DYNAMIC PROPERTIES OF HUMAN MOTONEURONS

by

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ABSTRACT

For limb muscles, α–motoneurons in the spinal cord are the last elements to integrate and modulate signals from other parts of the central nervous system. Animal research on the dynamic properties of α–motoneurons shows that α–motoneurons behave as differentiators or high pass filters to injected currents. In behaving animals or human subjects, one cannot control the input currents to α–motoneurons. Therefore, human studies have controlled the force output and examined the associated firing patterns of motoneurons or the population electromyography (EMG) activity of the muscle. A monotonic or linear relationship has been shown between the EMG activity and the force output. No studies have related the firing patterns of underlying single motor units to EMG and force output. The following study examined the relationship between simultaneously recorded population EMG and single motor units to the dynamic and the steady state phases of ramp-and-hold force trajectories.

The subjects traced ramp-and-hold isometric force trajectories using wrist flexion. The contraction speeds and amplitudes of force output were controlled. Surface EMG from wrist flexors and single motor unit (SMU) action potentials from flexor carpi radialis muscle were recorded. The background firing rate of SMU activity was controlled. Averaged responses of rectified surface EMG and single motor unit activities were constructed for each condition. EMG and SMU responses were quantified during the dynamic and the steady state phases.

The dynamic activity of EMG was linearly related to the contraction speed while the steady state activity of EMG was linearly related to the contraction amplitude. The dynamic activity of a SMU increased nonlinearly with the speed of contraction. An increase in the background firing rate of a SMU resulted in a decrease in its dynamic activity. The steady state activity of a SMU was affected by contraction amplitude but not by contraction speed.

The steady state activity increased nonlinearly with contraction amplitude. An increase in background firing rate decreased the magnitude of the steady state response.

The linear responses of EMG during the dynamic and the steady state phases cannot be completely explained by the nonlinear responses of tonically firing SMUs. The linearity of EMG is suggested to result from recruitment of additional SMUs contributing phasically during the ramp-and-hold contraction.

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INTRODUCTION

Force production and movement result when muscles contract according to commands from nervous system. Motoneurons in the spinal cord play an essential role to mediate the commands and are the last stations to modulate the commands. When a motoneuron is recruited, the corresponding muscle unit contracts. The force output of the muscle unit is determined by the firing pattern of the motoneuron. The force output of the whole muscle is determined by the number of motor units recruited and the firing pattern of each of these motor units.

Motoneuron discharge pattern depends on inputs to the motoneuron, whether they are synaptic or intracellularly injected currents. In the following overview of the literature, firing patterns of motoneurons will be separated into steady state and dynamic responses: the former refer to the firing responses to relatively nonchanging inputs to the motoneurons while the latter refer to responses to changing inputs. The firing patterns of single motoneurons have been studied in both animals and human subjects.

In cat experiments, currents of various shapes were injected into the cell bodies of motoneurons and the firing patterns were recorded with intracellular microelectrodes. In primate (both monkey and human) experiments, inputs to motoneurons can not be controlled. Consequently, the response patterns of motoneurons have been studied when the subject controlled the output of the muscle, that is, the force and rate of change of force. Fortunately, there is a one to one relationship between the motoneuron discharge and motor unit action potential in voluntary contraction. The motoneuron responses were computed indirectly by recording motor unit action potentials from within the muscle.

The introduction will first review literature on the steady state responses of motoneurons, in both animal and primate experiments. Then, dynamic properties of motoneurons will be reviewed. Finally, the introduction will focus on surface electromyography (EMG) activity which represents population activity of the motoneuron pool.

I. Steady State Responses of Motoneurons

Information on steady state firing of motoneurons will be presented separately for intracellular studies in the cat and extracellular studies in primates.

a) Intracellular studies in cat

When depolarizing currents are injected into the cell body of a motoneuron, the motoneuron fires action potentials. The minimum current needed to produce a single spike is defined as rheobase. The depolarization during the spike is followed by a transient hyperpolarization, called afterhyperpolarization. When a step current is injected into a motoneuron somata, the motoneuron responds with an initial high firing rate followed by adaptation to a steady state firing rate (Fig. 1.). Granit and coworkers (Granit et al., 1963) observed a linear relationship between the current intensity and the repetitive firing rate during the steady state firing in rat motoneurons. Since the rat motoneurons were small and easy to damage, Kernell (1965 a,b,c) extended the experiments to cat lumbosacral motoneurons. When currents were increased to threshold for repetitive firing, which was about 1.5 times the rheobase, motoneurons responded with long lasting and well maintained repetitive steady discharge (Kernell, 1965a). A linear relation between motoneuron steady state firing rate (f) and current strength (I) was observed over a considerable range of input currents (Kernell, 1965a). With further increase in current, the firing rate and current strength relation (f/I) remained linear but the slope (f/I slope) increased. The range from the point where the motoneuron began to fire repetitively to the point where the slope began to increase was defined as primary range of motoneuron firing. The range above that, at which the firing rate was more sensitive to injected current

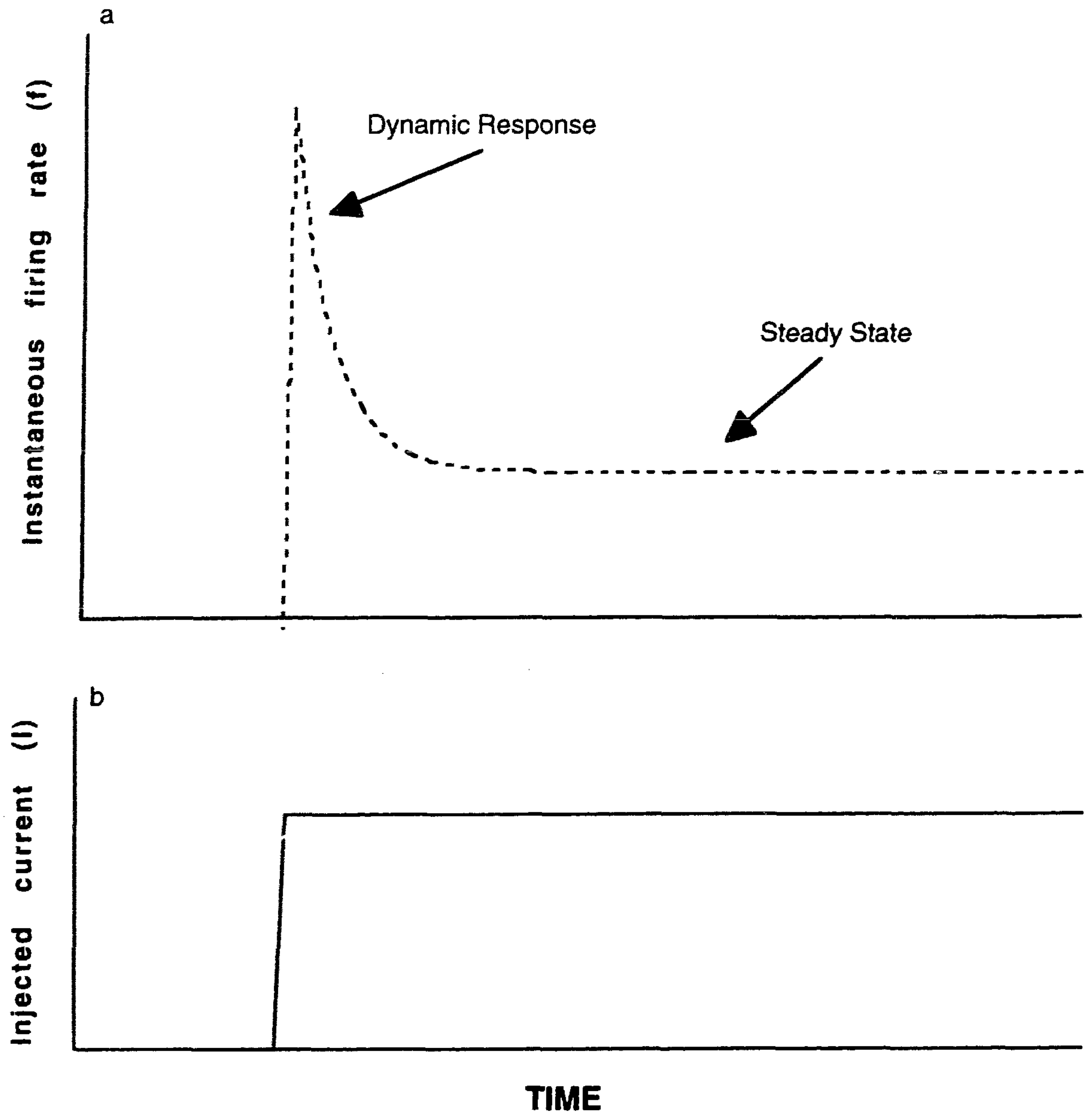

Fig. 1. When injected with step current (I) shown in (b), the motoneuron responds with an initial high instantaneous firing rate (f) which declines with time until a steady state firing is established as shown in (a). The decline in instantaneous firing rate is defined as adaptation.

strength, was defined as the secondary range of motoneuron firing (Kernell, 1965b). The limits of these two ranges of motoneuron firing have a close relation with the time course of afterhyperpolarization.

