects n_s=7, number of motor units, n_u=19.

differed between the F(0-1) and S(0-1) conditions when the subject was instructed to keep the unit's tonic background firing rate constant between the two conditions (figures 8A and 8B).

The relationship between magnitude of force and steady-state firing properties was investigated by having subjects complete the F(0-1) and F(0-2) conditions. Background firing rate was kept constant. When averaged across the thirteen units recorded, the steady-state firing rate during the F(0-2) trajectory (12.1 pps) was higher, but not significantly different from the F(0-1) condition (10.9 pps) (figure 9A). Therefore, since background firing rate was essentially constant between both conditions, static sensitivity values were significantly less for the F(0-2) than the F(0-1) condition ($p \leq 0.018$)(figure 9B). To determine whether the degree of adaptation, observable in the dynamic phase of the firing pattern, influenced the steady-state phase, four units were recorded from 3 subjects during S(0-1) and S(0-2) conditions. As with the fast conditions, static firing rates were slightly higher during the S(0-2) trajectory (range 10.0 - 19.1 pps) versus the S(0-1) condition (9.9 - 17.9 pps). Furthermore, three of the four units showed markedly higher static sensitivity values during the S(0-1) condition than the S(0-2) condition. This implies that the saturation in static firing rate observed during the F(0-2) condition was not related to the trajectory's faster

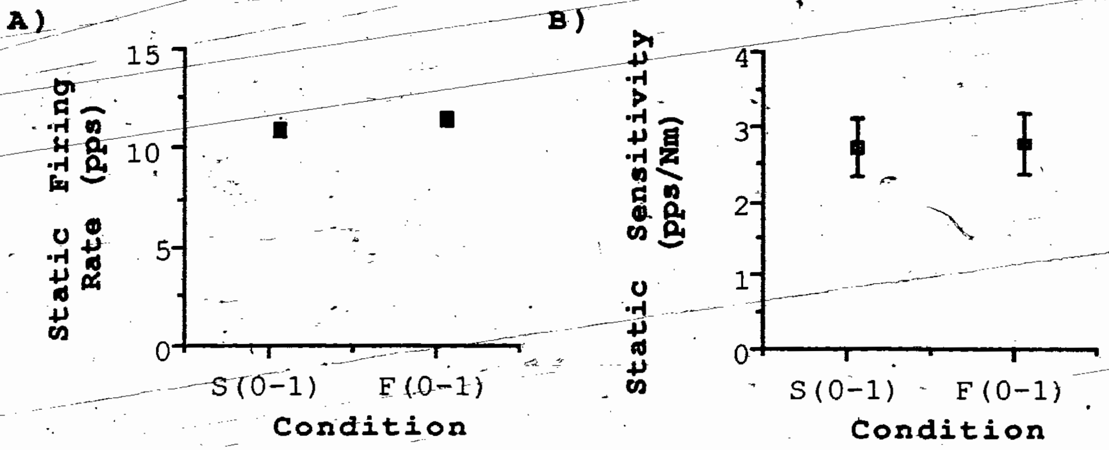


Figure 8 Mean and standard error of **A)** static firing rate ($p \leq 0.16$) and **B)** static sensitivity index ($p \leq 0.82$) for the F(0-1) and S(0-1) conditions when background firing rate was a low, tonic rate. Number of subjects, $n_s=6$, number of motor units, n=29.

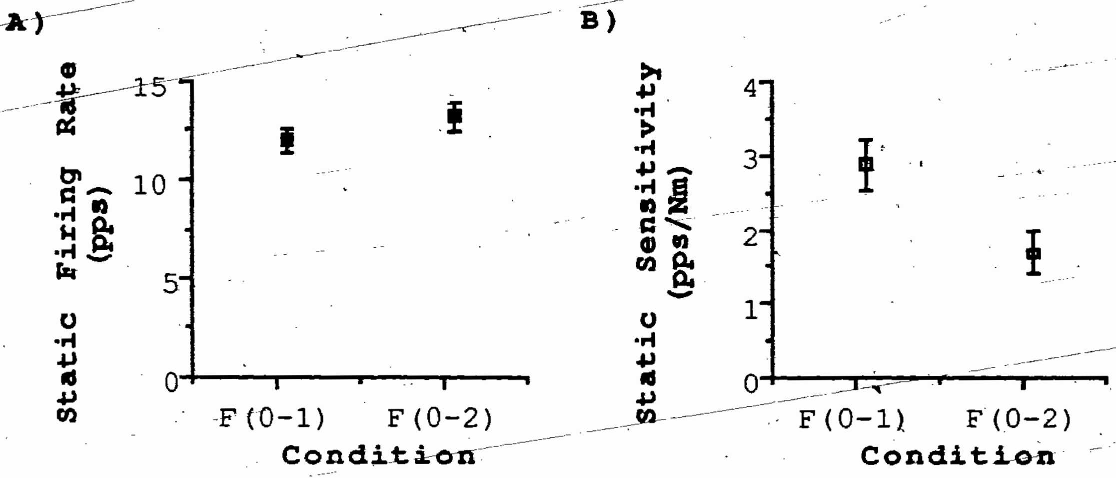


Figure 9 Mean and standard error of **A)** static firing rate ($p \leq 0.19$) and **B)** static sensitivity ($p \leq 0.018$) for the F(0-1) and F(0-2) conditions when background firing rate was a low, tonic rate. Number of subjects, $n_s=5$, number of motor units, n=13.

rate of rise, but rather it was related to it's greater force magnitude.

The influence of background excitation level on steady-state firing behaviour was also investigated during the F(0-1) trajectory as already described for the dynamic phase. Nineteen units, recruited during the trajectory fired significantly lower static firing rates ($p \leq 0.01$) than when they began the contraction from a minimal background firing rate; however, the large difference in background activity resulted in the static sensitivity index being significantly greater when the unit began from "zero" than when it began from a tonic firing rate ($p \leq 0.0001$). If the unit began from a high versus a low tonic background firing rate, its absolute static firing rate was significantly greater ($p \leq 0.02$), but its relative increase in static firing rate per increment in force, represented by the static sensitivity index, was less ($p \leq 0.0065$) than when the unit began from a lower background firing rate. A plot of the change in background firing rate versus the change in static sensitivity values, seen in figure 10, expands on these observed relationships. This figure shows a weak trend amongst the filled squares indicating that the difference in static sensitivity values is more marked when the tonic background firing rate is high compared to a "zero" background activity. Although the static sensitivity values become progressively smaller when the unit begins from higher

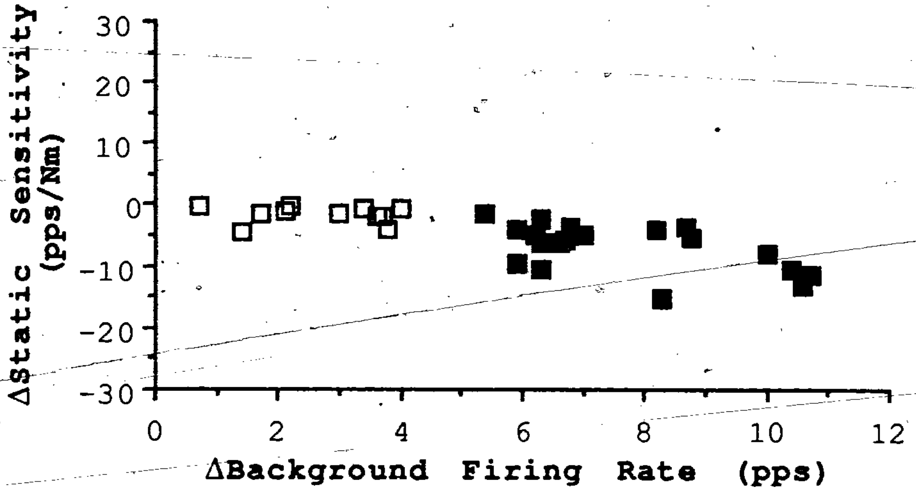


Figure 10 Each point represents the difference in background firing rate versus the difference in static sensitivity index for single motor units recorded during the F(0-1) condition. Unfilled squares (□) represent differences between a high and low, tonic background firing rate, whereas the filled squares (■) mark differences between a zero and a low, tonic background firing rate. Values obtained at the lower firing rate were always subtracted from values obtained when the unit fired at the higher background firing rate. Unfilled circles, number or subjects n_s=6, number of motor units, n_u=11. Filled circles, number or subjects n_s=7, number of motor units, n_u=19.

background firing rates, the open squares in figure 10 demonstrate that the magnitude of the difference in tonic, background firing rate between the two conditions was not related to the observed change in static firing behaviour.

Interdependence of Dynamic and Steady-state Phases: The dynamic phase of the single motoneuron firing pattern is related to the rate of rise of force whereas the static phase is related to magnitude of the force output. To confirm that the dynamic and static phases were not interdependent, static sensitivity and normalized dynamic index values, obtained during the F(0-1) condition, were plotted against each other (figure 11). The poor correlation (r=0.41) observed between these two indices, also seen if absolute values were plotted, suggests that dynamic and steady-state firing patterns maybe governed and/or generated by separate processes.

Simultaneously Firing Motor Units

Pairs of units firing simultaneously were recorded during the F(0-1) condition to assess whether the motoneuron's firing pattern was predictable based on its recruitment threshold. The background firing rates of the unit pairs were controlled. In one condition the low threshold unit began from a tonic background firing rate and the high threshold unit was recruited during the ramp phase. Unit pairs were only accepted if the high threshold unit, once recruited, maintained a tonic firing rate during the

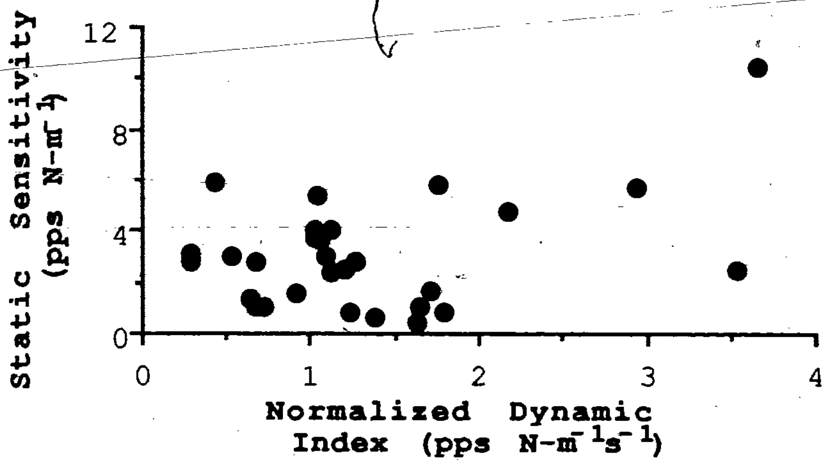


Figure 11 Static sensitivity and normalized dynamic index values for units recorded during the F(0-1) condition. The low correlation between the points (r=0.41) suggest that the dynamic and static phases are influenced by different factors. Number of subjects, n_s=6, number of motor units, n_u=29.

static portion of the trajectory. In a second condition both units fired tonically in the background.

Dynamic Phase: Only the absolute dynamic index was used to compare the dynamic firing behaviour between two units since both units were recorded during the same trajectory. Therefore, the normalized dynamic index would provide the same information. Fifteen pairs of units were recorded from seven subjects when only the low threshold unit fired tonically in the background. The absolute dynamic index values did not differ significantly between the two units, nor was there any observable relationships between their difference in background firing rate versus their difference in absolute dynamic index (closed triangles, figure 12). These relationships did not change in the second condition when both units fired tonically in the background (open triangles, figure 12). The scatter in figure 12, seen for both conditions, may have been due to the relatively small differences in recruitment thresholds between the recorded units. This plot does suggest that, among these low threshold motor units, recruitment threshold could not be used as a determinant of a unit's dynamic firing properties. This position is strengthened in figure 13 because the difference in recruitment threshold between the unit pairs was not correlated with their difference in absolute dynamic index.

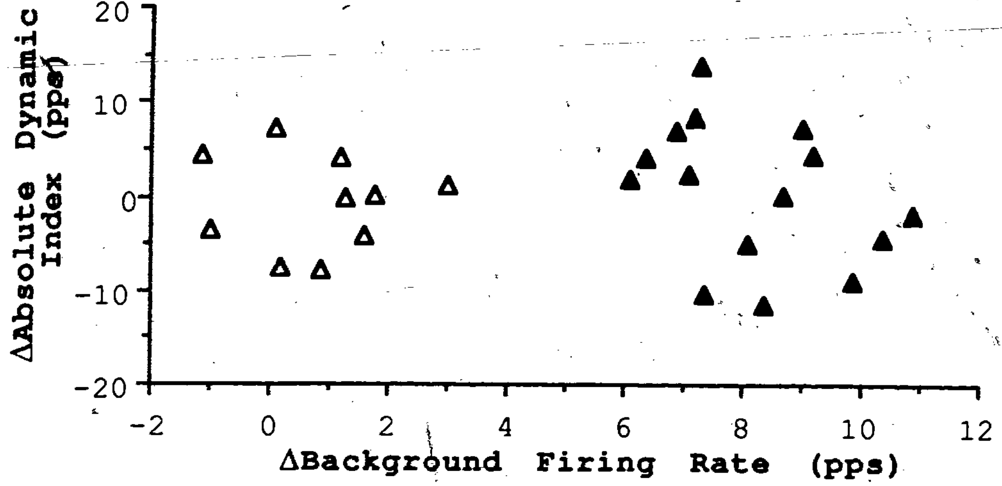


Figure 12 Each point is the difference between background firing rate and the absolute dynamic index of two simultaneously firing units. Either both units had fired in the background (unfilled triangles) or only the low threshold unit fired in the background and the high threshold unit was recruited during the ramp (filled triangles). High threshold motor unit values were subtracted from the low threshold motor unit values. Unfilled triangles, number of subjects, $n_s=6$, number of motor unit pairs, $n_u=10$. Filled triangles, number of subjects, $n_s=7$, number of motor unit pairs, $n_u=15$.

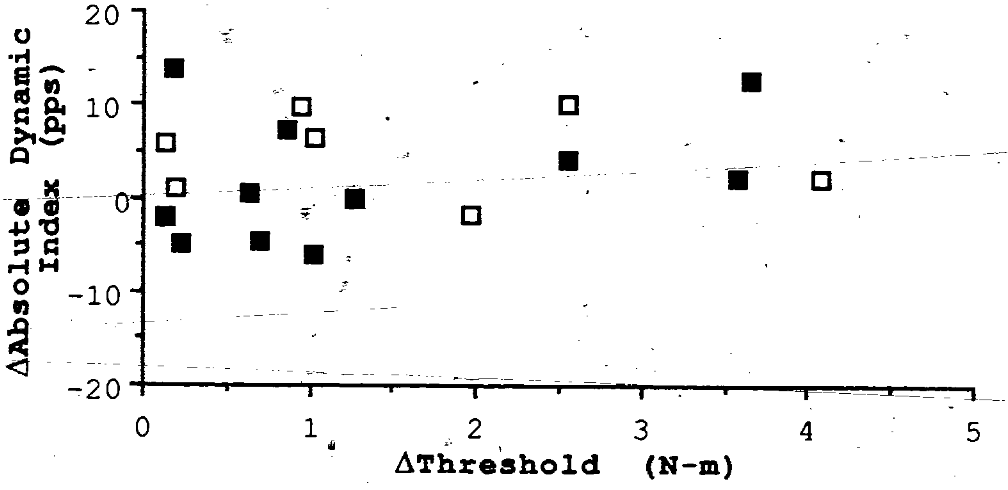


Figure 13 Each point is the difference between the absolute dynamic index and recruitment threshold of two simultaneously firing units for the same conditions as stated for figure 12. Low threshold values were subtracted from high threshold values. Unfilled squares, number of subjects, $n_s=5$, number of motor unit pairs, $n_u=8$. Filled triangles, number of subjects, $n_s=7$, number of motor unit pairs, $n_u=10$.