The duration of AHP was found to be negatively related to the size of motoneuron (Eccles et al., 1958). The larger the motoneuron, the shorter the duration of AHP (Eccles et al., 1958). Kernell (1965c) compared the duration of AHP after a single spike to the minimum and maximum firing rates of single motoneuron in response to intracellularly injected step currents. A highly significant inverse linear relationship was observed between the duration of AHP and minimum firing rate for repetitive firing. The same relationship was also observed between the duration of AHP and the maximal firing rate in the primary range of steady state firing. The shorter the duration of AHP, the higher the peak firing rate of motoneurons (Kernell, 1965c). Therefore, animal experiments showed that larger motoneurons had the ability to fire at higher rates than the smaller ones. The steady state f/I slope, on the other hand, was not related to the duration of AHP (Kernell, 1965a). This indicated that the steady state sensitivities, quantified by f/I slope, of motoneurons were not different in different motoneurons.

b) Single motoneuron responses under voluntary contraction

Corresponding to the intracellular studies, steady state responses of motoneurons in voluntary contractions have been studied by changing the force output level of muscle instead of the intensity of intracellularly injected current to the motoneurons. Most of the experiments have shown that all motoneurons are recruited at approximately the same firing rate (around 6-8 imp/sec). This lowest repetitive firing rate in voluntary contraction was not related to the threshold of motor units (Freund et al., 1975; Milner-Brown et al. 1973b). The mechanism for the almost same lowest firing rate was not very clear, though Renshaw inhibition was considered as a possible candidate (Freund, 1983).

With the increase of voluntary force, the firing rate of motoneurons increased over a considerable range (Monster and Chan, 1977; Freund et al., 1975; Milner-Brown et al., 1973b). The steady state maximal firing rates for slow contractions were between 20 and 35 impulses per second depending on the muscle and the recruitment threshold of the motor unit (Freund, 1983). In the first dorsal interosseous muscle, a linear relationship between the firing rate and force in the lower force region was observed (Milner-Brown, 1973b) though other experiments in different muscles showed different results. Freund et al. (1975), Person and Kudina (1972), and Monster and Chan (1977) found that the slope of firing rate versus force was higher at the lower force levels than at the higher force levels. When the force reached close to the maximum voluntary contraction, however, a higher increase of firing rate was observed again.

In intracellular experiments in cats, Kernell (1965c) found that the range of motoneuron firing rate was negatively related to the duration of AHP. In other words, the range of motoneuron firing rate was positively related to the size of motoneuron. However, in the human experiments, this was not always the case. It was observed that for the simultaneously recruited motoneurons, the lower threshold motoneurons fired at higher firing rates than larger ones in isometric contractions with intermediate contraction speed (Grimby and Hannerz, 1977; Deluca et al., 1985). Therefore, the lower threshold motor units are likely to fire in a wider range of firing rates than the higher threshold motor units. Monster (1979) observed that the lowest and highest firing rates of different motor units did not differ very much. Therefore, the firing range of motor units were approximately the same (Monster, 1979).

As mentioned before, the firing rate of motoneuron was linearly related to the force at lower force levels in some muscles. However, when the slope of the firing rate versus force was compared to the force threshold of motor units, different results were obtained. Monster (1979) found that the slope increased with the increase of threshold. This implied that a higher threshold motoneuron increases its firing rate more than a lower threshold motoneuron for the same change in force output. However, Milner-Brown et al. (1973) observed no relation and Freund et al. (1975) observed a negative correlation between the slope and the threshold.

II. Dynamic Responses of Motoneurons

a) Intracellular studies in cat

The dynamic responses of motoneurons have been studied by many authors when "step" or "ramp and hold" currents were injected into motoneuron soma. A motoneuron initially responds with a high instantaneous firing rate and then adapts to a lower firing rate during the hold period. Adaptation, which indicates dynamic response of a neuron, was first described by Granit (Granit et al. 1963) to explain the decrease of firing rate after the onset of injected step currents in rat motoneurons (Fig. 1.). Kernell (1965a,b; 1967) and Baldissera et al.(1975, 1982, 1984, 1987) systematically studied the phenomenon and mechanism of adaptation in cat motoneurons.

When step currents were injected into the soma of motoneurons, the motoneurons responded with high instantaneous firing rate which then decreased to a steady state repetitive firing rate. This adaptation in firing rate lasted from 2-3 intervals to 2 sec (Kernell 1965a,b). Step currents provide only one rate of current input. In order to examine the dynamic characteristics of motoneurons in detail, ramp and hold currents were used by Baldissera et al. (1982, 1985).

The instantaneous firing rate during the ramp exceeded that of the steady state level. The instantaneous firing rate increased during the whole ramp stimulus and was positively related not only to the current at that moment but also to the rate of rise of current. The higher the current slope, the higher the instantaneous firing rate. The slope of the instantaneous firing rate of the first interspike interval versus the rate of rise in current was defined as the dynamic sensitivity of motoneuron (Baldissera et al., 1982). The dynamic sensitivity was found higher in motoneurons with a longer duration of afterhyperpolarization (AHP) than in those with a shorter one (Baldissera et al., 1982). This suggests small motoneurons are more sensitive to the rate of rise of current.

Functionally, the dynamic response is very important in force generation (Baldissera et. al. 1975). It greatly enhance the muscle's ability for fast contraction. It was shown (Burke et al., 1970) that several short interspike intervals before a train of longer interspike intervals increased the speed of force generation considerably. Very short interspike intervals at the beginning of a spike train generated the force more rapidly and to a higher level than a train of stimulation with a same rate of steady firing (Baldissera et al., 1975). The mechanism of adaptation has been suggested to result from summation of AHP conductance (Baldissera et. al. 1982).

When a motoneuron is stimulated by a slowly rising current, sometimes, it does not generate a spike even if the current is larger than the rheobase for the motoneuron. The phenomenon of the increase in spike threshold by a slow rise of current was termed accommodation. Accommodation was first systematically studied by Araki and Otani (1959). Sasaki and Otani (1961) extended the work to cat by injecting slowly rising current and found two types of motoneurons. One with a higher threshold and a mean duration of AHP of 72 msec had a prominent sign of accommodation. This type of motoneurons actually was identical to large motoneurons and belongs to fast-twitch motor units. The other type of motoneurons with lower threshold and a mean duration of AHP of 102 msec did not show accommodation. This indicates that large motoneurons are easier to accommodate than small motoneurons. Accommodation is attributed to inactivation of Na^+ channels and activation of K^+ channels.

b) Single motoneuron responses under voluntary Contraction

In human subjects, dynamic properties of motoneurons firing were tested not for "known shapes of input currents" but for "controlled force trajectories". Tested by triangular profiles of isometric force, an increase in firing rate during the entire ramp period of force was observed by many authors (Person and Kudina, 1972; Milner-Brown et al. 1973b). The firing rates of motoneurons increased with the increase of contraction velocity. To distinguish clearly between the phasic and steady state responses of motoneurons in voluntary contraction, Tanji and Kato (1981) tested the activity of motor units using "ramp and hold" force trajectories. Each ramp started from zero force level and reached the maximum voluntary force at different speeds. They observed that the firing rate of motoneurons increased to a peak after being recruited and then decreased to a steady level. The higher the contraction speed, the higher the maximal instantaneous rate after the recruitment of motoneuron. In other words, the dynamic response of motoneuron in voluntary contraction is determined not only by desired force but also the desired contraction speed. At higher speed of contraction, the units became active earlier and had a lower force threshold (Milner-Brown et al., 1973b; Tanji and Kato, 1973; Freund et al., 1975).

Palmer and Fetz (1985) investigated the dynamic and steady state properties of motor units of wrist flexors in relation to "ramp and hold" force output in monkeys. They categorized motor units (MUs) into four types depending on different firing patterns: "phasic-tonic", "tonic", "decrementing" and "phasic". "Phasic-tonic MUs exhibited a phasic burst of activity during the torque ramp which exceeded the firing rate during the static hold period. Both phasic-tonic and tonic MUs exhibited a constant mean firing rate during the hold period; the discharge of decrementing MUs gradually decreased during the static hold. Phasic MUs fired only during the change in force." (Palmer and Fetz, 1985)

In Palmer and Fetz's experiment, although there was some evidence of different firing patterns of the same motor unit, they suggested that different firing patterns of motor unit discharge were the characteristics of motoneuron instead of depending on different contraction conditions. Several points should be mentioned about their experiments. Since they used monkeys as subjects, they did not get enough control of either the contraction speeds or the force output levels. Therefore, the comparison of different firing patterns of the same motoneuron under different conditions, such as different contraction speeds and force output levels, seemed impossible. Besides, their argument of the relation between the four types of primate corticomotoneuronal cells and the four kinds of a-motoneurons in spinal cord has less anatomical and physiological evidence of one to one representation. Furthermore, the background firing of motor units, which may affect the firing patterns of motor units, was not controlled in their experiment.

The phasic, and, phasic and tonic firing patterns were also observed in human subjects during "ramp and hold" force output (Gillies, 1972; Tanji and Kato, 1973). The firing rate of motoneuron increased in ramp period with an overshoot, then adapted to a steady state firing rate or ceased firing during the hold period. The higher the rate of rise of force, the higher the overshoot, the more the phasic firing motoneurons.

Grimby and Hannerz (1977) found that motor units with continuous firing pattern fired continuously throughout the force output while motor units with intermittent firing patterns fired only during the change of force. They observed that intermittent and continuous firing pattern could interchange in the same motor units under different speeds and strengths of force generation. If the contraction speed was very high but the destination force was not very strong, many motor units would fire intermittently during the ramp period of force then stop firing in the hold period of force. The threshold in the hold period was defined as tonic threshold. The results suggested that most motoneurons, except those with lowest threshold, were able to fire with different patterns, namely tonic or phasic, according to the strength of force and the contraction speed (Gillies, 1972; Freund et al., 1975; Grimby and Hannerz, 1977; Borg et al., 1978).

III. Surface Electromyography under Voluntary Contraction

Needle electrodes successfully and accurately record properties of single motoneuron or single motor units but fail to show the excitation level of the motoneuron pool as a whole. In human experiments, when force output rather than intracellular current to one motoneuron is controlled, population response of motoneurons may be better related to the force than the response of a single motor unit.

Surface electromyography (EMG) is a noninvasive method to record muscle activity and widely used in studies of human muscle activities. EMG, actually, is the spatial and temporal summation of action potentials of all active muscle fibers under surface electrodes. EMG informs about the overall excitation of one muscle or several muscles under study. Since there is one to one representation of muscle action potentials and the action potentials in motoneurons, EMG also shows the overall activity of motoneurons in the motoneuron pool. The magnitude of EMG is mainly determined by recruitment and the firing rate of motoneurons. The more motoneurons recruited and the higher their firing rates, the higher the EMG. The factors which also affect surface EMG include the distance between muscle fibers and the surface, the contributions to EMG from other muscles and the arrangement of electrodes.

The relationship of steady state EMG versus force was studied by keeping the force output steady for a period or during slow increases of force (Lawrence and Deluca et al., 1982a; Milner-Brown and Stein, 1975). It was shown that integrated EMG increased with the increase of force in all muscles. The relation of force and integrated EMG showed linear or nonlinear relationship in different muscles under study. A quasi linear relation was observed in first dorsal interosseous muscle while the relation was nonlinear for biceps and deltoid (Lawrence and Deluca et al., 1982a; Milner-Brown and Stein, 1975).

For slow ramp increases of force, EMG increased continuously during the ramp period. For contractions at high speeds, EMG formed a discrete burst. The onset time of EMG was much earlier than the onset time of force, and force continued to rise during the EMG silent period (Ghez and Gordon, 1987). In isotonic contractions, EMG, on the other hand, was related to movement velocity. In calf muscle under isotonic contraction, the relationship of EMG versus force was linear while the slope of the relation changed with different force modes (Bigland and Lippold, 1954). In muscle shortening at a constant velocity, slope of the EMG versus tension was higher than that in muscle lengthening. This implied that, for the same force output, shortening muscle needed more muscle activity than lengthening muscle at the same tension output (Bigland and Lippold, 1954).

IV. Summary

Motoneurons respond to steady synaptic or injected currents with steady firing rates. Steady state firing rates increase linearly with currents. The increase of firing rate in motoneurons increases the force output of motor units. During the dynamic phase of motoneuron response, the firing rate of motoneuron shows an overshoot above the steady state phase. The dynamic firing pattern enhances the muscle contraction speed and is one of prominent factors for high speed voluntary contraction.

In voluntary isometric contractions, the steady state firing rate of a motor unit is positively related to the force level. During the dynamic phase, the maximal firing rate is related to not only the desired force but also the desired contraction speed. The higher the contraction speed, the higher the over shoot in the motoneuron firing rate.

Surface EMG activity is also related to the contraction amplitudes and contraction speeds. A positive relation has been observed between the surface EMG activity and the force output of muscle. A high contraction speed is accompanied by a peak in surface EMG before or during the build up of force.

OBJECTIVES

Prior studies in man have established a proportionate relation between surface EMG and force output in both dynamic and steady state conditions (Lawrence and Deluca et al., 1982a; Milner-Brown and Stein, 1975; Bigland and Lippold, 1954; Brown and Cooke, 1980). Discharge patterns of underlying single motor units show that for ramp and hold contractions, motor units respond with a dynamic phase and a steady state phase. No study has related the firing patterns of SMUs to both the surface EMG and force output.

The main objective of the following study was to relate the firing patterns of single motor units to the surface EMG activity and force output. How does the activity of single motor units lead to the linear relationships between surface EMG and force both during the dynamic and the steady state phases of isometric contractions?

The linearity of EMG responses holds irrespective of the background activity. How do changes in background activity of single motor units change their responses during dynamic and steady state phases?

METHODS

Seven volunteer subjects (4 male and 3 female) participated in these experiments. They ranged in age from 22-45 years and were free of any known neuromuscular disorders. The experiments were approved by the Ethics Committee for Human Experiments at Simon Fraser University. Each subject signed the Ethics Consent form.

Data Collection

The main purpose of the experimental protocol was for the subject to trace isometric force trajectories by activating wrist flexor muscles. To achieve this, the subject was seated with his right forearm supported by a padded horizontal platform (Fig. 2.). The right forearm rested on the platform such that the axis of rotation of the wrist was kept vertical to the platform. The wrist was further clamped to avoid lateral movement of wrist. A vertical handle was placed in front of the subject's palm at the metacarpi-phalangeal joint. The subject exerted isometric force against the handle with wrist flexion while the fingers were relaxed. Force of wrist flexion, surface electromyography (EMG) activity of the wrist flexors and single motor unit (SMU) activity from the flexor carpi radialis (FCR) muscle were recorded for off line analysis.

Strain gauges (EA-13-250MQ-350) were attached to a horizontal bar attached to the vertical handle. The signal from the force gauges were fed to a bridge amplifier (Vishay Instrument, DC-1000 Hz band pass). The force signal after amplification was displayed on an oscilloscope, which was placed at a reasonable distance (around 1.5 meters), for visual feedback to the subject.

Surface EMG activity was recorded from the wrist flexors using two Ag-AgCl electrodes (8 mm in diameter). These electrodes were placed 2 cm apart on the skin over