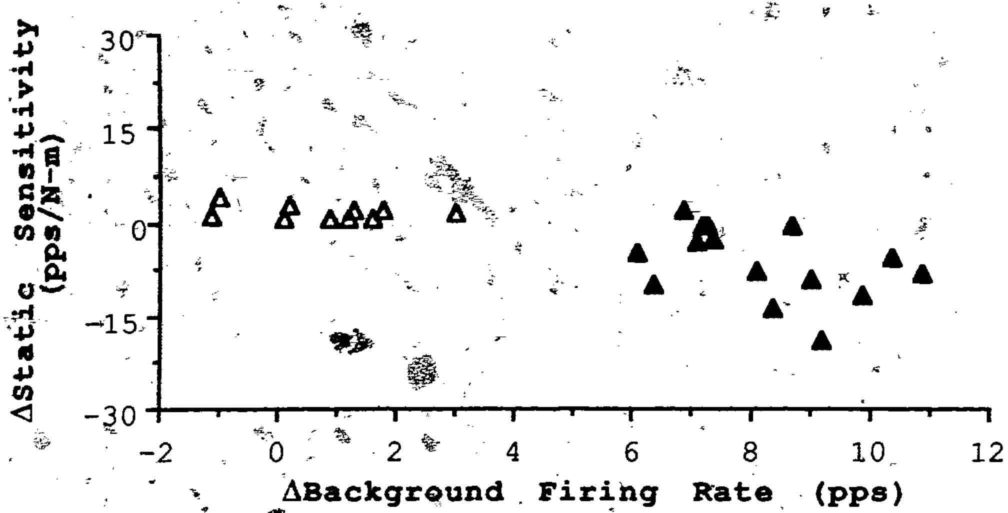


Figure 14 Each point is the difference between background firing rate and the static sensitivity index of two simultaneously firing units. Either both units fired in the background (open triangles) or only the low threshold unit fired in the background and the high threshold unit was recruited during the ramp (filled triangles). High threshold motor unit values were subtracted from the low threshold motor unit values. Unfilled triangles, number of subjects, $n_s=6$, number of motor unit pairs, $n_u=10$. Filled triangles, number of subjects, $n_s=7$, number of motor unit pairs, $n_u=15$.

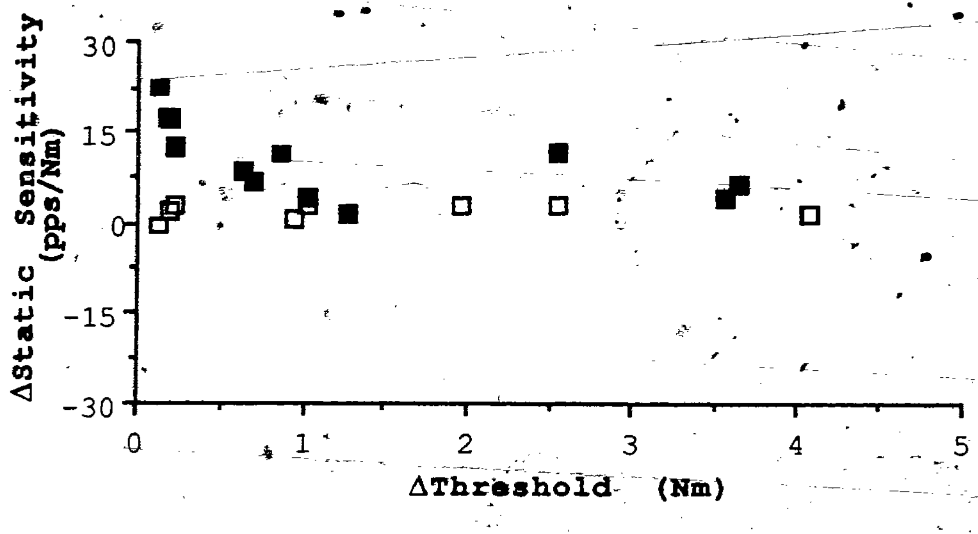


Figure 15 Each point is the difference between the static sensitivity index and recruitment threshold of two simultaneously firing units for the same conditions as stated for figure 14. Low threshold values were subtracted from high threshold values. Unfilled squares, number of subjects, $n_s=5$, number of motor unit pairs, $n_u=8$. Filled triangles, number of subjects, $n_s=7$, number of motor unit pairs, $n_u=10$.

Steady-state Phase: The steady-state phase of the firing pattern was also compared between two simultaneously firing units. The lower threshold unit generated significantly higher absolute static firing rates ($p \leq 0.02$) compared to the higher threshold unit when it was recruited during the trajectory; however, similar to the trend observed with single motor units at different excitation levels, the static sensitivity index was greater ($p \leq 0.0003$) for the higher threshold unit when it was recruited during the trajectory. The static sensitivity values, however, compared when both units began from very similar background firing rates, did not differ. The difference in background firing rate plotted against the difference in static sensitivity values between the unit pairs is shown in figure 14. This plot has a very similar trend to figure 10 (although with more scatter) suggesting that the steady-state behaviour of the unit was not related to its recruitment threshold, but rather to its background excitation level. This is supported by figure 15 which displays the very poor relationship between difference in recruitment threshold and difference in static sensitivity.

Surface Electromyogram Activity

The trajectories completed for the single motor unit experiments did not range widely enough in magnitude or rate of rise of force to provide sufficient information on surface EMG activity. Therefore, in order to investigate surface EMG activity during a number of different conditions, these experiments were completed separately in two different force ranges. Due to limitations of the experimental arrangement, maximum voluntary contractions could only be obtained from three subjects who generated relatively small maximum voluntary contractions. From their maximum voluntary contraction values, one force range was approximately 15% of MVC and the other force range was approximately 30% of MVC.

Dynamic Phase - Low Force Range: The first set of results were obtained when subjects produced force trajectories to approximately 15% of MVC. The relationship between the dynamic phase of the surface EMG activity and the rate of rise of isometric force was investigated by having subjects complete force trajectories at three different speeds of contraction. Typical average response histograms of rectified surface EMG and force for all four trajectories are shown in figure 16. It is evident from this figure that the dynamic phase of the EMG activity was greatest during the fastest rate of rise of force ($p \leq .05$) and was least at the slowest rate of rise of force. The absolute dynamic index used to quantify the average response histogram activity concurred with these qualitative observations (Fig. 17A).

The rates of rise of force generated during these trajectories were fastest for the F(0-2) condition ($p \leq .002$) and approximately seven times slower in the S(0-2) condition.

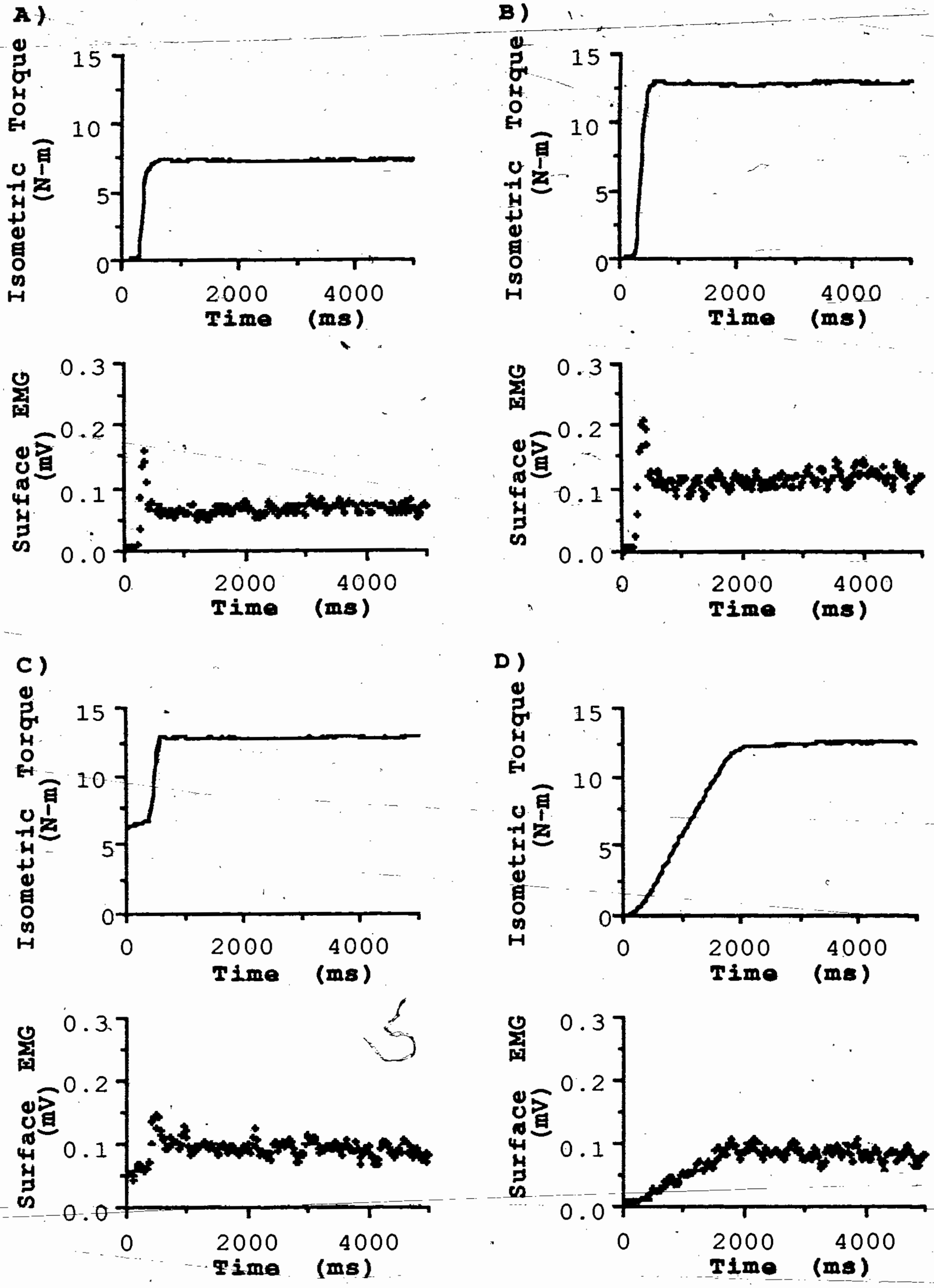


Figure 16 Typical average response histograms for **A)** F(0-1) **B)** F(0-2) **C)** F(1-2) **D)** S(0-2) trajectories. The force outputs were approximately 15% of MVC. Isometric torque is displayed on top and surface EMG on the bottom for each condition. Number of sweeps = 30.

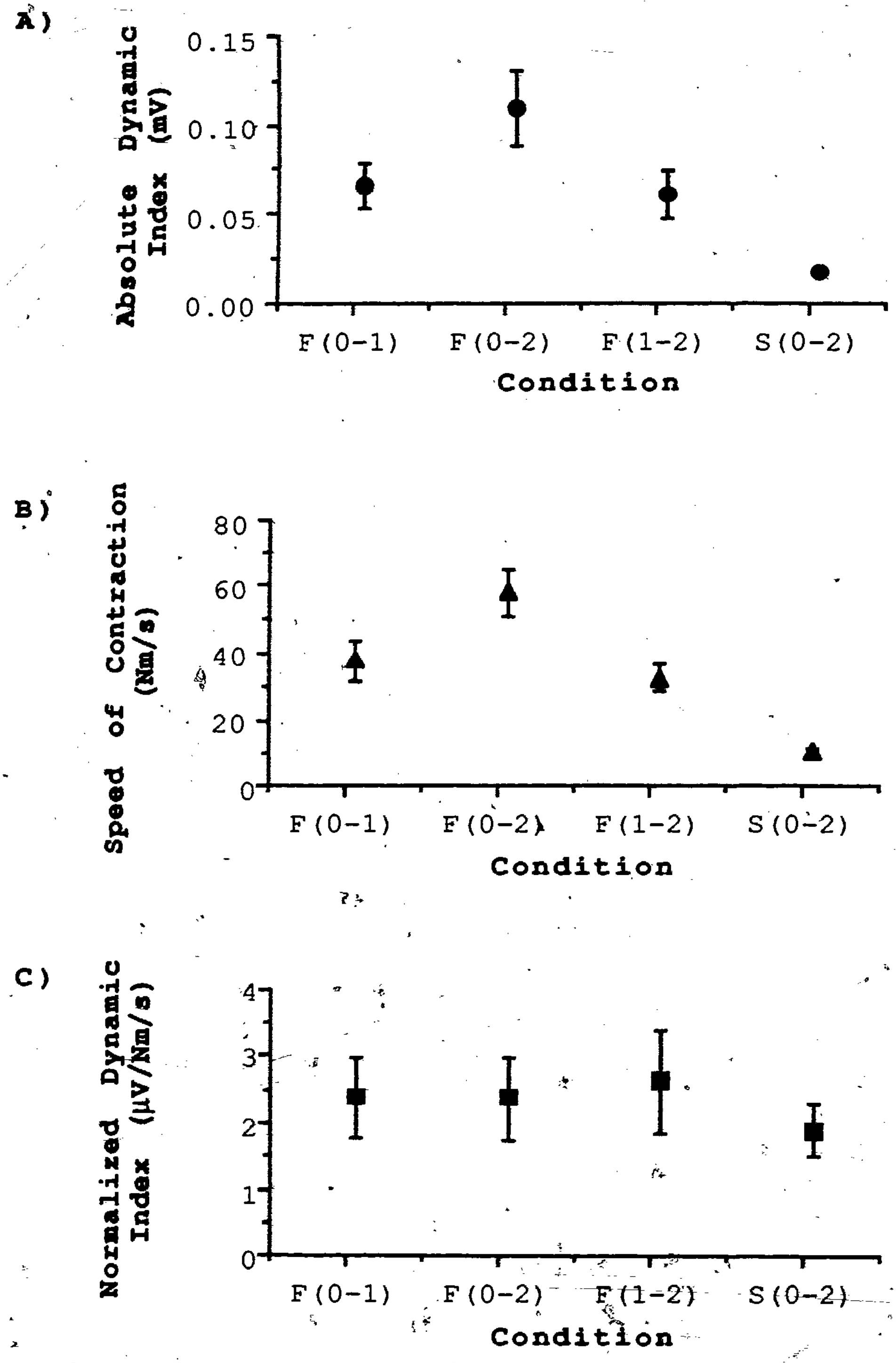


Figure 17 Mean and standard error of **A)** absolute dynamic index **B)** speed of contraction of trajectory and **C)** normalized dynamic index for four different isometric force trajectories completed to approximately 15% of MVC. Number of subjects, n_s=9, number of experiments, n_e = 11.

Consequently, when the absolute dynamic index was normalized to the speed of contraction (Fig. 17B) there was no significant difference between the normalized dynamic index values calculated for any of the conditions (figure 17C) ($p \leq .90$). This suggested that the dynamic phase of the EMG was linearly related to the speed of contraction at low force outputs.

Within this force range the influence of background motoneuronal activity on the dynamic phase of the EMG activity was investigated by controlling the background force level. The absolute dynamic index values between F(0-1) and F(1-2) ($p \leq .90$) did not differ significantly, nor did the normalized dynamic indices ($p \leq .90$) (figures 17A and 17C). These results would confirm that speed of contraction is the only parameter related to the dynamic phase of the surface EMG activity.

Higher Force Range - The relationship between speed of contraction and dynamic EMG activity was also investigated at larger force outputs. For these experiments it was assumed that the dynamic behaviour observed during the slow condition was not unique to small force outputs and, therefore, would also be observed at larger force outputs. Therefore, this condition was omitted.

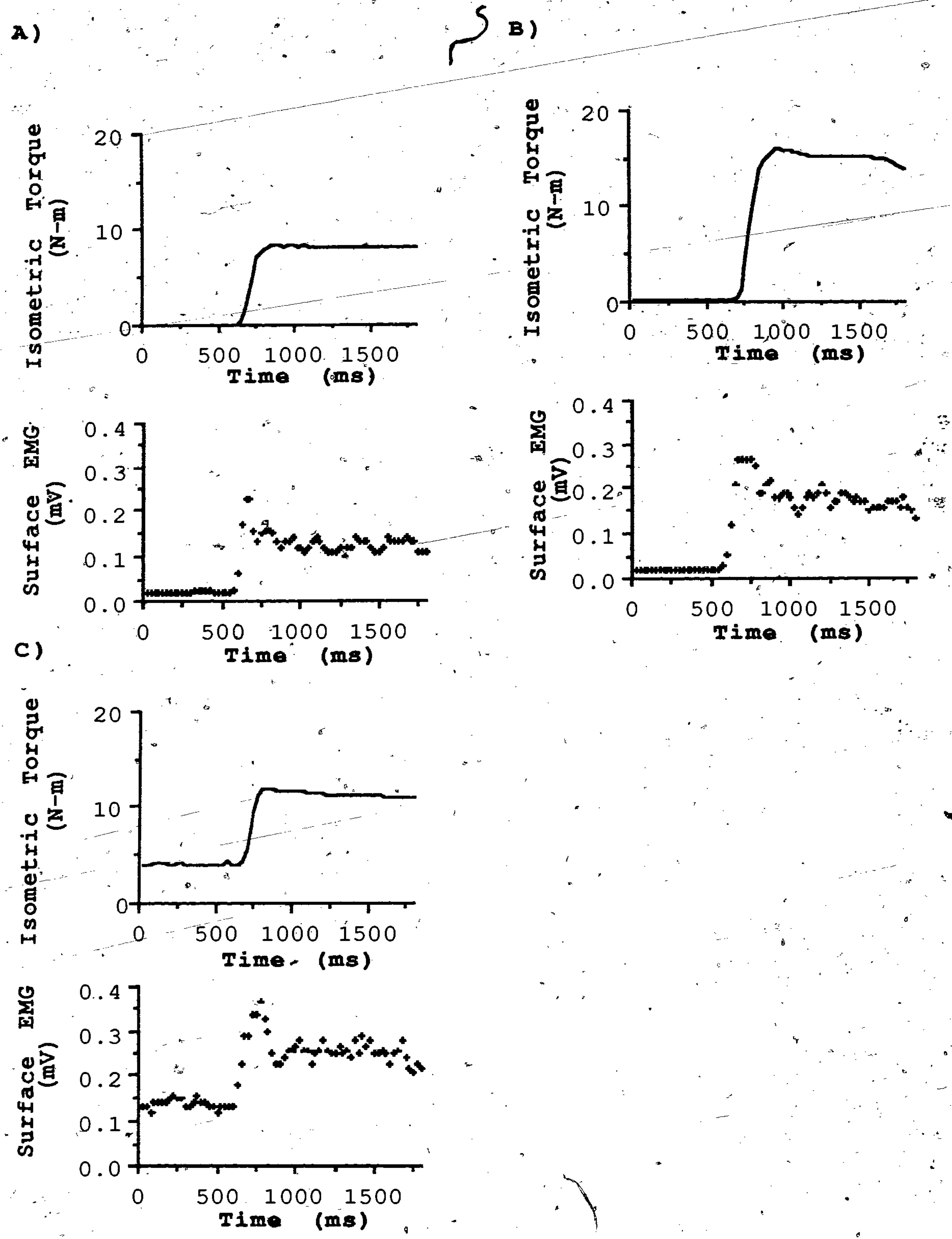


Figure 18 Typical average response histograms for **A)** F(0-1) **B)** F(0-2) **C)** F(1-2) trajectories. The force outputs were approximately 30% of MVC. Isometric torque is displayed on top and surface EMG on the bottom for each condition. Number of sweeps = 20.

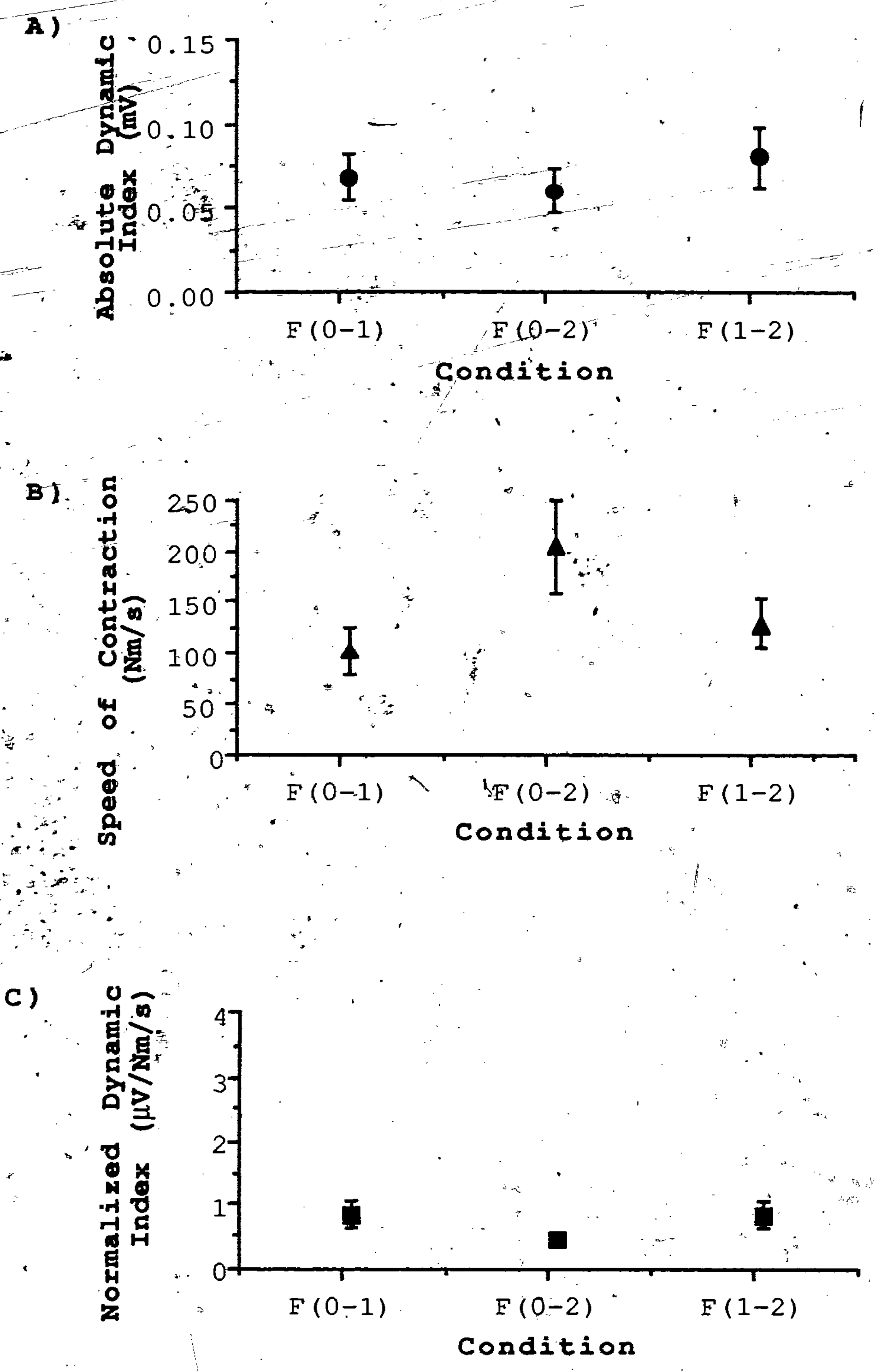


Figure 19 Mean and standard error of **A)** absolute dynamic index **B)** speed of contraction and **C)** normalized dynamic index for three different isometric force trajectories completed to approximately 30% of MVC. Number of subjects, n_s=10, number of experiments, n_e = 11.

Typical average response histograms constructed for the F(0-1), F(0-2) and F(1-2) conditions are shown in figure 18. As was confirmed by the absolute dynamic index values (figure 19A),this figure indicates that there was no marked difference in the dynamic EMG activity between the three conditions ($p \leq .90$); however, the speeds of contractions were nearly two times faster during the F(0-2) trajectory ($p \leq .01$) than either the F(0-1) or F(1-2) conditions (figure 19B). Therefore, when the absolute dynamic index was normalized to the speed of contraction, the relative increment in the dynamic index value was markedly less during the F(0-2) ($p \leq .04$) than during the other two conditions (Fig. 19C). The F(0-1) and F(1-2) conditions did not significantly differ from one another ($p \leq .90$). From these results there appears to be a non-linear relationship between the rate of rise of isometric force and the dynamic EMG activity during faster rates of rise of force generated in this force range. The non-significant difference between the dynamic index values of the F(0-1) and F(1-2) conditions would suggest, that within this force range, the background excitation level of the motor unit population did not influence the dynamic phase of the surface EMG activity when the same rate of rise and magnitude of force were completed. However, since these trajectories were not completed at the same time as those in the fifteen percent of MVC force range the two sets of results can not be compared.

Changes in the duration of the dynamic phase of the EMG activity between the F(0-2) and F(0-1) conditions completed to 30% of MVC, were also examined to determine if duration of the dynamic phase during the F(0-2) condition increased to compensate for the saturation observable in the amplitude of the dynamic phase. This was achieved by calculating the ratio of the absolute amplitude of the dynamic phase between the F(0-2) and the F(0-1) condition against the ratio of the area of the dynamic phase between the same two conditions. Since the absolute dynamic index did not significantly differ between the two trajectories completed in this force range, the ratio was approximately 1. Therefore, a ratio value greater than 1 between the values of the integrated dynamic phase would suggest that the area of the dynamic phase was larger during the F(0-2) trajectory, possibly due to its greater duration. Figure 20 does not demonstrate any clear relationship between the ratio of the EMG amplitudes and the ratio of the areas of the dynamic phase between the F(0-2) and F(0-1) trajectories. If duration of the dynamic phase was not greater during the F(0-2) than the F(0-1) condition, the relationship in figure 20 would yield a regression with a slope approaching 1. In comparing the absolute values between the two trajectories, however, it was observed that for five of nine subjects, the dynamic phase of the surface EMG activity was greater during the F(0-2) condition.

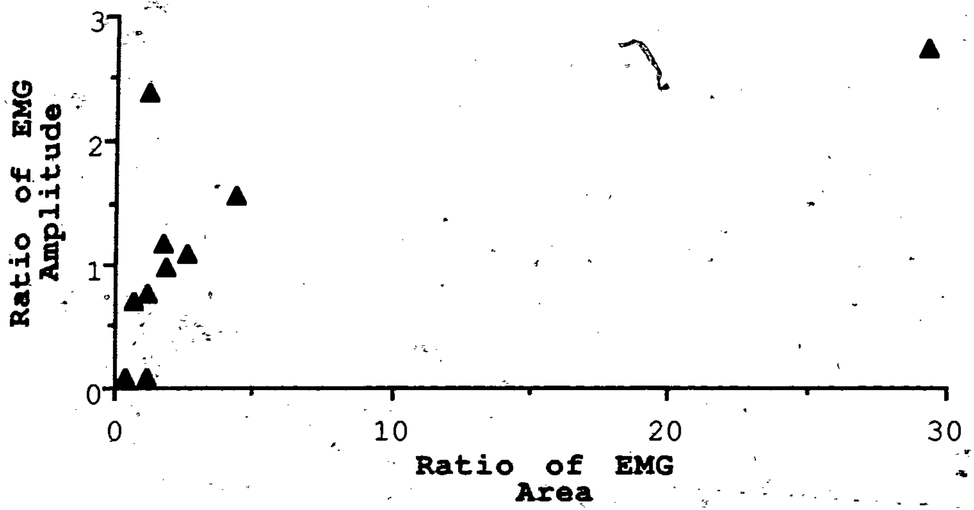


Figure 20 The ratio of the absolute dynamic index, representing the amplitude of the EMG dynamic phase, of the F(0-2) to F(0-1) conditions plotted against the ratio of the area of the EMG dynamic phase of the F(0-2) to F(0-1) conditions. This was done for the force trajectories taken to 30% of MVC. Number of experiments, n_e=10.