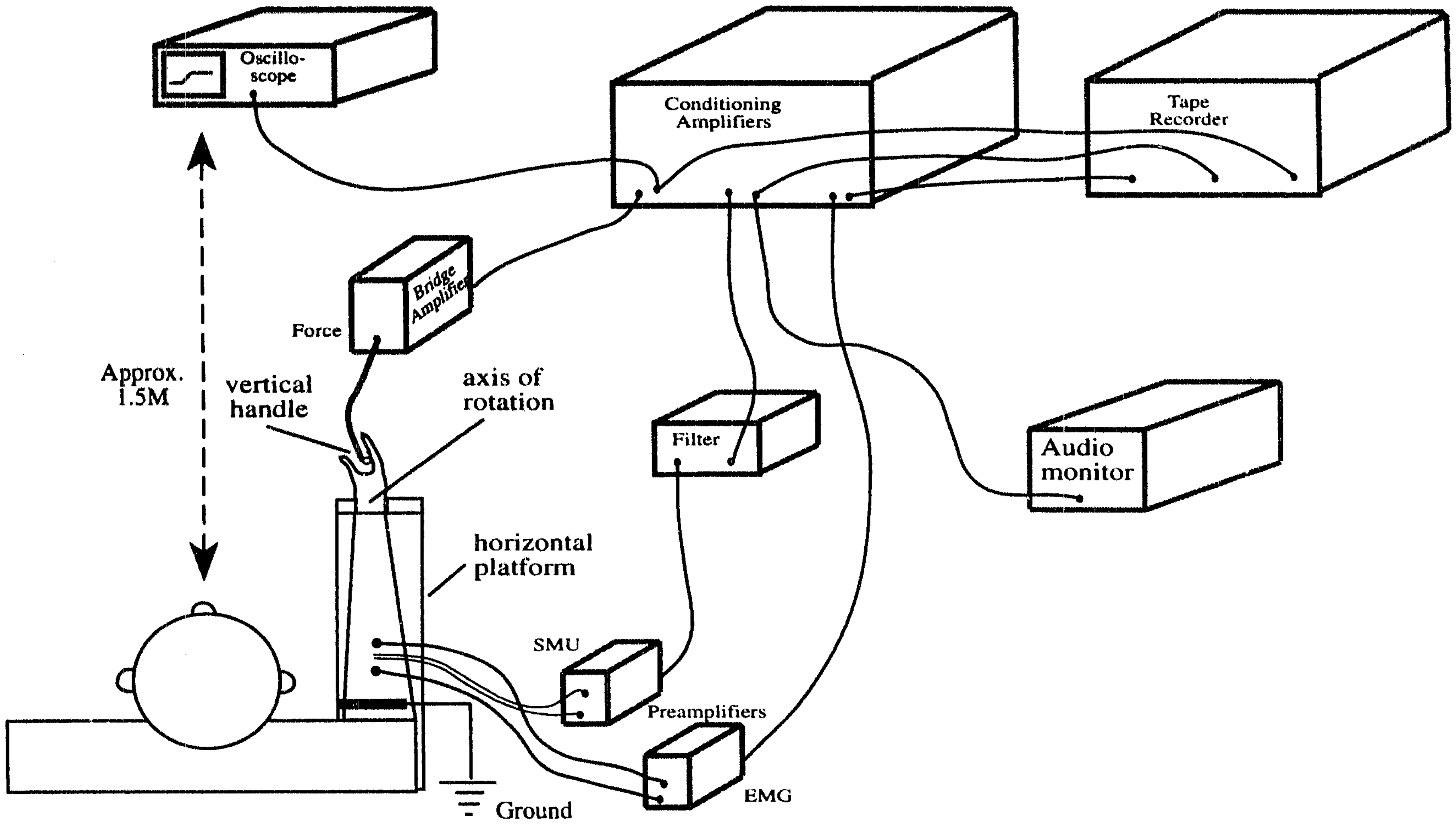

Fig. 2. The block diagram for data collection. The subject exerted force to the vertical handle while the force was displayed on an oscilloscope for feedback. The single motor unit (SMU) and surface electromyography (EMG) activities were collected from flexor carpi radialis (FCR) muscle and amplified before being recorded on to a tape recorder. The SMU action potentials were also forwarded to an audio amplifier for the ease of controlling background firing rate.

FCR muscle. The signal was fed to a preamplifier (Grass P15 AC, 30Hz-3KHz band pass). The amplified signal was forwarded to a conditioning amplifier.

Single motor unit (SMU) action potentials were recorded from FCR with the help of bipolar intramuscular electrodes. The electrode consisted of two Teflon coated stainless steel wires (75 micrometers in diameter). The wires were embedded within the barrel of a needle (25 gauge) with epoxy (Calancie and Bawa, 1985). The action potentials were fed to a preamplifier (Grass P15 AC, 100Hz-10KHz band pass). To filter more low frequency noise such as 60 Hz signal, a filter (Wavetek Rockland, set 100Hz high pass) was used to improve the signal clarity when needed. The high pass filtered action potentials were amplified using a conditioning amplifier. The action potentials were then displayed on an oscilloscope for visual feedback and fed to a loudspeaker for audio feedback. With the help of audio and visual feedback, the subject could control the activity of SMUs under study.

The force, surface EMG and single motor unit action potentials were recorded on a video tape recorder (Sony SLV-555UC) using Vetter Digital PCM Recording Adapter 4000A or an 8 channel instrumentation tape recorder (HP 3968A) for off-line analysis.

Procedures

After all the electrodes were in place, the subject first had a period of training (5-15 minutes) so he/she could trace the required force trajectories comfortably. The subject was asked to recruit and maintain one or two distinct motor units. If there were more than one motor units recruited, the motor units were labeled according to their recruitment thresholds. These SMUs could be distinguished by their shapes and amplitudes.

As shown in Figure 3, four different force trajectories were traced by the subject. For the fast trajectories F(0-1; 0-2), the subject was instructed to contract wrist flexors as fast as possible from baseline level (0) by one step [F(0-1)] or two steps [F(0-2)]. The magnitude of the step was determined by the convenience of each subject. For the slow trajectories, the subject traced a known force trajectory indicated on the oscilloscope keeping the same amplitude of contraction as for the fast contractions. Level zero of the trajectory was not zero force because with a tonically firing SMU, it is impossible to have a silent muscle.

For motor unit recording, the subject was asked to control the background firing rate with the help of audio and video feedback and then, superimpose contraction of the muscle on the controlled background firing rate of the SMU under study. When examining the effect of the background firing rate on the dynamic properties of the motoneuron, the subject maintained the motor unit discharge at two distinct rates.

Analysis

All data were analyzed using a 486 PC computer, a CED (Cambridge Electronics Design Co.) 1401 computer interface and CED software, SIGAVG and SPIKE2. In order to average all the responses in each condition, the rising phase of force record was discriminated at certain level, usually at the middle of force trajectory, to generate a trigger signal (trigger TTL) for the computer interface. This trigger signal was used for averaging the surface EMG, the SMU activity and the force records. Since the trigger occurred during the rising phase of the force, pretrigger time was used in order to average pretrigger phase or the baseline activity.

The force and surface EMG were collected on computer using CED software SIGAVG (sample rate 1000Hz) (Fig. 4.). EMG was rectified while being collected. For the fast contractions, the pretrigger time was generally 1.5 seconds while the total acquisition time was 4 seconds. For slow contractions, the pretrigger time was 2.5 seconds while the total acquisition time was 7 seconds. All data were saved on hard drive and reviewed for appropriate responses. The inappropriate sweeps (e.g. when the contraction

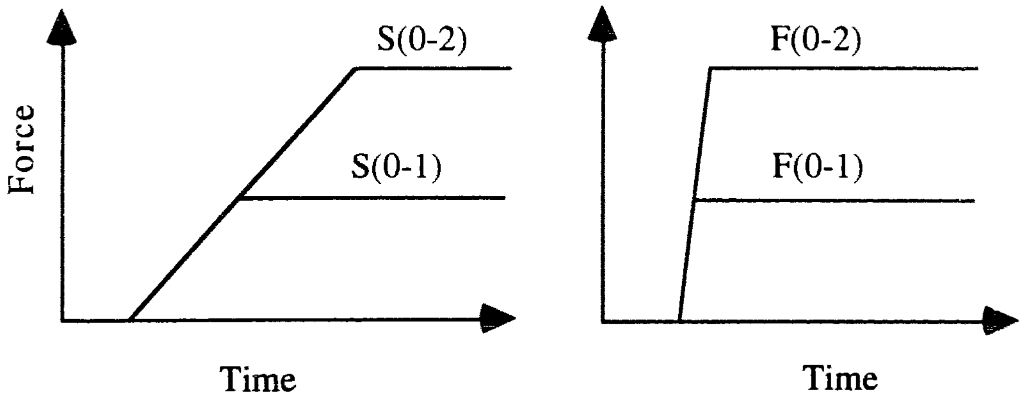

Fig. 3. The force trajectories for experiments. Force 0 was the background force (not zero force). The amplitude from force 0 to force 2 was twice as large as that from force 0 to force 1. In fast contractions, the subject was asked to contract as fast as possible while in slow contractions, subject traced "ramp and hold" force trajectories on the scope with a significantly slower speed in the ramp phase.

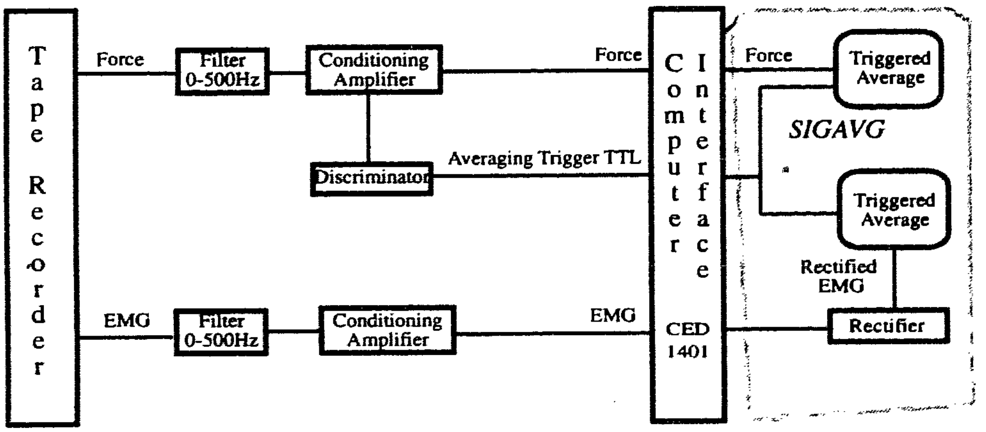

Fig. 4. Block diagram for surface EMG and force processing. Raw EMG and force were acquired through computer interface CED 1401 according to each trigger signal. EMG was rectified by software SIGAVG right after being acquired. Then, the appropriate sweeps of force and the appropriate sweeps of rectified EMG were averaged.

was of wrong duration or amplitude) were rejected and the rest of the data were averaged to generate averaged force and averaged surface EMG records.