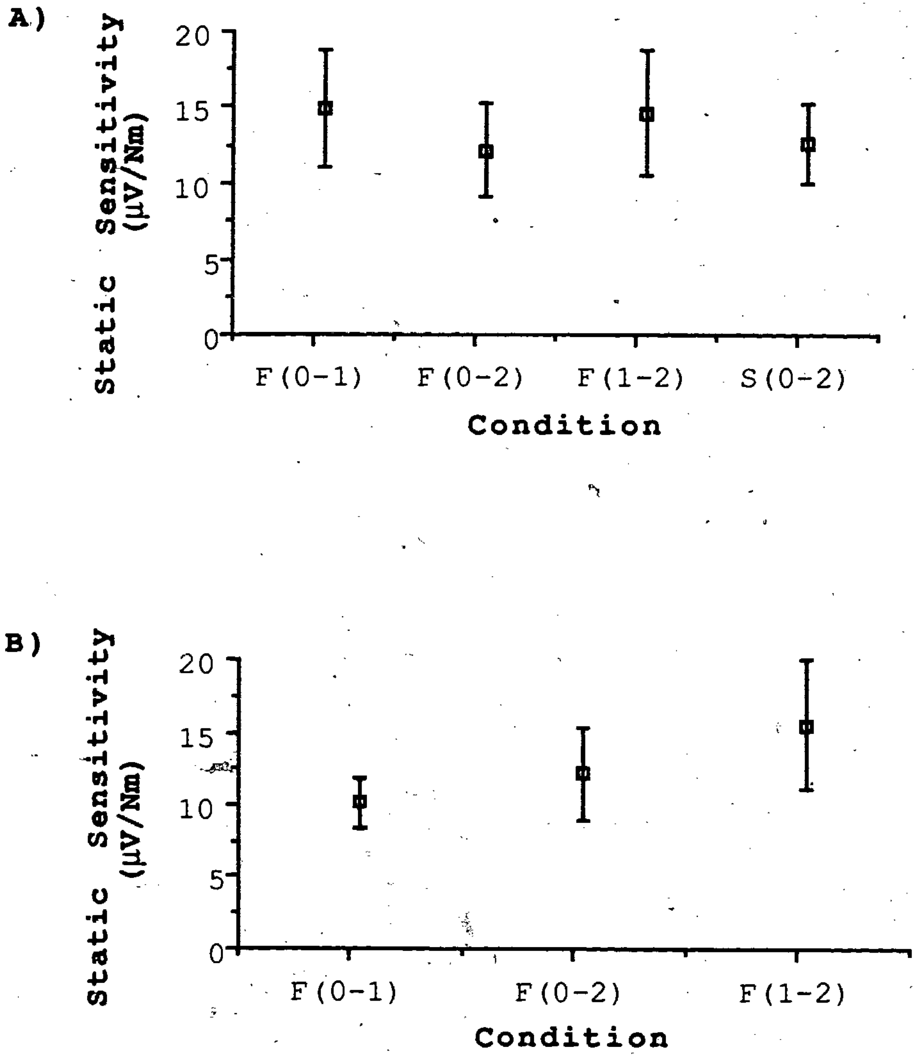


Figure 21 Mean and standard error for **A)** static sensitivity index from surface EMG activity recorded during four different isometric force trajectories completed to 15% of MVC. Number of subjects, $n_s=9$, number of experiments, $n_e=11$. **B)** static sensitivity index from surface EMG activity recorded during three different isometric force trajectories completed to 30% of MVC. Number of subjects, $n_s=10$, number of experiments, $n_e=11$.

Steady-state Phase: The steady-state phase of the surface EMG activity was also investigated for trajectories completed to small and large force magnitudes and was quantified with the static sensitivity index.

The static sensitivity index indicates the increment in static EMG per desired increment in force. No significant difference in the static sensitivity index was observed between any of the trajectory conditions at either low ($p \leq .90$) or high force outputs ($p \leq .06$) (figures 21A and 21B). This strongly suggests that static EMG activity is related only to the magnitude of the force output and is not influenced by the rate of rise of force which precedes the attained force level, nor is it influenced by the background activity level.

Constraints on Maximum Rate of Rise of Force

Freund and Budigen (1979) showed that when a subject was instructed to contract "as fast as possible", maximum speed of contraction was constrained by the magnitude of the isometric force trajectory. This was confirmed in this study; however, visual cues can also constrain the maximum speed of contraction (Fitts, 1954). Therefore, nine subjects were instructed to produce the same force trajectory "as fast as possible" during three conditions in which the time scale on the oscilloscope was used to alter the visual feedback. The results showed that when the timebase was very fast (0.1 sec/div) the subject was able to produce significantly faster

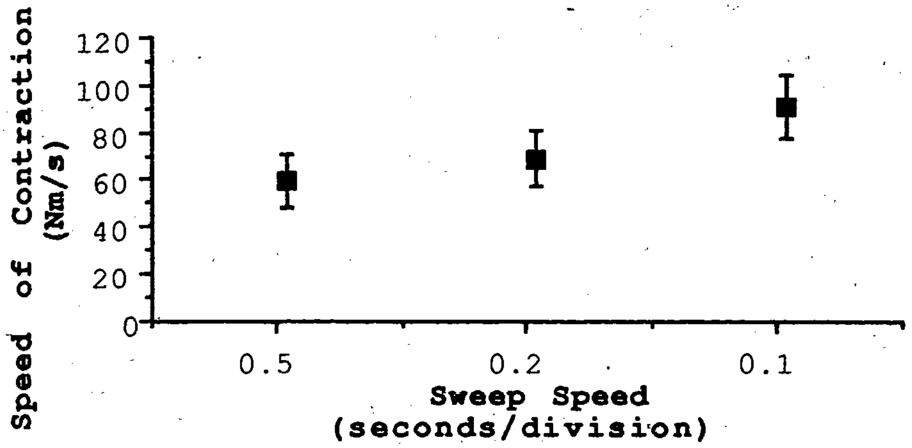


Figure 22 Mean and standard error of maximum speed of contraction for the F(0-2) trajectory traced "as fast as possible" during three different settings of the oscilloscope timebase: 0.5 sec/div, 0.2 sec/div and 0.1 sec/div. Number of subjects, n_s=5, number of experiments, n_e=7.

maximum speeds of contraction ($p \leq .002$) than when he completed the exact same trajectory with the timebase set at 0.5 sec/div (figure 22).

DISCUSSION

The results of this study indicated that the dynamics of low threshold motoneuron firing patterns were not only sensitive to changes in trajectory parameters, but were also influenced by changes in the motoneuron's background excitation level. Surface EMG activity was also related to trajectory parameters although different levels of background excitation level of the motor unit population did not affect the relative dynamic or static EMG behaviour. Furthermore, unlike single motor unit activity, at low force outputs, EMG activity was linearly related to components of the force output, although saturation non-linearity was observable during the dynamic phase at faster rates of rise of force within the thirty percent of MVC force range. The following discussion will concern the possible mechanisms contributing to, and the functional implications of, the observed dynamic and steady-state phases of the single motor unit and surface EMG activities. The results will then be addressed in terms of speculated central input patterns to the motoneuron pool or the synergistic motoneuron pools.

Single Motor Unit Discharge Behaviour

This work has shown that low threshold single motor units are capable of a range of firing pattern during controlled ramp- and-hold force trajectories. The motoneuron firing patterns observed during these trajectories included a dynamic and steady-state phase, each of which was influenced by different factors in a non-linear manner.

Dynamic Phase: The absolute dynamic phase of the single motor unit pattern was shown to increase during faster rates of rise of isometric force. This activity was quantified by the difference between the maximal instantaneous firing rate and the mean static firing rate. Therefore, changes in the absolute dynamic index would reflect changes in either one or both of these values. Mean static firing rate was shown to be unaffected by speed of contraction (figure 8); therefore, an increase in the absolute dynamic index value would indicate an increase in maximum instantaneous firing rate. Motor units were recorded over three different speeds of contraction: two fast conditions , one of which was twice as fast as the other and a slow condition. The difference in absolute dynamic index values between the F(0-2) and the F(0-1) trajectories, was not as marked as the difference in this index between the F(0-1) and the S(0-1) conditions. The trends of these results may suggest that only relatively small increases in the maximum instantaneous firing rate are necessary to produce large changes in the rate of rise of the force output. If this was the case, it could explain why only clear differences in the absolute dynamic index were seen when there was a six-fold difference in speed of contraction such as between F(0-1) and S(0-1). A two-fold difference in the speed of contraction between the F(0-1) and

F(0-2) trajectories may not have been large enough to detect significant differences. Desmedt and Godaux (1977) and Oishi et al. (1988) showed a large increase in tibialis anterior and adductor pollicus motor unit initial instantaneous firing rates, respectively, over a range of slow to very fast rates of rise of force such that between any two successive force trajectories an increment in firing rate between approximately 5 to 15 pps was observed. These larger increments in instantaneous firing rate as compared to those seen in this study maybe attributable to the faster rates of rise of force completed by their subjects and/or the motor unit population studied.

Possible Controls over Dynamic Phase: The changes in instantaneous firing rates can be affected by rate of synaptic input, accommodation, after-hyperpolarization, Renshaw cell inhibition as well as other factors. In human work the contribution of these various factors can only be speculated.

Accommodation (Bradley and Somjen, 1961; Burke and Nelson, 1969) may have influenced the dynamic phase of the firing pattern during the slow force trajectory. In cat, accommodation has been shown to have the greatest influence on F type motor units (Burke and Nelson, 1971). The population investigated in this study were low threshold units presumably innervated by small motoneurons; therefore, it is possible that accommodation may not have had a profound effect on the dynamics of the motoneuron firing pattern. It is also possible that accommodation may have a greater effect during ramp phases much slower than those investigated in this study and therefore, its influence on these motor units was not particularly evident.

After-hyperpolarization (AHP) conductance was proposed by Kernell (1969) and Baldissera and Gustafsson (1974a;b) to regulate repetitive firing behaviour. For instance, the minimal rhythmic firing rate of a motoneuron was suggested to be the inverse of the time course of afterhyperpolarization (Kernell, 1965c). Further, adaptation in firing rate was attributed to the summation of after-hyperpolarization conductance when successive spikes impinged on the after-hyperpolarization time course of the preceding spike (Baldissera and Gustafsson, 1971;1974). These proposals, however, came from results obtained with current injections into the motoneurons of anesthetized or decerebrated cats: not particularly ideal physiological models. More recently, cat and human investigators (Bussel and Pierrot-Deseilligny, 1977; Hultborn et al., 1979) have relegated the after-hyperpolarization conductance changes to a more minor role in the control of motoneuronal firing and shifted the emphasis to synaptic controls.

Impinging on the motoneuron are many different sources of excitatory and inhibitory synaptic input. Renshaw cells are inhibitory interneurons which are excited by motoneuron collaterals and feedback onto motoneurons. The close proximity of the these interneurons and their monosynaptic recurrent inhibition onto the motoneuron soma (Baldissera et al., 1981) would suggest that their response could be fast enough to control all phases of the motoneuronal firing pattern (Eccles et al., 1961). Furthermore, work with human subjects has delineated a difference in the potency of Renshaw cell inhibition during weak and stronger force outputs. Hultborn and Pierrot-Deseilligny (1979) observed that recurrent inhibition was greatest during weak contractions of the soleus muscle. Therefore, since the majority of the force trajectories completed during the single motor unit recordings for this thesis were approximately 5 to 10% of MVC, it is possible that Renshaw cell activity could have been a factor in controlling firing rate. In addition to Renshaw cell inhibition, Ib afferents are also inhibitory to human motoneurons (Pierrot-Deseilligny et al., 1979); however, the latency time for this feedback on changes in force is estimated at 17 msecs (Pierrot-Deseilligny et al., 1979). This time course may be too long to effect the interspike intervals between, perhaps, the first 3 or 4 spikes. The potential influence of Ib afferents will be discussed in the next section.

The initial excitation level of the motoneuron was also shown to influence the dynamic phase of the firing pattern in a non-linear manner. Dynamic firing rate behaviour was not significantly different regardless of whether the unit was recruited during the force trajectory or fired at a minimal rhythmic firing rate preceding the contraction. However, at background firing rates greater than the unit's minimal discharge rate dynamic index values were much less. These results may suggest that the factors influencing the dynamic firing pattern generated from a minimal background firing rate versus from a "zero" background activity were similar. Possibly, the influence of AHP summation (Baldissera and Gustaffson, 1974a) and Ib muscle afferent inhibition (Grimby and Hannerz, 1979), generated during the period of low tonic background firing rate, does not have a particularly significant effect on the dynamic firing pattern as compared to when the unit begins from rest. This could suggest that recurrent inhibition may have the predominant effect when background excitation level is low. However, the filled circles in figure 7 indicate that at higher, tonic background firing rates, compared to "zero" background activity, the dynamic firing behaviour decreased, possibly suggesting a greater influence of AHP accumulation and Ib muscle afferent inhibition. This is supported by the consistently lower dynamic firing behaviour observed after the unit began from a much higher background firing rate. Therefore, the factors already considered may have an even greater hyperpolarizing effect on the motoneuron resulting in lower maximum firing rates. For instance, during the high background firing rates, AHP conductances may sum to hyperpolarize the cell before the superimposed contraction. In addition, during the increased force generated during the higher background firing rates, Ib inhibitory feedback from the homonymous and synergistic muscle(s) may also be greater (Pierrot-Deseilligny et al., 1979; Grimby and Hannerz, 1979). The inhibitory effect of these inputs, as already alluded to, could result in longer interspike intervals. Further, cat experiments (Hultborn and Pierrot-Deseilligny, 1979) demonstrated that tonic discharges from the motoneuron can facilitate Renshaw cells such that the gain of the recurrent inhibition pathway is increased. Therefore, it is possible that when the trajectory was preceded by high background firing rates, Renshaw cell inhibition was greater than when the unit began from low firing rates or "zero".

Functional Implications of Dynamic Phase: The functional implications of the motoneuron's adapting firing behaviour was addressed by normalizing the absolute dynamic index value to the rate of rise of isometric force. The normalized dynamic index indicated that although the absolute instantaneous firing rate increased during faster speeds of contraction the actual firing rate increments were less. This same saturation non-linearity could also be seen when the instantaneous firing rates of human tibialis anterior and adductor pollicus motor units were normalized to speed of contraction (Desmedt and Godaux, 1977; Oishi et al., 1988). The insertion of a short-interspike interval into an experimentally generated stimulation train has been shown in cats (Burke et al., 1976; Stein and Parmiaggini, 1979; Zajac and Young, 1980) and humans (Gurfinkel and Levik, 1972) to produce a fast, non-linear increase in force output. This effect is optimal in cat motor units if the interspike interval is around 10 milliseconds (Burke et al., 1976; Zajac and Young, 1980) and approximately 20 milliseconds for human muscle (Gurfinkel and Levik, 1972). Zajac and Young (1980) demonstrated that modulation of only the first interspike interval was necessary to produce maximal rate of rise of force from S type cat gastrocnemius motor units. This was unlike the F type motor units which required at least the initial two intervals to be of particular lengths for fast, rates of rise of force. Therefore, if the same behaviour was also true for human low threshold motor units, small changes in the dynamic phase of the motoneuron firing pattern may be sufficient to produce non-linear increases in the speed of contraction.

Steady-state Phase: The steady-state firing behaviour of low threshold single motor units showed saturation non-linearity during larger force outputs or when the unit began from high background excitation levels. The relatively lower increment in static firing rate during the F(0-2) condition versus the F(0-1) condition was not due to the faster speed of contraction during the F(0-2) trajectory. This was confirmed when static sensitivity values were less during a S(0-2) versus a S(0-1) condition. Bigland and Lippold (1954b) observed a similar trend, but over a larger range of force outputs. They recorded a very small total increase (approximately 10 pps) in the abductor digiti minimi motor unit firing rate across steady-state isometric force outputs ranging between 15 and 75% of MVC. Therefore, if they had normalized mean firing rate to the corresponding static force output they would have observed a non-linearity in the relative static firing behaviour.

Minimum and maximum firing rates were not determined during any of the thirty-seven single motor unit experiments; however, two additional experiments were conducted on two subjects to obtain a rough gauge of the firing rate range of low threshold FCR motor units. Five motor units recorded during slow increases in force consistently fired from a minimum firing rate of 8 pps to a maximum of 20 pps. This firing rate range during slow increases in force is comparable to that seen by Milner-Brown et al. (1973) from first dorsal interosseus low threshold units. These results may suggest that static firing rates approaching near maximum would have been seen if subjects had produced greater torque outputs.

Possible Controls over Steady-state Phase: The time between the initiation of the contraction and the steady-state phase of the trajectory was approximately 300 milliseconds during the fastest speeds of contraction. Therefore, peripheral feedback, perhaps conveyed by Ib muscle afferents (Pierrot-Deseilligny et al., 1979), could contribute in the control of the static firing rate of the unit (Grimby and Hannerz, 1979). The inhibitory influence of the Ib muscle afferents could begin at the onset of contraction such that it could have an even greater effect when the unit fired tonically before the superimposed ramp-and-hold trajectory, possibly resulting in the small increment in static firing rate.

Functional Implications of Steady-state Phase: The functional significance of the steady-state firing behaviour observed between the F(0-1) and F(0-2) conditions maybe alluded to in rate - tension curves constructed for animal (Rack and Westbury, 1969; Botterman et al,1988) and human muscles (Bigland and Lippold, 1954b; Bellemare et al., 1983). Botterman et al. (1988) stimulated ventral roots at different rates and plotted them against percentage of maximum integrated tension for type F and type S cat flexor carpi radialis muscle units. Although the curves for the type S muscle units were shifted to the left compared to the F type muscle units, the relationship was sigmoid for all muscle unit types. Rack and Westbury (1969) observed a similar shape in the rate - tension curve obtained from cat soleus muscle. In human abductor digiti minimi muscle Bigland and Lippold (1954b) demonstrated a linear increase in force output at stimulation rates between 8 and 30 pps with a plateau at stimulation rates greater than 45 pps. A similar rate-tension plot has also been constructed for adductor pollicus (Bellemare et al., 1983). Both animal and human rate-tension curves displayed a steep, linear portion indicating that small increments in stimulation rate generate large increases in force output. Furthermore, the FCR type S cat motor units appeared to generate even greater increments in force per increase in firing rate than type F motor units (Botterman et al., 1988). Bellemare et al. (1983) speculated from the rate - tension curve of the adductor pollicus and its much higher mean firing rates as compared to the soleus, that the rate - tension curve of the soleus, which is composed of type S motor units, would be shifted towards lower stimulation rates and would display a much steeper slope. Therefore, our results, obtained from low threshold human FCR motor units during the F(0-1) and F(0-2) conditions, may suggest that during the force increments generated by our subjects, only small increments in steady-state firing rate were required to achieve large increases in force output.

The same increment in force required smaller relative increments in firing rate when the unit began from a tonic firing rate particularly a high background firing rate. Burke et al. (1976) demonstrated that the same pattern of experimentally generated depolarizing pulses injected into cat gastrocnemius motoneurons, yielded greater force outputs when applied after a series of depolarizing stimuli than when applied to a motoneuron which had been quiescent. When a motoneuron fires before a superimposed contraction its muscle unit contracts such that the inertial effects of activating muscle fibers are overcome before greater force outputs are required. In addition, calcium release will have already been initiated (Burke et al., 1976; Zajac and Young, 1980). Therefore, small increases in firing rate from an already active state may be sufficient to produce desired increases in force output from the muscle unit, versus when the unit must begin from rest.

Human Versus Cat Studies: Baldissera et al. (1987) injected ramp-and-hold patterns of current input into anesthetized cat gastrocnemius motoneurons and intracellularly recorded the resulting discharge patterns. Currents were applied to quiescent neurons and the outputs were quantified in terms of the input. This group found, that under these conditions, each of the dynamic and static phases could be described by a single value taken as the slope of the linear relationship between current input and motoneuron output.

In this human study with flexor carpi radialis motor units, ramp-and-hold patterns of isometric contraction were controlled and the motoneuron firing patterns were recorded. Therefore, unlike the Baldissera et al. (1987) experiments, the input, i.e. the motoneuron firing patterns, were quantified in terms of the torque outputs. Our results indicate that motoneuron firing patterns change in a non-linear manner with respect to both the output parameters and the unit's excitatory level before the superimposed contraction.

The linearity seen in the dynamic and steady-state components of the cat motoneuron firing pattern in relation to current input parameters may reflect the predominate influence of afterhyperpolarization on the motoneuron's repetitive firing properties. In their experiments afterhyperpolarization would probably be the primary controlling factor as compared to Ib muscle afferent or Renshaw cell inhibition because these two inputs are known to be compromised during anaesthesized preparations. In addition, only the activity of a single, functionally isolated, motor unit was investigated which would limit the intensity of Ib muscle afferent input. This is unlike the human model where the motor unit activity was investigated with the controlled output of not only the flexor carpi radialis, but also its synergists during wrist flexion. Therefore, in these studies, Ib muscle afferent and Renshaw cell inhibition may have had a large role in controlling the motoneuron firing pattern because Ib muscle afferents from throughout the muscle, as well as from synergists, have wide synaptic connection within a motoneuron pool (Baldissera et al., 1981). In addition, Renshaw cells are facilitated by collaterals of other motoneurons within a motoneuron pool as well as by the collaterals of the motoneuron it feedbacks onto (Baldissera et al., 1981). The saturation observed in the dynamic and steady-state firing pattern of the single motor unit studied in these experiments may, therefore, be due to inhibition from Ib muscle afferents and Renshaw cells as well as afterhyperpolarization.

Simultaneously Firing Motor Units

Dynamic and steady-state phases of the firing patterns of simultaneously recorded motor unit pairs were compared in terms of their background excitation levels and their recruitment thresholds.

Dynamic Phase: Within the low threshold population investigated no significant differences were observed in the dynamic phase of motor unit firing patterns regardless of whether both units or only the low threshold unit fired tonically in the background. Differences between recruitment threshold was also unable to explain the scatter observable in the data. Within the population of cat gastrocnemius motoneurons investigated by Baldissera et al. (1987), smaller motoneurons had greater dynamic sensitivity values than larger motoneurons: however, Palmer and Fetz (1985) indicated that low threshold rhesus macaque motor units displayed less dynamic firing rate behaviour than higher threshold motor units. Observed distributions of dynamic firing rate behaviours across a motoneuron pool may, however, be an artefact because motoneuronal background excitation level was not controlled in either study. Two examples will be presented to emphasize the importance of background excitation level on motoneuron firing rate behaviour. These examples may also explain the discrepancy between the Baldissera et al. and the Palmer and Fetz studies. Large motoneurons have small input resistances (Kernell, 1966) and, therefore, require greater current inputs to reach their rhythmic threshold than small motoneurons. If the dynamic firing rate behaviour of a large and small motoneuron are investigated with identical current inputs, of a moderate rate of rise and intensity, the smaller motoneuron would reach rhythmic threshold quicker and display much shorter interspike intervals than the larger motoneuron. This may explain the observations of Baldissera et al.(1987) better than their suggestion of "neuronal intrinsic properties" graded across the motoneuron pool. On the other hand, if the input had a very fast rate of rise to a large intensity the firing properties of the smaller motoneuron may saturate and not display any dynamic phase in its firing pattern. This could have been the type of behaviour observed from low threshold units by Palmer and Fetz (1985). Therefore, unless excitation level of the motoneuron is controlled preceding the application of a current or a synaptic input it may not be valid or physiologically accurate to suggest that dynamic firing rate behaviour can be predicted from just recruitment threshold.

Steady-state Phase: Steady-state firing properties compared between concurrently active motor units were also not found to be correlated with motor unit recruitment threshold. Instead, these experiments supported the observations made when the single motor unit behaviour was recorded from different levels of background firing rate (figure 10). The higher threshold unit, if recruited during the trajectory, displayed a greater static sensitivity value than the lower threshold unit; however, there was no difference in the static sensitivity values of the units if they both preceded the superimposed contraction with tonic background firing rates. This would suggest that each motoneuron recorded in this investigation was capable of a similar range of static sensitivity behaviours and have had similar rate-tension curves.

The functional implications of concurrently active motor units will be discussed with the surface EMG data.

Surface Electromyogram Activity

Activity of a motor unit population can be measured via surface EMGs (Milner-Brown and Stein, 1975). Although surface EMGs were recorded from over the belly of the flexor carpi radialis, it was recognized that other wrist flexor muscles particularly palmaris longus, flexor digitorum superficialis and flexor carpi ulnaris may also have contributed to the surface EMG activity. If this did occur, the surface EMG activity observed would not have necessarily reflected the behaviour of flexor carpi radialis; however, a study by Gielen et al. (1985), recorded simultaneously from brachialis, biceps brachaii and brachioradialis during isotonic movements about the elbow. They found that the integrated EMG activity from each muscle was linearly related to velocity of movement. Therefore, any contamination of the surface EMG record due to contributions by other wrist flexors may not have obscured the true behaviour of the flexor carpi radialis muscle.

As with the single motor unit data, the surface EMG activity was investigated in terms of a dynamic and steady-state phase of activity. Each component was related to a different force parameter which suggested functional differences between the dynamic and steady-state phases.

Dynamic Phase: Surface EMG activity recorded during force outputs to approximately 15% of maximum voluntary contraction (MVC) was linearly related to only the rate of rise of isometric force. This relationship did not change when background surface EMG activity was altered. This was unlike the single motor unit dynamic firing behaviour which changed in a non-linear manner in relation to both speed of contraction and background excitation level. The dynamic phase of the surface EMG activity, however, did reflect the single motor unit behaviour during the fastest rates of rise of force completed to approximately thirty percent of MVC by displaying saturation non-linearity. The dynamic index values were not different when the subject completed the same force trajectory from two different levels of background EMG activity. Therefore, unlike the single motor unit the dynamic phase of the total motor unit population activity appeared to be related only to the speed of contraction and not to the population's activity level preceding the superimposed contraction.

Linearity in the dynamic surface EMG activity is most likely maintained at moderately fast speeds of contraction by the wide range of firing patterns displayed by motor units. Motor unit firing behaviour in this study was quantified only for those units which displayed steady-state firing behaviour; however, during the rate of rise of the force trajectory motor units were consistently observed to be recruited, fire a short series of spikes at relatively fast instantaneous firing rates and then drop out when the ramp portion of the trajectory was completed. Similar behaviour has been observed from adductor pollicus (Gillies, 1972), first dorsal interosseus (Freund et al., 1975; Deluca et al.,

1982) and rectus femoris (Person and Kudina, 1973) motor units. Therefore, assuming each motoneuron is capable of a range of dynamic firing patterns, (where one end of the range includes the very phasic activity just described and the other end approaches saturation), the surface EMG recorded during moderately fast speeds of contraction will not display saturation as long as higher threshold motor units can be recruited to contribute very phasic firing patterns.

It has been suggested that the linearity between dynamic surface EMG activity and speed of contraction maybe dependent on the underlying recruitment and discharge properties of the motor unit population. During the dynamic phase of the trajectory to even very small increments in force, it was observed that several motor units were recruited and active even though the subject was well practised in isolating a single unit at a particular background firing rate. Therefore, if the majority of FCR motoneurons are recruited during low force outputs then it would be expected that the primary contribution to the dynamic phase of EMG would shift from the recruitment of additional motoneurons to firing rate modulation during greater force outputs. The result would be that the dynamic phase of EMG would not continue to increase proportionally during faster speeds of contraction because the majority of the recruited units could achieve large increments in rate of rise of force with small increases in instantaneous firing rate. That is, it is possible that although the maximum instantaneous firing rates increases relatively little during faster rates of rise of force, the muscle unit has not achieved fused tetanus and is sensitive to small changes in input.

Steady-state Phase: The increment in steady-state surface EMG activity was proportional to the magnitude of the force trajectory, whereas the relative increment in single motor unit static firing rate per N-m of torque was extremely non-linear. The maintained linearity between static EMG activity and torque magnitudes of upto 30% of MVC can be best explained by the recruitment of additional motor units. Motor units recruited during the rate of rise of force will continue to fire if the magnitude of the trajectory's static component is equal to or greater than the unit's recruitment threshold (Gillies, 1972; Freund and Budigen, 1975). In this study, units recruited during the trajectory displayed the greatest static sensitivity values. Therefore, even though motor units already active before the contraction would have contributed relatively little to the static EMG activity, motor units recruited during the trajectory which continued to fire during the static phase, would have provided an increase in the static EMG activity. Presumably non-linearities in the static phase of EMG activity may occur during force outputs to large percentages of MVC: however, Bigland and Lippold (1954b) demonstrated that during force outputs of 80 to 100% of MVC, abductor digiti minimi motor units produced larger increments in firing rate than when force outputs ranged from 15 to 75% of MVC. This type of behaviour may also be possible from human FCR motoneurons, although the low threshold motor units investigated did not display a large range of steady-state firing rates.

The suggestion that significant increments in steady-state surface EMG activity may result from the recruitment of additional motor units is supported by the comparative behaviour of simultaneously recorded units. The static sensitivity index between two motor units of different recruitment threshold did not differ when both these units began from a tonic background firing rate; however, the static sensitivity index was significantly greater when the higher threshold unit was recruited during the contraction. Bigland and Lippold (1954b) further support this postulation by suggesting that the recruitment of additional motoneurons is more metabolically efficient for abductor digiti minimi motor units than rate-coding for grading muscle force outputs. This may, however, only be valid during low force outputs.

Central Inputs to Motoneurons

Freund and Budigen (1979) demonstrated that for the fastest force impulses or movements the maximum speed of contraction was constrained in a linear manner, to the magnitude or the distance of the contraction. This was also supported by Milner (1986) for isotonic movements. Small motor units, which have slower contraction times and smaller twitch tensions, are recruited before larger motor units. Therefore, the maximum speed of contraction attainable for a small force output will be lower than for larger force outputs because the lower threshold motor units, contributing to the small force output, generate lower maximum rates of rise of force. This relationship established by Freund and Budigen, however, describes a constraint between two output parameters. Movement time was shown by Fitts (1954) to be constrained by target width. This thesis has demonstrated that maximum speed of contraction was limited by the speed of the visual cue. Both pieces of evidence suggest that central inputs to the motoneuron pool can be influenced by perceptual constraints (Warren, 1988); however, the form of those central inputs has yet to be determined. The following discussion will speculate on the pattern of central inputs to the motoneuron pool based on the results of this study.

The distinction of two phases in the surface EMG activity recorded during ramp and hold force trajectories [also observed during isotonic movements by Lesteinne et al.

(1981)] suggests that the underlying single motor unit activity is also constrained to two distinct phases. Therefore, it is suggested that the pattern of central inputs applied to the motoneuron pool occur in two components: a pulse and a step. It should be emphasized that it is uncertain what parameters (such as length, velocity, stiffness (Stein, 1982)) are contained in the central inputs. Therefore, the following discussion will be based solely on the assumption that central inputs to the motoneuron pool influence motor unit recruitment and rate-coding to produce force outputs of particular rates of rise and magnitudes.

The majority of the literature present central input models for very fast (ballistic) contractions. The following are several examples of these types of models. A pulse-step model was proposed by Ghez and Vicario (1978) from EMG recordings obtained when cats completed ramp and hold isometric trajectories. In this model the pulse was of constant duration and modulated in intensity to govern the recruitment and dynamic firing patterns of motoneurons and ultimately, the rate of rise of isometric force. Inextricably linked to the pulse was a step, which varied in duration and was also modulatable in intensity to control increments in the static firing rate and thereby govern the steady-state magnitude of the contraction. Freund and Budigen (1979) discussed a pulse model based on their results from human subjects who completed isometric and isotonic impulse contractions. This pulse was also considered constant in duration and variable in intensity to control motoneuron activity. Their pulse component was modelled to control both the rate of rise and the magnitude of the contraction. This kind of model has also been suggested by Lesteinne (1979) and Brown and Cooke (1981). Recently Gottlieb et al. (1989) suggested a pulse model where both the pulse amplitude and duration varied depending on whether velocity of movement or movement distance was the controlled parameter.