SMU action potentials were discriminated to produce TTL pulses (Fig. 5.). The trigger TTL pulses from force were used for averaging SMU responses. During fast contractions, either some action potentials of motor units other than the one under study were discriminated or some action potentials of the motor unit under study were not discriminated. To correct such errors, raw SMU and force data were collected on A/D channels while the TTL pulses representing SMUs and force triggers were collected on digital channels. The sample rate for the channel acquiring the SMU raw data was set at 10 KHz. The sample rate for the channel acquiring force was set at 1 KHz. After acquisition, all the data were reviewed with SPIKE2 software. According to distinct shapes of different motor unit action potentials, the TTL channels were corrected by adding missing TTL pulses and deleting incorrect TTL pulses in the array of pulses representing action potentials.

The following histograms were constructed from the SMU responses. To determine mean firing rates, first order interval histograms were constructed (200 bins, 1 ms bin width). In order to average patterns of SMU firing related to contraction, two kinds of histograms were constructed. Peri-Stimulus Time Histograms (PSTHs) were computed using the force TTL as stimulus (1 ms bin width, pretrigger time and sweep duration were the same as those for EMG analysis). Using the same TTL, average response histograms (ARHs) of instantaneous firing rates were constructed. To construct the ARH of instantaneous firing rate, the instantaneous firing rate for each trial was calculated by the inverse of interspike intervals (Fig.5b). Average response histogram of the instantaneous firing rate was constructed using force TTL. The pretrigger times, the total processing time and bin width were the same as those in PSTH construction.

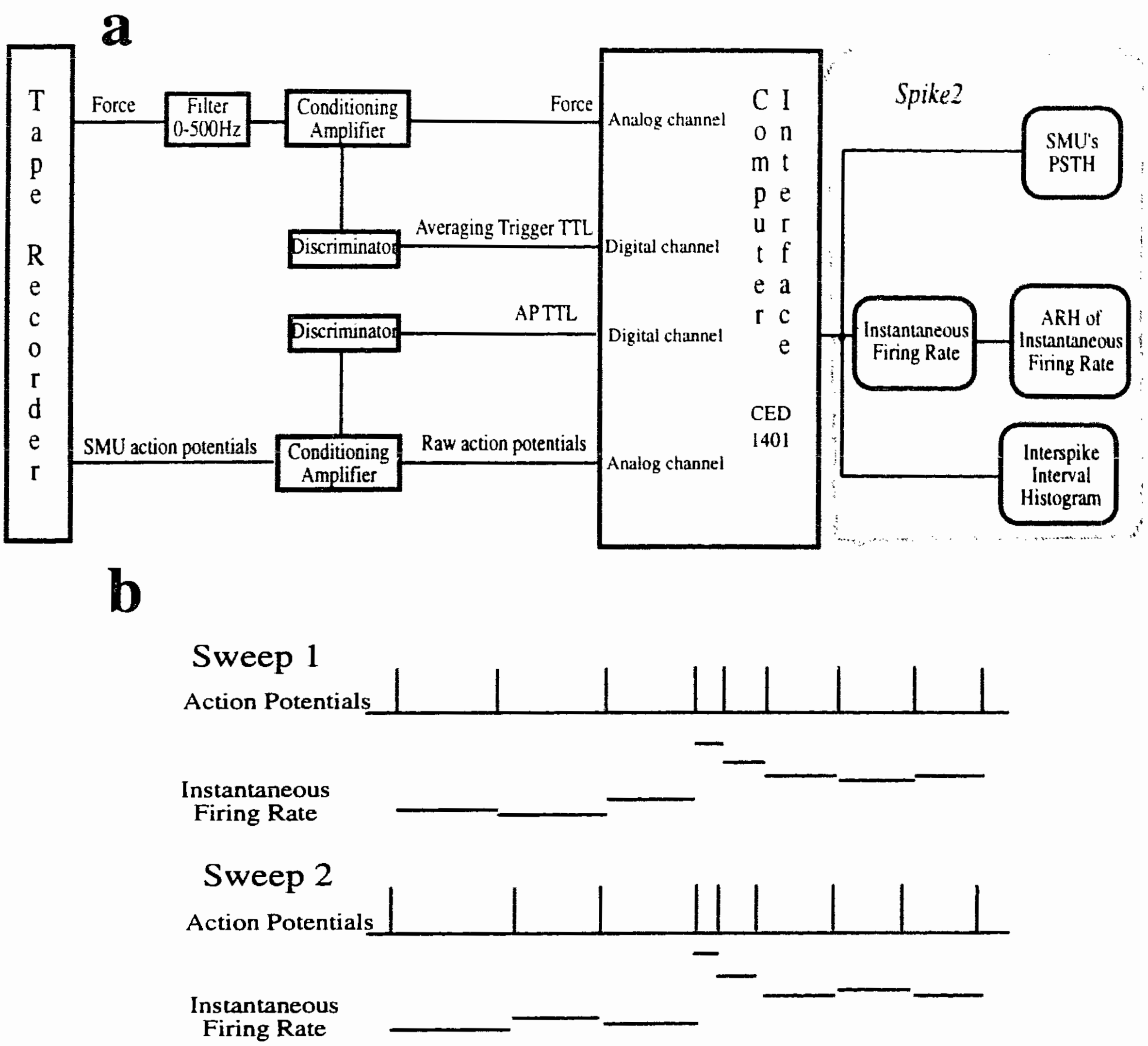

Fig. 5. (a) Block diagram for signal processing of SMU activity. Force and SMU raw action potentials were acquired through two A/D channels on CED 1401. The TTL pulses for SMUs and force were acquired on two digital channels on CED 1401. The TTL signals were corrected in SPIKE2 software off-line. TTL SMU signals were used to establish Interspike Interval Histogram (ISIH), Peri-Stimulus Time Histogram (PSTH) and Averaged Response Histogram (ARH) of SMU instantaneous firing rates. (b) Two sweeps are illustrated to show timings of action potentials (SMU spikes) and corresponding interspike intervals below.

The magnitude of contraction, A, (Fig. 6.) was obtained by subtracting the averaged background force (FB) from the averaged maximal steady state force (FS). The rate of change of force was obtained by

$$R = \frac{\Delta F}{\Delta t} = \frac{F(90\%) - F(10\%)}{\Delta t}$$

where F(90%) is the force level of (FB+90%A), F(10%) the force level of (FB+10%A), and Δt the time difference between the time of F(90%) and the time of F(10%) (Fig. 6). Because of the noise in the force trace, df/dt was not obtained by differentiating the force trace.

Due to the dynamic properties of a motor unit, a peak was observed in the averaged rectified EMG or SMU activity. For EMG activity, moving averages (in SIGAVG, 5 points, 3 times) were applied to it before the peak value was obtained. For SMU activity, the peak in ARH of instantaneous firing rates was much clearer than that in PSTH. Therefore, ARHs of instantaneous firing rate were considered better indicators of dynamic activity of a motor unit, and were used to compute dynamic and steady state properties of SMU activity. From EMG and SMU histogram, three parameters were measured: background activity B by averaging at least 1200 ms of the background; steady state level S by averaging over at least 1500 ms during the steady state and the peak value P. Then the following parameters were calculated for both EMG and SMU activities:

Absolute dynamic response amplitude = P-S,
Normalized dynamic response amplitude = (P-S)/R
Steady state response amplitude = (S-B)/A.

The absolute dynamic response amplitude (ADRA), the normalized dynamic response amplitude (NDRA) and the steady state response amplitude (SSRA) of SMUs were compared and statistical analysis were carried out for the following conditions: (i). the same motor unit for two different contraction speeds; (ii). the same motor unit for two