The pulse-step model proposed in the present study is different from those presented above in a number of respects. To start, it addresses a range of contraction speeds, not just ballistic-type contractions. A pulse-step model which can include a wide range of contraction speeds seems valid for two reasons: (1) ballistic contractions mark the extreme end of a continuum of contraction speeds and have been demonstrated to vary dependent on a number of constraining factors; (2) the observations of this thesis demonstrate two phases in the EMG activity throughout an eight-fold range in the rate of rise of force. This model also differs from most of the others by including two components: a pulse and a step. The pulse and step are not considered to be dependent on each other. The pulse is to have a modulatable intensity for controlling the recruitment and firing patterns of the motoneurons during the dynamic phase. Therefore, the larger the intensity of the pulse, the more motoneurons recruited and the shorter the interspike intervals in the unit's firing pattern. A pulse of constant duration was first proposed by Ghez and Vicario (1978) and later supported by Freund and Budigen (1979), Lestienne (1979) and Brown and Cooke (1981) based on an EMG burst of constant duration during isometric and isotonic contractions of different rates of rise. Five of nine of our experiments demonstrated a greater duration in the dynamic phase during the F(0-2) condition. Therefore, it is suggested that duration of the pulse as well as the step may also be modulatable. A pulse of greater duration could yield a series of very short interspike intervals resulting in the production of greater rates of change of force. This maybe particularly effective for higher threshold motor units (Zajac and Young, 1980). An example will be presented to describe the workings of our central inputs model in terms of force output parameters.

This example focuses on two force trajectories both equal in magnitude of the steady-state force output, but varied in rate of rise of force (our F(0-1) and S(0-1) conditions). In this situation only the pulse would be modulated, linked to a step of constant magnitude. For the S(0-1) trajectory the intensity of the pulse would be small, and therefore recruit few motoneurons, each contributing relatively few spikes with long interspike intervals during the dynamic phase such that the input of predominate influence would be the step component. This would result in a slow rate of rise of force. The speed of contraction in the F(0-1) condition would then be increased by a pulse of greater intensity and/or greater duration which would recruit more motoneurons, each generating shorter interspike intervals within the dynamic phase. The constant magnitude of the step would yield the same static firing rates in both the S(0-1) and F(0-1) conditions.

Presumably these proposed central inputs would be the output of a system working within the constraints already discussed (i.e. the influence of visual cues). Pulse amplitude and duration may also be constrained to a maximum dependent on the magnitude of the contraction to be produced (Freund and Budigen, 1979).

APPENDIX I - SINGLE MOTOR UNIT DATA

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Table 1: Background firing rate, absolute dynamic and normalized dynamic indices (DI) for motor units recorded during F(0-1) and S(0-1) force trajectories when subjects were instructed to keep background firing rate constant. Means and standard errors are given at bottom of table. The background firing rates, the absolute dynamic index values and the normalized dynamic index values were significantly different ($p \leq 0.003$, $p \leq 0.0002$ and $p \leq .0001$ respectively).

Subject	**Background (pps)**		**Absolute DI (pps)**		**Normalized DI (pps/N-m/s)**	
	F(0-1)	**S(0-1)**	**F(0-1)**	**S(0-1)**	**F(0-1**	**S(0-1)**
TP 16/03/89 178/183	7.6	8.2	10.3	7.7	.57	3.66
TP 05/04/89 199/207	7.1	7.3	19.2	3.6	.65	1.34
TP 05/04/89 233/239	5.6	5.8	21.3	9.2	.61	1.11
TP 02/06/89 114/129	6.7	8.1	23.5	12.1	1.20	2.80
TP 02/06/89 161/165	7.7	7.2	21.6	8.4	.96	1.70
LS 11/10/88 161/165	7.5	10	4.7	8.1	.47	3.31
LS 27/10/88 226/225	5.2	5.9	10.7	7.6	1.02	3.33
LS 06/06/89 100/104	8.9	9.2	9.9	2.6	2.11	2.05
LS 20/09/89 205/210	7.5	8.6	9.9	3.1	3.60	5.00
SF 27/11/88 259/260	6.9	8.1	2.5	3.6	.23	1.68
SF 27/11/88 13/12	9.9	7.4	6.4	8.3	.61	3.90
SF 14/03/89 94/98	9.1	10.4	8.2	5.2	2.88	11.50
SF 05/04/89 24/33	7.9	7.5	9.1	4.6	1.13	3.96
SF 01/06/89 67/73	7.5	9.3	2.7	9.6	.23	6.36
VL 06/03/89 104/118	5.4	5.7	16.4	7.8	.98	1.79
VL 06/03/89 120/127	6.4	8.4	10.2	8.8	1.05	3.09
VL 15/03/89 136/150	6.6	8.3	10.3	4.8	1.70	4.70
BH 02/06/89 36/48	5.9	6.5	16.4	4.6	.96	1.30
PB 02/14/87 45/54	7.1	8.7	3.4	5.2	.37	1.14
PB 02/14/87 58/59	9.1	9.9	6.5	4.3	1.06	3.94

PB 02/21/87 66/67	7.2	7.9	8.9	5.8	.85	2.12
PB 02/21/87 75/76	7.2	9.4	11.8	9.2	1.59	4.6
PB 02/21/87 82/83	10.6	10.7	13.8	14.2	1.65	7.63
PB 02/12/88 112/113	6	7.5	10.9	8.3	1.00	4.61
PB 02/12/88 126/132	8.9	8.7	10.6	5.1	1.31	2.77
PB 02/12/88 128/134	10.5	14.1	9.5	9.6	1.17	5.2
PB 02/12/88 138/142	8.0	9.0	13.8	8.7	1.72	4.78
PB 02/13/88 167/171	6.9	6.6	16.7	10	1.57	5.68
PB 27/11/88 167/171	9.9	8.0	10.7	6.5	3.47	9.15
MEAN	**7.6**	**8.3**	**11.4**	**7.1**	**1.27**	**3.94**
STANDARD ERROR	**0.27**	**0.32**	**1.0**	**0.50**	**.16**	**.45**

Table 2: Background firing rate, absolute dynamic and normalized dynamic indices for motor units recorded during F(0-1) and F(0-2) force trajectories when background firing rate was kept constant. Means and standard errors are given at bottom of table. Neither background firing rate nor the absolute dynamic index was significantly different (p≤0.17) and (p≤0.56), respectively. Normalized dynamic index values were significantly different (p≤.023).

SUBJECT	**Background (pps)**		**Absolute DI (pps)**		**NDI (pps/N-m/s)**	
	F0-1	**F0-2**	**F0-1**	**F0-2**	**F(0-1)**	**F(0-2)**
BH 02/06/89 36/42	5.9	6.3	16.4	10.1	.96	.36
BH 5/10/89 49/67	8.6	8.9	10.1	10.9	1.30	.61
BH 5/10/89 52/70	8.5	8.2	16.8	19.8	2.17	1.12
DT 07/09/89 223/227	6.7	8.6	7.9	11.6	.70	.66
PB 11/27/88 30/35	9.9	7.2	10.7	19.4	3.47	4.11
SF 05/04/89 24/27	7.9	7.8	9.1	13.2	1.13	.99
SF 01/06/89 67/70	7.5	8.9	2.7	1.1	.23	.04
SF 27/08/89 9/5	9.6	9.7	7.2	5.1	1.12	.57
SF 04/10/89 27/32	10.5	11.3	14.7	2.1	1.12	.13
TP 05/04/89 199/200	7.1	7.4	19.2	14.1	.65	.31
TP 02/06/89 114/119	6.7	10.9	23.5	27.0	1.20	.76
TP 7/09/89 233/239	6.9	7.4	15.7	22.8	.40	.49
TP 7/09/89 243/247	7.8	9.2	11.1	21.9	.80	.76
MEAN	**8.0**	**8.6**	**12.7**	**13.8**	**1.17**	**0.84**
STANDARD ERROR	**0.37**	**0.38**	**1.50**	**2.16**	**0.23**	**0.28**

Table 3: Background firing rate, absolute dynamic and normalized dynamic indices when unit completed the F(0-1) trajectory from a low, tonic firing rate (Low FR) versus when the unit was recruited during the contraction (Zero). Means and standard errors are given at bottom of table. Background firing rate was significantly different ($p \leq .0001$), but absolute and normalized dynamic index values were not ($p \leq .36$).

SUBJECT	**Background (pps)**		**Absolute DI (pps)**		**Normalized DI (pps/N-m/s)**	
	Low FR	**Zero**	**Low FR**	**Zero**	**Low FR**	**Zero**
BH 02/06/89 36/39	5.9	0.0	16.4	16.2	.96	.86
BH 05/10/89 52/75	8.5	2.2	16.8	16.9	2.17	1.93
BH 05/10/89 43/62	8.2	0.0	15.8	15.1	1.48	1.65
DT 07/09/89 216/212	10.0	0.0	14.6	10.3	1.30	.80
DT 03/10/89 14/18	10.8	0.4	6.8	15.6	1.47	3.47
LS 22/02/89 61/62	7.0	0.0	14.7	24.2	1.73	2.43
LS 04/03/89 154/146	6.7	0.0	12.6	13.5	1.11	1.13
LS 01/06/89 7/3	6.4	0.1	18.1	19.0	4.83	3.66
LS 06/06/89 100/110	8.9	0.6	9.9	10.9	2.11	2.38
LS 27/08/89 183/179	10.6	0.0	13.9	20.1	1.97	2.82
MW 05/10/89 91/96	8.8	0.0	17.8	17.8	.93	.96
MW 05/10/89 115/123	10.7	0.0	25.0	21.0	1.52	2.40
PB 14/02/87 58/48	9.1	0.4	6.5	2.4	1.06	.24
SF 05/03/89 88/87	6.4	0.5	9.8	0.7	2.15	.16
SF 05/04/89 12/11	6.3	0.05	9.1	5.1	1.35	.75
VL 06/03/89 120/121	6.4	0.1	10.2	20.8	1.05	1.49
VL 06/03/89 104/110	5.4	0.0	16.4	5.4	.98	.27
VL 15/03/89 136/133	6.6	0.0	10.3	9.2	1.70	1.40
VL 01/06/89 258/250	6.8	0.0	22.8	6.6	1.70	.55
MEAN	**7.9**	**0.23**	**14.1**	**13.2**	**1.66**	**1.54**
STANDARD ERROR	**0.41**	**0.12**	**1.14**	**1.57**	**0.20**	**0.24**

Table 4: Background firing rate, absolute dynamic and normalized dynamic indice values when unit completed the F(0-1) trajectory from a low, tonic background firing rate (low FR) versus a higher, tonic rate (high FR). Background firing rates are significantly different ($p \leq 0.0001$). Absolute dynamic index values are not statistically different ($p \leq 0.06$), but when normalized with respect to the maximum dT/dt, the means of the NDI values are significantly different ($p \leq 0.039$).

SUBJECT	**Background (pps)**		**Absolute DI (pps)**		**Normalized DI (pps/N-m/s)**	
	Low FR	**High FR**	**Low FR**	**High FR**	**Low FR**	**High FR**
BH 05/10/89 52/57	8.5	10.6	16.8	12.0	2.17	1.31
LS 04/03/89 143/151	7.0	8.1	20.6	7.4	1.72	.65
MW 05/10/89 102/107	6.4	10.4	21.7	19.2	1.07	1.13
MW 05/10/89 112/120	9.0	9.7	13.5	11.0	2.04	1.26
MW 23/11/89 66/73	7.9	11.7	14.9	12.3	3.10	2.60
SF 05/03/89 173/184	7.6	9.3	15.0	6.7	3.30	1.53
SF 04/10/89 32/36	11.3	14.3	3.4	2.1	.13	.21
TP 19/12/88 146/151	6.3	9.7	18.2	10.6	.25	.16
TP 05/04/89 199/214	7.1	9.3	19.2	9.7	.67	.32
TP 07/09/89 233/130	6.9	10.6	15.7	24.6	.40	.89
VL 15/03/89 136/142	6.6	10.1	10.3	11.4	1.70	1.50
MEAN	**7.7**	**10.3**	**15.4**	**11.5**	**1.50**	**1.05**
STANDARD ERROR	**0.45**	**0.48**	**1.55**	**1.81**	**0.33**	**0.22**

Table 5: Mean steady-state firing rate and static sensitivity index during the F(0-1) and S(0-1) conditions. Means and standard errors are given at bottom of table and did not significantly differ ($p \leq 0.16$ and $p \leq 0.82$).

Subject	**Steady-state firing rate (pps)**		**Static sensitivity (pps/N-m)**	
	F(0-1)	**S(0-1)**	**F(0-1)**	**S(0-1)**
TP 16/03/89 178/183	8.9	9.9	.90	1.31
TP 05/04/89 199/207	8.5	9.9	.67	1.26
TP 05/04/89 233/239	8.5	9.9	.67	.56
TP 02/06/89 114/129	9.8	10.5	2.40	1.70
TP 02/06/89 161/165	13.7	10.3	3.60	2.10
LS 11/10/88 161/165	11.8	11.9	2.61	2.71
LS 27/10/88 226/225	10.1	11.4	2.58	3.23
LS 06/06/89 100/104	11.4	12.1	4.31	5.37
LS 20/09/89 205/210	11.5	12.0	10.00	10.00
SF 27/11/88 259/260	10.8	12.3	2.42	2.41
SF 27/11/88 13/12	13.9	12.5	2.37	3.07
SF 14/03/89 94/98	11.0	12.3	5.28	5.60
SF 05/04/89 24/33	10.4	10.0	2.10	2.34
SF 01/06/89 67/73	11.4	12.7	2.69	2.31
VL 06/03/89 104/118	11.8	12.0	4.96	4.88
VL 06/03/89 120/127	11.5	11.6	3.57	2.04
VL 15/03/89 136/150	10.0	11.7	5.40	4.90
BH 02/06/89 36/48	9.9	10.1	3.28	2.88
PB 02/14/87 45/54	13.9	8.9	5.44	.14
PB 02/14/87 58/59	11.1	12.1	1.92	2.13
PB 02/21/87 66/67	9.1	9.7	1.16	1.10
PB 02/21/87 75/76	7.8	10.3	.63	.82
PB 02/21/87 82/83	11.8	10.5	1.19	0.0

PB 02/12/88 112/113	10.3	10.9	3.16	2.46
PB 02/12/88 126/132	9.2	9.5	.20	.53
PB 02/12/88 128/134	11.1	16.7	.40	1.73
PB 02/12/88 138/142	8.6	10.4	.39	.94
PB 02/13/88 167/171	6.3	8.8	0.0	1.47
PB 27/11/88 167/171	10.7	9.8	2.10	4.74
MEAN	**10.5**	**11.0**	**2.63**	**2.57**
STANDARD ERROR	**0.33**	**0.31**	**0.40**	**0.39**

Table 6: Mean steady-state firing rate and static sensitivity index during the F(0-1) and F(0-2) conditions. Included in this table are four units (marked with *) recorded during S(0-1) and S(0-2) conditions. Means and standard errors are given at bottom of table. Although static firing rates did not differ ($p \leq 0.095$), static sensitivity index values were significantly different ($p \leq 0.0031$).