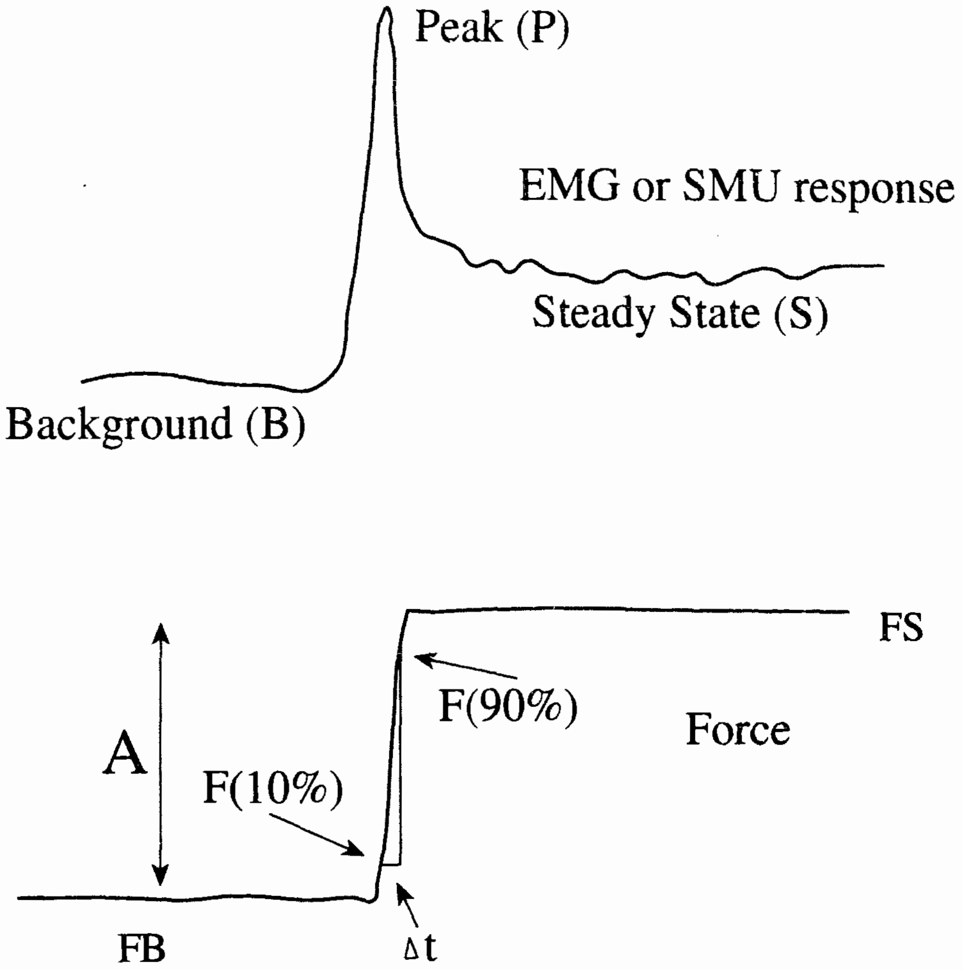

Figure 6. Schematic diagram for averaged response histogram of rectified EMG or SMU activity is shown in the top while the corresponding force trajectory is shown in the lower trace. The amplitude of contraction is given by A. F(10%) is the force at 10% of the A and F(90%) is the force at 90% of A. Δt is the time taken from F(10%) to F(90%). For EMG or SMU activity, B is the average background, P is the peak value while S is the average steady state value of the averaged histogram.

different force magnitudes; (iii). the same motor unit at two different background firing rates; (iv). pair of different threshold motor units recorded simultaneously. The ADRA, NDRA and SSRA of surface EMG were compared for condition (i) and (ii) only.

Statistical Analysis

The mean values of the quantified SMU and EMG activities, which were the ADRA, NDRA and SSRA of motor units and EMG, were compared under each condition. T-test was used since it is a statistical test for mean values. In the four sets of comparisons for SMU and two comparisons for EMG mentioned before, the comparisons were between either SMU or EMG activities of two constraints on the same motor unit or same constraint but two different threshold motor units. Therefore, the paired t-test was used for the purpose. The formula for the paired t-test is:

$$t = \frac{\frac{\Sigma d}{n}}{S_{\bar{d}}} = \frac{\frac{\Sigma d}{n} \bullet \sqrt{n}}{\sqrt{\frac{\Sigma\left(d - \frac{\Sigma d}{n}\right)^2}{n-1}}}$$

where d is the difference between SMU or EMG activities of two constraints or two different threshold SMUs in each condition; $S_{\bar{d}}$ is the standard error of mean of d; n is the number of samples used for comparison.

Paired T-test on Microsoft Excel Macros was used to compare single motor unit behaviours and EMG activities across pairs of conditions. A null hypothesis, that was there was no difference between the mean values of single motor unit behaviours (or EMG activities) across pairs of constraints, was made. With the t value calculated by the above formula and (n-1) degree of freedom, P value was obtained. The hypothesis was rejected if the p value was smaller than 0.05. In other words, mean values were considered significantly different at $p<0.05$.

RESULTS

I. General:

Data for surface EMG activity were obtained from a total of 60 separate conditions of 15 experiments with 6 subjects. Of these 60 conditions, 13 of them were for slow contractions, 34 of them for F[0-1] contractions and 13 of them for F[0-2] contractions. EMG data have been categorized into 2 groups for comparisons, (i) slow contractions to fast contractions i.e. S(0-1) to F(0-1), and (ii) fast contractions of different amplitudes i.e. F[0-1] contractions to F[0-2] contractions.

The response characteristics of SMUs were analyzed from 43 motor units in 23 experiments with 7 subjects. There were a total of 113 averaged responses. Of these 113 histograms, 88 were for tonically firing motor units and the rest, 25, for phasic responses. In the 88 sets of data for tonically firing units, 20 of them were recorded for S(0-1) force trajectories, 50 of them in F(0-1) force trajectories, the rest, 18, of them in F(0-2) trajectories. In the 25 sets of data for phasically firing units, 3 of them were recorded in S(0-1) force trajectories, 14 of them in F(0-1) force trajectories, the rest, 8, of them in F(0-2) trajectories. The SMU data were categorized into four groups for comparisons: (i) same SMU in slow and fast contractions, (ii) same SMU in fast one and two division contractions, (iii) same SMU with different background firing rates, either two non zero rates or zero and non zero rates, and (iv) two SMUs recorded simultaneously. The results of comparisons were summarized in Appendix: SMU Results Table.

Forces used in these experiments were relatively low. For 77 of different one division conditions (both fast and slow) the amplitudes ranged from 0.283 N to 2.522 N with a mean of 1.23 N. In 22 of two division conditions (only in fast contraction speed) the amplitudes ranged from 1.522 N to 4.806 N with a mean of 2.57 N. When rates of contraction were calculated, they were significantly different not only between slow and fast contraction conditions but between F[0-1] and F[0-2] conditions also. The rates for slow contractions ranged from 0.26 to 5.50 with a mean of 1.16 N/s. The rates for the F[0-1] contractions ranged from 1.39 to 34.42 with a mean of 9.28 N/s. The rates for F[0-2] contractions ranged from 7.85 to 31.95 with a mean of 18.54 N/s.

II. Surface EMG Responses

At high contraction rates, the average rectified surface EMG showed a large overshoot during its dynamic phase. The peak of EMG appeared around the start of trajectories (Fig. 7.). When muscle contracted at a slower speed with the same amplitude, the average rectified surface EMG showed same activity for the steady state. In the dynamic phase, however, the overshoot was much smaller or even hard to detect (Fig. 7.).

a) EMG responses in slow and fast contractions

A total of 12 pairs of average rectified EMG were used for comparison. For the rest of the data, EMG amplitude was small, and hence, signal-to-noise ratio was poor. Averages were not obtained for such records. Absolute Dynamic Response Amplitude, Normalized Dynamic Response Amplitude and Steady State Response Amplitude of surface EMG were calculated and compared. Paired t-tests were carried out for each comparison.

Absolute Dynamic Response Amplitude. The Absolute Dynamic Response Amplitude (ADRA) of average rectified surface EMG in fast contraction conditions ranged from 4.7 μV to 62.9 μV with a mean of 16.65 μV. The ADRA of EMG in slow contraction ranged from 0.3 μV to 10.5 μV with a mean of 1.67 μV. Paired t-test showed that the mean ADRA of fast contractions was significantly different from that of slow contractions at level of $p \leq 0.02$. This result indicates that the dynamic activity of motoneuron pool