SUBJECT	**Steady-state firing rate (pps)**		**Static sensitivity (pps/N-m)**	
	F0-1	**F0-2**	**F0-1**	**F0-2**
BH 02/06/89 36/42	9.9	10.3	3.28	1.56
BH 5/10/89 49/67	11.1	11.8	2.45	1.41
BH 5/10/89 52/70	12.5	13.5	3.98	2.58
DT 07/09/89 223/227	10.8	12.0	3.87	1.40
PB 11/27/88 30/35	10.7	6.6	2.10	0.0
SF 05/04/89 24/27	10.4	10.7	2.10	1.43
SF 01/06/89 67/70	11.4	12.8	2.69	1.38
SF 27/08/89 9/5	13.5	13.4	5.34	2.64
SF 04/10/89 27/32	14.2	15.0	3.39	1.82
TP 05/04/89 199/200	8.5	10.1	.67	.63
TP 02/06/89 114/119	9.8	11.6	2.40	.27
TP 7/09/89 233/239	8.3	18.5	.74	4.12
TP 7/09/89 243/247	10.9	11.2	2.50	.94
* TP 05/02/90 195/199	12.2	13.0	.86	.94
* SR 05/02/90 177/181	14.3	16.4	8.10	4.20
* SR 05/02/90 185/189	17.9	19.1	5.40	2.80
* LS 06/02/90 212/208	9.9	10.0	4.30	3.50
MEAN	**11.5**	**12.7**	**3.19**	**1.86**
STANDARD ERROR	**0.58**	**0.77**	**0.46**	**0.31**

Table 7: Steady-state firing rate and static sensitivity index values compared between when unit completed F(0-1) trajectory from a background of a low, tonic rate (low FR) versus being recruited during the contraction (zero). Means and standard errors given at bottom of table were significantly different (p≤.010 and p≤.0001, respectively).

SUBJECT	**Steady-state firing rate (pps)**		**Static sensitivity (pps/N-m)**	
	Low FR	**Zero**	**Low FR**	**Zero**
BH 02/06/89 36/39	9.9	8.1	3.28	7.23
BH 05/10/89 52/75	12.5	12.4	3.98	10.30
BH 05/10/89 43/62	11.8	12.9	3.56	12.93
DT 07/09/89 216/212	15.4	15.0	4.42	12.19
DT 03/10/8 14/18	13.2	13.0	4.80	25.50
LS 22/02/89 61/62	11.4	10.3	3.83	8.70
LS 04/03/89 154/146	9.0	5,8	3.96	9.84
LS 01/06/89 7/3	10.1	8.3	8.04	18.40
LS 06/06/89 100/110	11.4	11.9	4.31	19.51
LS 27/08/89 183/179	13.9	10.2	6.87	20.00
MW 05/10/89 91/96	12.3	13.6	2.56	8.00
MW 05/10/89 115/123	12.9	13.7	3.57	15.9
PB 14/02/87 58/48	11.1	7.1	1.92	5.44
SF 05/03/89 88/87	10.5	10.6	6.83	16.50
SF 05/04/89 12/11	8.9	7.9	2.50	7.38
VL 06/03/89 120/121	11.5	9.6	3.57	6.11
VL 06/03/89 104/110	11.8	8.4	4.96	6.50
VL 15/03/89 136/133	10.0	7.7	5.40	11.60
VL 01/06/89 258/250	13.3	11.0	5.00	8.46
MEAN	**11.6**	**9.24**	**4.38**	**12.1**
STANDARD ERROR	**0.39**	**0.83**	**0.36**	**1.30**

Table 8: Steady-state firing rate and static sensitivity index values compared between when unit completed F(0-1) trajectory from a background of a low, tonic rate (low FR) versus a higher, tonic firing rate (high FR). Means and standard errors given at bottom of table are significantly different ($p \leq 0.02$ and $p \leq 0.0065$, respectively).

SUBJECT	**Steady-state firing rate (pps)**		**Static sensitivity (pps/N-m)**	
	Low FR	**High FR**	**Low FR**	**High FR**
BH 05/10/89 52/57	12.5	13.3	3.98	2.70
LS 04/03/89 143/151	11.4	9.9	7.46	3.10
MW 05/10/89 102/107	10.3	12.8	2.35	1.56
MW 05/10/89 112/120	11.0	11.7	2.74	2.32
MW 23/11/89 66/73	11.3	13.0	6.92	2.71
SF 05/03/89 173/184	12.0	12.8	7.21	5.74
SF 04/10/89 32/36	15.3	15.0	1.82	.48
TP 19/12/88 146/151	12.4	13.0	1.01	.52
TP 05/04/89 199/214	8.5	10.3	.65	.38
TP 07/09/89 233/130	8.3	11.9	.74	1.20
VL 15/03/89 136/142	10.0	12.8	5.40	3.50
MEAN	**11.2**	**12.4**	**3.66**	**2.14**
STANDARD ERROR	**0.59**	**0.43**	**0.80**	**0.50**

Table 9: Static sensitivity and normalized dynamic index values of each unit recorded during the F(0-1) condition to assess whether there is an observable dependency between motoneuron static and dynamic firing properties. Means and standard errors are given at bottom of table.

SUBJECT	**Static Sensitivity (pps/N-m)**	**Normalized DI (pps/N-m/s)**
	F(0-1)	**F(0-1**
TP 16/03/89 178/183	.90	.57
TP 05/04/89 199/207	.67	.65
TP 05/04/89 233/239	.67	.61
TP 02/06/89 114/129	2.40	1.20
TP 02/06/89 161/165	3.60	.96
LS 11/10/88 161/165	2.61	.47
LS 27/10/88 226/225	2.58	1.02
LS 06/06/89 100/104	4.31	2.11
LS 20/09/89 205/210	10.00	3.60
SF 27/11/88 259/260	2.42	.23
SF 27/11/88 13/12	2.37	.61
SF 14/03/89 94/98	5.28	2.88
SF 05/04/89 24/33	2.10	1.13
SF 01/06/89 67/73	2.69	.23
VL 06/03/89 104/118	4.96	.98
VL 06/03/89 120/127	3.57	1.05
VL 15/03/89 136/150	5.40	1.70
BH 02/06/89 36/48	3.28	.96
PB 02/14/87 45/54	5.44	.37
PB 02/14/87 58/59	1.92	1.06
PB 02/21/87 66/67	1.16	.85
PB 02/21/87 75/76	.63	1.59

PB 02/21/87 82/83	1.19	1.65
PB 02/12/88 112/113	3.16	1.00
PB 02/12/88 126/132	.20	1.31
PB 02/12/88 128/134	.40	1.17
PB 02/12/88 138/142	.39	1.72
PB 02/13/88 167/171	0.0	1.57
PB 27/11/88 167/171	2.10	3.47
MEAN	**2.63**	**1.27**
STANDARD ERROR	**0.40**	**0.16**

Table 10: Background firing rate and absolute dynamic index values for low and higher threshold motor units simultaneously recorded during the F(0-1) trajectory. The low threshold unit fired tonically in the background whereas the higher threshold unit was recruited during the contraction. Background firing rate values were significantly different ($p \leq 0.0001$) but absolute dynamic index values were not different ($p \leq 0.73$). Correction for the rate of rise of the force trajectory was not considered to be necessary since both units were recorded under the same condition; therefore, normalized dynamic index values were not included.

SUBJECT	**Background (pps)**		**Absolute DI (pps)**	
	Low Threshold	**High Threshold**	**Low Threshold**	**High Threshold**
BH 05/10/89 57/62	10.6	0.0	12.0	15.1
LS 04/03/89 143/146	7.0	0.0	20.6	13.5
LS 15/03/89 164/163	5.9	0.0	8.9	8.3
LS 01/06/89 4/3	8.3	0.1	6.4	19.0
LS 01/06/89 7/8	6.4	0.2	18.1	15.0
MW 07/09/89 205/203	9.2	1.3	6.9	13.0
MW 05/10/89 120/123	9.7	0.0	11.0	21.0
PB 14/02/87 45/48	7.1	0.4	3.7	2.4
PB 21/02/87 66/69	7.2	0.3	8.9	3.0
SF 05/03/89 84/87	9.3	0.5	6.7	0.7
SF 14/03/89 94/95	9.1	0.1	8.2	4.9
TP 04/03/89 134/137	8.6	1.5	18.0	5.5
TP 16/03/89 171/172	8.5	0.0	27.1	28.0
TP 16/03/89 178/177	7.6	0.4	10.3	21.8
VL 15/03/89 142/143	10.1	0.0	11.4	17.0
MEAN	**8.3**	**0.3**	**11.9**	**12.5**
STANDARD ERROR	**0.4**	**0.1**	**1.6**	**2.5**

Table 11: Background firing rate and absolute dynamic index values for low and higher threshold, simultaneously recorded motor units during the F(0-1) trajectory. Both units fired tonically in the background. Neither background firing rate nor absolute dynamic index values were significantly different ($p \leq 0.17$ and $p \leq 0.35$, respectively) . Correction for the rate of rise of the force trajectory was not considered to be necessary since both units were recorded under the same condition; therefore, normalized dynamic index values were not included.

SUBJECT	**Background (pps)**		**Absolute DI (pps)**	
	Low Threshold	**High Threshold**	**Low Threshold**	**High Threshold**
BH 05/10/89 67/70	8.9	8.2	10.9	19.8
BH 05/10/89 45/43	9.2	8.2	18.8	15.8
DT 07/09/89 221/223	7.8	6.7	7.8	7.9
LS 04/03/89 168/167	8.1	6.7	7.4	12.6
LS 15/03/89 151/154	7.9	7.9	10.0	18.7
MW 05/10/89 112/115	9.0	10.3	13.5	10.1
PB 02/12/88 128/126	10.5	8.9	9.5	10.6
SF 05/03/89 173/177	7.6	7.7	15.0	8.9
SF 07/09/89 253/255	8.6	9.8	7.3	11.7
SF 07/09/89 259/1	10.3	7.5	7.9	7.8
MEAN	**8.8**	**8.2**	**10.8**	**12.4**
STANDARD ERROR	**0.3**	**0.4**	**1.2**	**1.3**

Table 12: Torque threshold values for two simultaneously recorded motor units labelled as low threshold and high threshold. The low threshold unit fired tonically before the contraction whereas the higher threshold unit was recruited during the contraction. Included in the table is the difference in background firing rates between the two units as well as their difference in absolute dynamic index values. High threshold values were subtracted from low threshold values.

SUBJECT	Low Threshold (N-m)	High Threshold (N-m)	ΔBkgd (pps)	ΔAbsolute DI (pps)
BH 05/10/89 57/62	2.63	5.11	10.7	-3.1
LS 04/03/89 143/146	.19	1.14	[illegible].0	7.1
LS 15/03/89 164/163	.41	.98	5.9	0.6
LS 01/06/89 4/3	.24	.35	8.2	-12.6
LS 01/06/89 7/8	.35	>.35	6.2	3.1
MW 07/09/89 205/203	1.65	2.45	7.9	-6.1
MW 05/10/89 120/123	not obtained	not obtained	9.7	-10.0
PB 14/02/87 45/48	.43	1.63	6.7	1.3
PB 21/02/87 66/69	.25	.88	6.9	5.9
SF 05/03/89 84/87	.49	.67	8.8	6.0
SF 14/03/89 94/95	.18	.25	9.0	3.3
TP 04/03/89 134/137	3.68	>3.68	7.1	12.5
TP 16/03/89 171/172	2.04	5.55	8.5	-0.9
TP 16/03/89 178/177	1.85	4.44	7.2	-11.5
VL 15/03/89 142/143	1.18	>1.18	10.2	-5.6

Table 13: Torque threshold values for two simultaneously recorded motor units labelled as low threshold and high threshold. Both units fired tonically before the force trajectory was traced. Included in the table are the difference in background firing rates between the two units as well as their difference in absolute dynamic index values. High threshold values were subtracted from low threshold values.

SUBJECT	**Low Threshold (N-m)**	**High Threshold (N-m)**	**Δ Bkgd. (pps)**	**ΔAbsolute DI (pps)**
BH 05/10/89 67/70	2.63	5.11	.7	-8.9
BH 05/10/89 45/43	.73	2.63	1.0	3.0
DT 07/09/89 221/223	<1.15	1.15	1.1	-.1
LS 04/03/89 151/154	.19	1.14	1.4	5.2
LS 15/03/89 168/167	.25	1.12	0.0	8.7
MW 05/10/89 112/115	not obtained	not obtained	-1.3	-3.4
PB 02/12/88 128/126	1.34	5.35	1.6	1.1
SF 05/03/89 173/177	.49	.67	-0.1	-6.1
SF 07/09/89 253/255	.13	.19	-1.2	-4.7
SF 07/09/89 259/1	.13	.26	2.8	.1

Table 14: Steady-state firing rate and static sensitivity index values for low and higher threshold, simultaneously recorded motor units during the F(0-1) trajectory. The low threshold unit fired tonically in the background whereas the higher threshold unit was recruited during the contraction. Means and standard error values given at bottom of table are significantly different ($p \leq .02$ and $p \leq .0003$, respectively).

SUBJECT	**Steady-state firing rate (pps)**		**Static sensitivity (pps/N-m)**	
	Low Threshold	**High Threshold**	**Low Threshold**	**High Threshold**
BH 05/10/89 57/62	13.3	12.9	2.70	12.93
LS 04/03/89 143/146	11.4	5.8	7.46	9.84
LS 15/03/89 164/163	8.7	8.2	3.21	10.00
LS 01/06/89 4/3	9.5	8.3	2.67	18.40
LS 01/06/89 7/8	10.1	9.3	8.04	19.78
MW 07/09/89 205/203	12.0	11.9	3.25	12.77
MW 05/10/89 120/123	11.7	13.7	2.32	15.90
PB 14/02/87 45/48	13.9	7.1	5.44	5.36
PB 21/02/87 66/69	9.1	9.9	1.16	5.90
SF 05/03/89 84/87	12.8	10.6	5.74	16.50
SF 14/03/89 94/95	11.0	9.5	5.28	26.10
TP 04/03/89 134/137	9.8	9.7	.45	2.80
TP 16/03/89 171/172	10.0	7.3	.55	2.70
TP 16/03/89 178/177	8.9	8.8	.90	5.56
VL 15/03/89 142/143	12.8	8.7	3.50	11.00
MEAN	**11.0**	**9.4**	**3.51**	**11.70**
STANDARD ERROR	**0.4**	**0.5**	**0.62**	**1.74**

Table 15: Steady-state firing rate values for low and higher threshold, simultaneously recorded motor units during the F(0-1) trajectory. Both units fired tonically before contraction was completed. Means and standard error values given at bottom of table were not significantly different ($p \leq 0.43$ and $p \leq 0.68$, respectively).

SUBJECT	**Steady-state FR (pps)**		**Static sensitivity (pps/N-m)**	
	Low Threshold	**High Threshold**	**Low Threshold**	**High Threshold**
BH 05/10/89 67/70	11.8	13.5	1.41	2.58
BH 05/10/89 45/43	11.9	11.8	2.57	3.56
DT 07/09/89 221/223	12.2	10.8	4.15	3.87
LS 04/03/89 168/167	9.9	9.0	3.10	3.96
LS 15/03/89 151/154	9.6	8.6	2.07	.85
MW 05/10/89 112/115	11.3	13.3	2.74	3.57
PB 02/12/88 128/126	11.1	9.2	0.40	.20
SF 05/03/89 173/177	12.0	12.7	7.21	8.20
SF 07/09/89 253/255	13.4	12.9	6.63	4.26
SF 07/09/89 259/1	13.4	10.9	4.25	4.62
MEAN	**11.7**	**11.3**	**3.45**	**3.57**
STANDARD ERROR	**0.4**	**0.6**	**0.68**	**0.69**

Table 16: Torque threshold values for two simultaneously recorded motor units labelled as low threshold and high threshold. The low threshold unit fired tonically before the contraction whereas the higher threshold unit was recruited during the contraction. Also included are the difference in background firing rates between the two units as well as their difference in static sensitivity (SS) values (high threshold unit subtracted from low threshold unit).

SUBJECT	**Low Threshold (N-m)**	**High Threshold (N-m)**	**ΔBkgd (pps)**	**Δ SS (pps/N-m)**
BH 05/10/89 57/62	2.63	5.11	10.7	-10.20
LS 04/03/89 143/146	.19	1.14	7.0	-2.38
LS 15/03/89 164/163	.41	.98	5.9	-6.79
LS 01/06/89 4/3	.24	.35	8.2	-15.73
LS 01/06/89 7/8	.35	>.35	6.2	-11.74
MW 07/09/89 205/203	1.65	2.45	7.9	-9.52
MW 05/10/89 120/123	not obtained	not obtained	9.7	-13.58
PB 14/02/87 45/48	.43	1.63	6.7	.08
PB 21/02/87 66/69	.25	.88	6.9	-4.74
SF 05/03/89 84/87	.49	.67	8.8	-10.76
SF 14/03/89 94/95	.18	.25	9.0	-20.82
TP 04/03/89 134/137	3.68	>3.68	7.1	-2.35
TP 16/03/89 171/172	2.04	5.55	8.5	-2.15
TP 16/03/89 178/177	1.85	4.44	7.2	-4.66
VL 15/03/89 142/143	1.18	>1.18	10.2	-7.50

Table 17: Torque threshold values for low threshold and high threshold motor units simultaneously recorded during the F(0-1) trajectory. Both units fired tonically before contraction was completed. Included in the table are the difference in background firing rates between the two units as well as their difference in static sensitivity (SS) values. High threshold values were subtracted from low threshold values.

SUBJECT	**Low Threshold (N-m)**	**High Threshold (N-m)**	**ΔBkgd. (pps)**	**Δ SS (pps/N-m)**
BH 05/10/89 67/70	2.63	5.11	.7	-1.17
BH 05/10/89 45/43	.73	2.63	1.0	-.99
DT 07/09/89 221/223	<1.15	1.15	1.1	.28
LS 04/03/89 168/167	.19	1.14	1.4	-.86
LS 15/03/89 151/154	.25	1.12	0.0	1.22
MW 05/10/89 112/115	not obtained	not obtained	-1.3	-.83
PB 02/12/88 128/126	1.34	5.35	1.6	.20
SF 05/03/89 173/177	.49	.67	-0.1	-.99
SF 07/09/89 253/255	.13	.19	-1.2	2.37
SF 07/09/89 259/1	.13	.26	2.8	-.37

APPENDIX II - SURFACE EMG DATA

Table 18: Absolute dynamic index for surface electromyograms recorded during four different traced trajectories completed to small force magnitudes. Means and standard errors are given at the bottom of the table. The absolute DI for all the fast conditions was greater than the S(0-2) condition ($p \leq .05$). The F(0-2) condition was significantly greater ($p \leq .05$) than either the F(0-1) or the F(1-2) trajectories which were not significantly different ($p \leq .90$).

SUBJECT	**Absolute Dynamic Index (mV)**			
	F0-1	**F0-2**	**F1-2**	**S0-2**
PS 19/5/88	.078	.111	.013	.005
KM 17/5/88	.036	.053	.018	.014
TP 13/5/88	.082	.19	.122	.034
NG 17/5/88	.011	.012	.057	.014
PM 13/5/88	.146	.242	.138	.010
SB 15/5/88	.031	.060	.022	.014
MC 19/5/88	.057	.129	.081	.011
JC 19/7/88	.044	.048	.030	.002
PS 19/7/88	.112	.147	.053	.006
DT 18/7/88	.023	.037	.025	0.0
MW 19/7/88	.045	.111	.043	.018
MEAN	**0.06**	**0.104**	**0.055**	**0.012**
STANDARD ERROR	**0.012**	**0.021**	**0.013**	**0.003**

Table 19: Maximum rates of rise of isometric torque for four different traced trajectories completed to small force magnitudes. Means and standard errors are given at the bottom of the table. The maximum dT/dt for the fast conditions were significantly greater than the S(0-2) condition ($p \leq .001$). The F(0-2) condition was significantly faster ($p \leq .002$) than either the F(0-1) or the F(1-2) trajectories which were not significantly different from one another ($p \leq .90$).

SUBJECT	**Maximum speed of contraction (N-m/s)**			
	F0-1	**F0-2**	**F1-2**	**S0-2**
PS 19/5/88	62.4	87.2	47.6	9.4
KM 17/5/88	15.0	27.6	14.7	3.4
TP 13/5/88	18.5	43.2	17.2	8.7
NG 17/5/88	21.5	34.4	20.5	6.3
PM 13/5/88	20.5	34.2	18.0	8.5
SB 15/5/88	13.3	26.9	12.2	5.5
MC 19/5/88	23.8	47.3	38.0	7.4
JC 19/7/88	49.1	72.2	36.2	8.9
PS 19/7/88	53.1	63.2	25.6	4.9
DT 18/7/88	43.3	77.7	39.4	11.0
MW 19/7/88	64.0	94.4	55.0	8.7
MEAN	**35.0**	**55.3**	**29.5**	**7.5**
STANDARD ERROR	**5.9**	**7.4**	**4.3**	**0.7**

Table 20: Absolute dynamic index normalized with respect to the rate of rise of isometric force (normalized dynamic index) for surface electromyograms recorded during four different traced trajectories completed to small force magnitudes. Means and standard errors are given at the bottom of the table and were not significantly different from one another ($p \leq .90$).

SUBJECT	**Normalized DI (µV/N-m/s)**			
	F(0-1)	**F(0-2)**	**F(1-2)**	**S(0-2)**
PS 19/5/88	1.25	1.27	.27	.53
KM 17/5/88	2.41	1.92	1.22	4.1
TP 13/5/88	4.43	4.39	7.07	3.88
NG 17/5/88	.51	.35	2.78	2.22
PM 13/5/88	7.12	7.06	7.66	1.18
SB 15/5/88	2.33	2.23	1.80	2.56
MC 19/5/88	2.39	2.72	2.13	1.48
JC 19/7/88	.90	.66	.83	.22
PS 19/7/88	2.11	2.32	2.07	1.21
DT 18/7/88	.53	.47	.63	0.0
MW 19/7/88	.70	1.18	2.48	1.77
MEAN	**2.24**	**2.23**	**2.48**	**1.77**
STANDARD ERROR	**0.60**	**0.60**	**0.76**	**0.41**

Table 21: Absolute dynamic index for surface electromyograms recorded during three different traced trajectories completed to large force magnitudes. Means and standard errors are given at the bottom of the table, and were not significantly different from one another (p≤.90).

	Absolute Dynamic Index (mV)		
SUBJECT	**F0-1**	**F0-2**	**F1-2**
BH 09/11/89	.038	.10	.12
CS 29/11/89	.039	.027	.031
DT 29/11/89	.065	.04	.06
LS 14/11/89	.027	.010	.024
LS 29/11/89	0.0	.006	0.0
MW 09/11/89	.059	.086	.12
PB 14/11/89	.15	0.0	.14
PS 09/11/89	.10	.09	.10
RC 09/11/89	.12	.13	.18
SR 14/11/89	.073	.072	.018
YZ 29/11/89	.017	.039	.028
MEAN	**0.063**	**0.055**	**0.075**
STANDARD ERROR	**0.014**	**0.013**	**0.018**

Table 22: Maximum rates of rise of isometric torque for three different traced trajectories completed to large force magnitudes. Means and standard errors are given at the bottom of the table. The F(0-2) trajectory was significantly faster (p≤.01) than either the F(0-1) or the F(1-2) conditions which were not significantly different (p≤.90).

SUBJECT	**Maximum speed of contraction (N-m/s)**		
SUBJECT	**F0-1**	**F0-2**	**F1-2**
BH 09/11/89	111.7	270.2	173.9
CS 29/11/89	77.1	136.6	100.6
DT 29/11/89	45.2	117.5	73.9
LS 14/11/89	63.6	88.5	75.0
LS 29/11/89	25.4	46.7	37.9
MW 09/11/89	210.7	537.5	255.3
PB 14/11/89	84.5	173.4	89.7
PS 09/11/89	83.3	136.4	83.3
RC 09/11/89	109.1	189.5	128.6
SR 14/11/89	253.5	398.0	267.3
YZ 29/11/89	27.9	51.9	25.1
MEAN	**93.3**	**195.1**	**119.1**
STANDARD ERROR	**21.8**	**45.9**	**24.4**

Table 23: Absolute dynamic index normalized with respect to rate of rise of isometric torque (normalized DI) for three different traced trajectories completed to large force magnitudes. Means and standard errors are given at the bottom of the table. The normalized dynamic index for the F(0-2) condition was significantly less ($p \leq .04$) than either the F(0-1) or F(1-2) conditions which did not significantly differ from one another ($p \leq .90$).

SUBJECT	**Normalized DI (µV/N-m/s)**		
	F0-1	**F0-2**	**F1-2**
BH 09/11/89	.34	.37	.69
CS 29/11/89	.50	.19	.31
DT 29/11/89	1.40	.34	.80
LS 14/11/89	.42	.11	.32
LS 29/11/89	0.0	.13	0.0
MW 09/11/89	.28	.16	.47
PB 14/11/89	1.80	0.0	1.50
PS 09/11/89	1.20	.66	1.20
RC 09/11/89	1.10	.67	1.40
SR 14/11/89	.29	.18	.04
YZ 29/11/89	.61	.75	1.10
MEAN	**0.70**	**0.30**	**0.70**
STANDARD ERROR	**0.20**	**0.10**	**0.20**

Table 24: The area of the dynamic phase of the surface EMG during F(0-1) and F(0-2) trajectories completed within the thirty percent of MVC force range..

SUBJECT	**Area of dynamic phase (V*ms - not calibrated)**	
	F(0-1)	**F(0-2)**
BH 09/11/89	0.8	23.1
CS 29/11/89	8.4	6.6
DT 29/11/89	13.5	4.6
MW 09/11/89	3.0	11.9
PB 14/11/89	5.9	4.6
PS 09/11/89	25.2	37.4
RC 09/11/89	12.0	17.0
SR 14/11/89	10.7	24.2
YZ 29/11/89	3.6	2.7

Table 25: Static sensitivity for surface electromyograms recorded during four different traced trajectories completed to small force magnitudes. Means and standard errors given at the bottom of the table are not significantly different (p≤.90).

SUBJECT	**static sensitivity (µV/N-m)**			
	F(0-1)	**F(0-2)**	**F(1-2)**	**S(0-2)**
PS 19/5/88	4.14	4.16	3.60	3.39
KM 17/5/88	13.60	11.44	11.90	11.58
TP 13/5/88	47.10	37.20	50.50	27.00
NG 17/5/88	9.8	7.9	15.1	16.2
PM 13/5/88	20.80	12.00	12.50	8.40
SB 15/5/88	20.45	17.24	17.24	16.80
MC 19/5/88	19.45	19.15	22.58	26.03
JC 19/7/88	3.67	2.77	3.89	3.40
PS 19/7/88	5.40	5.49	6.81	8.44
DT 18/7/88	7.02	5.65	5.31	5.51
MW 19/7/88	5.00	3.50	4.10	5.20
MEAN	**14.20**	**11.46**	**13.89**	**11.92**
STANDARD ERROR	**3.86**	**3.07**	**4.11**	**2.56**

Table 26: Static sensitivity for surface electromyograms recorded during three different traced trajectories completed to large force magnitudes. Means and standard errors given at the bottom of the table are not significantly different (p≤.06).

SUBJECT	**static sensitivity (µV/N-m)**		
	F(0-1)	**F(0-2)**	**F(1-2)**
BH 09/11/89	4.6	4.9	5.8
CS 29/11/89	3.5	4.7	3.8
DT 29/11/89	13.0	14.0	18.0
LS 14/11/89	10.0	9.9	12.7
LS 29/11/89	3.9	4.0	3.8
MW 09/11/89	6.8	9.0	11.0
PB 14/11/89	23.0	42.0	58.0
PS 09/11/89	11.0	10.0	16.0
RC 09/11/89	11.0	10.0	14.0
SR 14/11/89	4.9	6.3	8.3
YZ 29/11/89	12.0	9.0	11.0
MEAN	**9.4**	**11.3**	**14.8**
STANDARD ERROR	**1.7**	**3.2**	**4.5**

Table 27: Maximum rate of rise of isometric torque during the F(0-1) and F(0-2) trajectories completed at an oscilloscope sweep speed of 0.2 seconds/division. Means and standard errors are given at bottom of table. The F(0-2) trajectory was significantly faster ($p \leq .0056$) than the F(0-1) trajectory.

SUBJECT	**Maximum dT/dt (N-m/s)**	
	F(0-1)	**F(0-2)**
BH 02/06/89	16.1	30.8
BH 09/11/89	54.5	90.8
LS 02/04/89	29.0	62.7
MW 06/06/89	47.1	87.2
MW 09/11/89	58.6	110.4
PB 02/04/89	6.3	10.8
PS 09/11/89	57.5	100.6
RC 09/11/89	25.9	41.7
RH 02/04/89	16.5	90.8
MEAN	**34.6**	**69.5**
STANDARD ERROR	**6.7**	**11.6**

Table 28: Maximum rate of rise of isometric force during the F(0-2) trajectory completed at three different timebase settings on the oscilloscope: 0.5 seconds/division, 0.2 seconds/division, 0.1 seconds/division. Means and standard errors are given at bottom of table. In the seven experiments when it was completed, the F(0-2) trajectory traced with the oscilloscope timebase at 0.1 seconds/division was significantly faster than the F(0-2) trajectory traced with timebase set at 0.5 seconds/division ($p \leq .009$).

SUBJECT	**Maximum speed of contraction (N-m/s)**		
	F(0-2) .5 sec/div	**F(0-2) .2 sec/div**	**F(0-2) .1 sec/div**
BH 02/06/89	31.6	30.8	31.7
BH 09/11/89	94.4	90.8	123.5
LS 02/04/89	25.9	62.8	54.0
MW 06/06/89	81.2	87.2	118.2
MW 09/11/89	89.7	110.4	120.7
PB 02/04/89	9.3	10.8	did not do
PS 09/11/89	97.7	100.6	112.1
RC 09/11/89	38.8	41.7	46.0
RH 02/04/89	26.2	42.1	did not do
MEAN	**55.0**	**64.1**	**86.6**
STANDARD ERROR	**11.7**	**11.6**	**13.5**

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