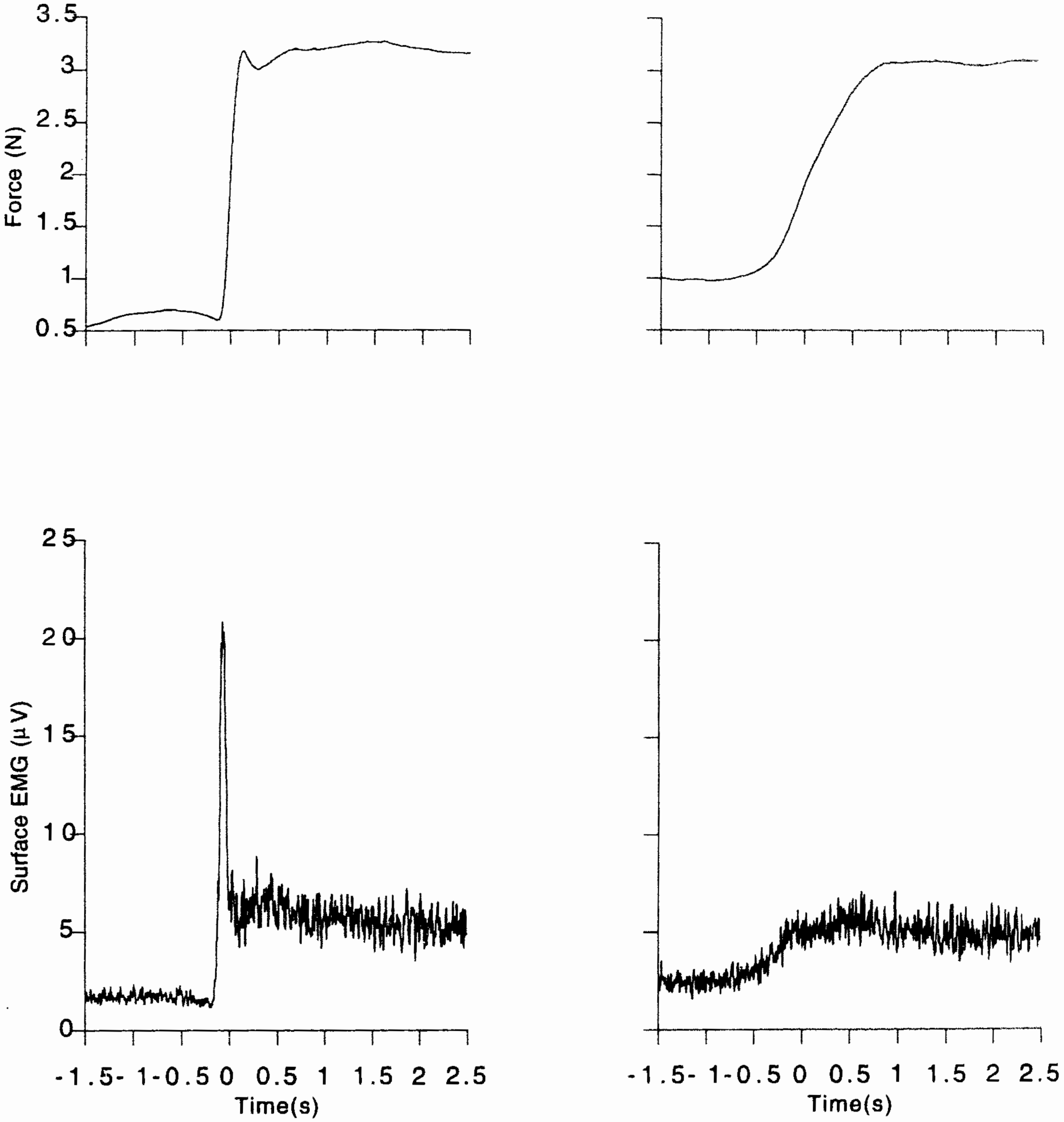

Fig. 7. The force trajectory (top)and surface EMG (bottom) in fast contraction (left) and slow contraction (right). The lower figure is the typical average responses of EMG (28 sweeps for the left one and 29 sweeps for the right one, 5 points moving average applied three times) Subject: SF.

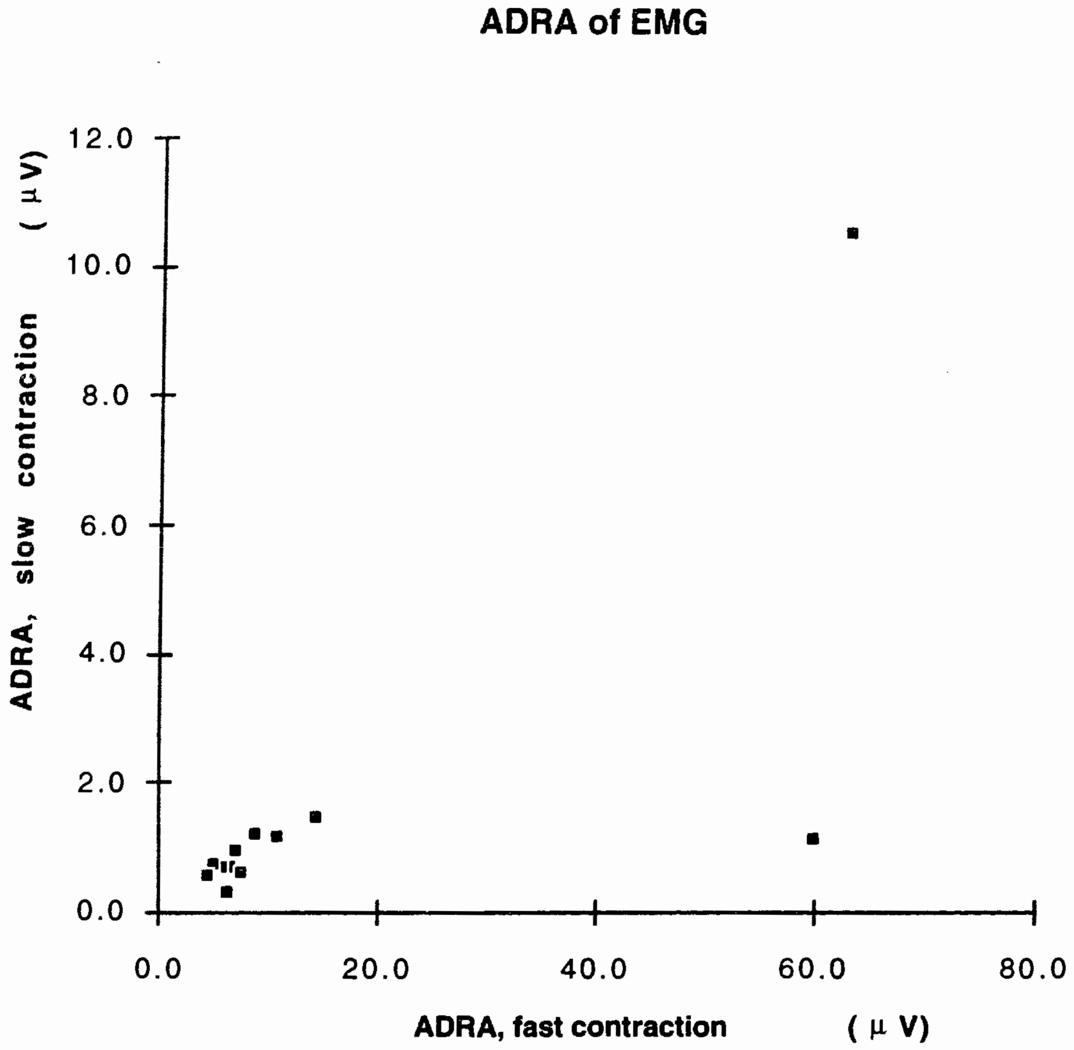

Fig. 8. Comparison of Absolute Dynamic Response Amplitude (ADRA) of EMG in fast and slow contractions. ADRA in fast contractions is much larger than that in slow contractions.

increases with the increase of contraction speed. The higher the contraction speed, the larger the dynamic activity of the motoneuron pool. The results are shown in Fig. 8.

Normalized Dynamic Response Amplitude. Since the magnitude and the rate of contraction varied for each condition and from experiment to experiment, dependence on the rate of contraction was computed by normalizing ADRA with the speed of contraction. The Normalized Dynamic Response Amplitude (NDRA) of average rectified surface EMG in fast contractions ranged from 0.8 μV/(N/s) to 4.5 μV/(N/s) with a mean of 1.64 μV/(N/s). The NDRA of EMG in slow contractions ranged from 0.2 μV/(N/s) to 7.9 μV/(N/s) with a mean of 1.67 μV/(N/s). Paired t-test showed that the mean NDRA of fast contractions was not significantly larger than that of slow contractions at level of $p \geq 0.49$. This result indicates that the dynamic activity of EMG increases linearly with the increase of contraction speed. The results are shown in Fig. 9.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of average rectified surface EMG in fast contraction conditions ranged from 0.7 μV/N to 6.9 μV/N with a mean of 2.30 μV/N. The SSRA of EMG in slow contraction conditions ranged from 0.6 μV/N to 6.1 μV/N with a mean of 2.28 μV/N. Paired t-test showed that the mean SSRA of fast contractions was not significantly different from that of slow contractions at level of $p \geq 0.93$. The SSRA of fast contraction and that of the slow contraction was highly correlated ($r=0.94$). This result indicates that the SSRA of motoneuron pool was not related to the contraction speed but only to the contraction amplitude. The results are shown in Fig. 10.

b) EMG in F[0-1] and F[0-2] contractions

The following results were obtained from the data of F[0-1] and F[0-2] contractions. As mentioned in general part of the results, the contraction speeds of F[0-2] contractions were much larger than those of F[0-1] contractions. On the average, the

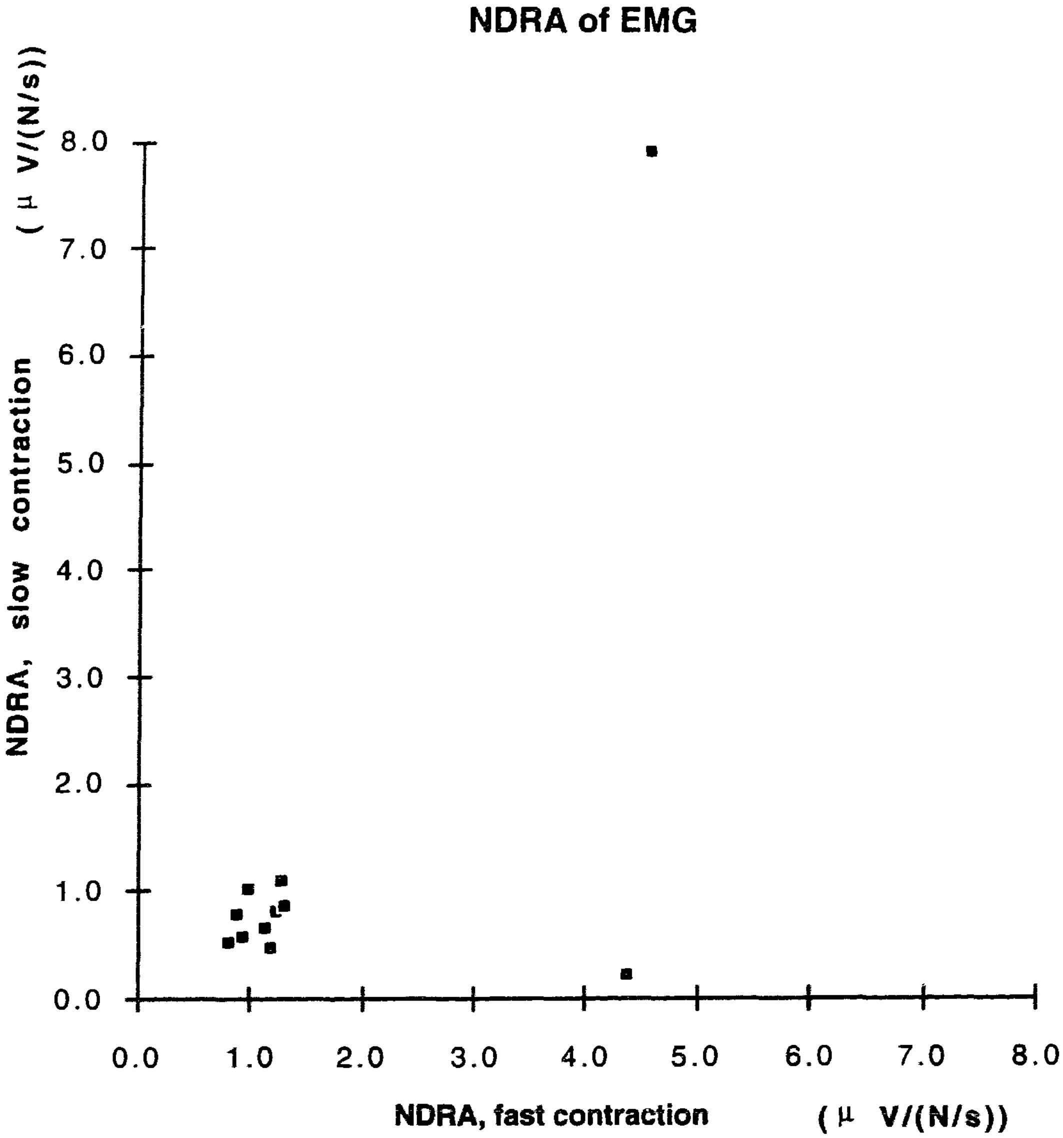

Fig. 9. Normalized Dynamic Response Amplitude (NDRA) of EMG in slow and fast contraction. No significant difference was observed in the means of NDRA for the two conditions.

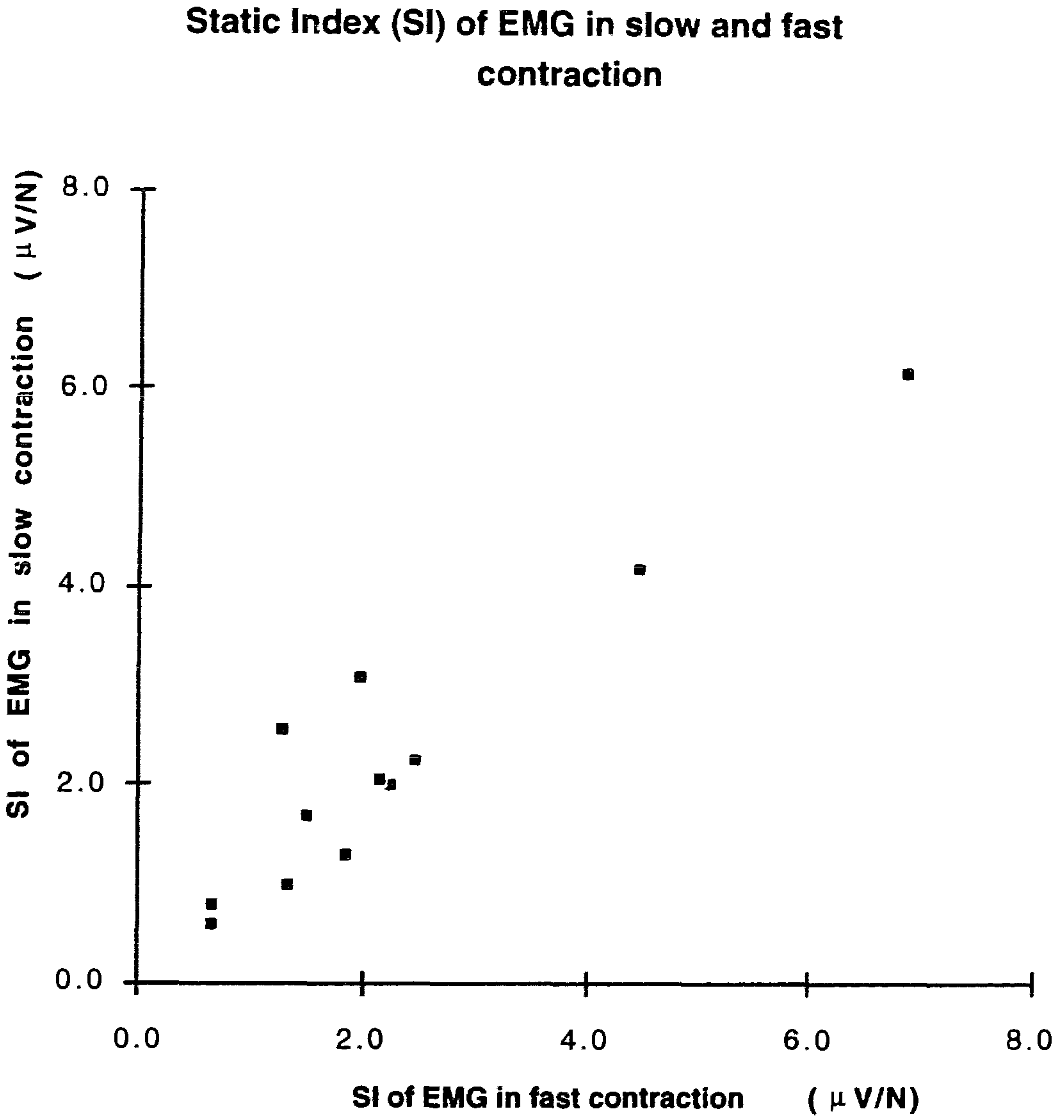

Fig. 10. Steady State Response Amplitude (SSRA) of EMG in slow and fast contractions. The data is highly correlated (r=0.94). There is no significant difference between the SSRA of EMG in slow contraction and that in fast contraction (paired t-test, p=0.933).

former were 1.9 times as large as the latter. At the same time, the effects of amplitudes on the Steady State Response Amplitude could be assessed. A total of 12 pairs of averaged rectified EMG were used for comparison. Absolute Dynamic Response Amplitude, Normalized Dynamic Response Amplitude and Steady State Response Amplitude of surface EMG were calculated and compared.

Absolute Dynamic Response Amplitude. The Absolute Dynamic Response Amplitude (ADRA) of average rectified surface EMG in F[0-1] contraction ranged from 3.1 μV to 97.5 μV with a mean of 34.16 μV. The ADRA of EMG in F[0-2] contractions ranged from 14.1 to 87.4 μV with a mean of 46.63 μV. Paired t-test showed that the mean ADRA of EMG in F[0-1] contractions was significantly smaller than that in F[0-2] contractions at level of $p \leq 0.0046$. The results are shown in Fig. 11.

Normalized Dynamic Response Amplitude (Normalized with contraction speed). The Normalized Dynamic Response Amplitude (NDRA) of average rectified surface EMG in F[0-1] contractions ranged from 0.4 μV/(N/s) to 4.5 μV/(N/s) with a mean of 2.78 μV/(N/s). The NDRA of EMG in F[0-2] contractions ranged from 0.7 μV/(N/s) to 5.8 μV/(N/s) with a mean of 2.94 μV/(N/s). Paired t-test showed that the mean NDRA of EMG in F[0-1] contractions was not significantly different from that in F[0-2] contractions at level of $p \geq 0.64$. This result indicates that the dynamic activity of motoneuron pool increases with the increase of contraction speed. However, NDRA, which equals ADRA divided by contraction speed, was not related to the contraction speed. This implies that motoneuron pool dynamic activity, quantified by ADRA, kept linear even when contraction speed increase further from F[0-1] to F[0-2] contractions. The results are shown in Fig. 12.

Normalized Dynamic Response Amplitude (Normalized with amplitude). During ballistic contractions, it was found that the time taken to complete the contraction kept constant (Freund and Budigen, 1979). In the range of contraction speeds

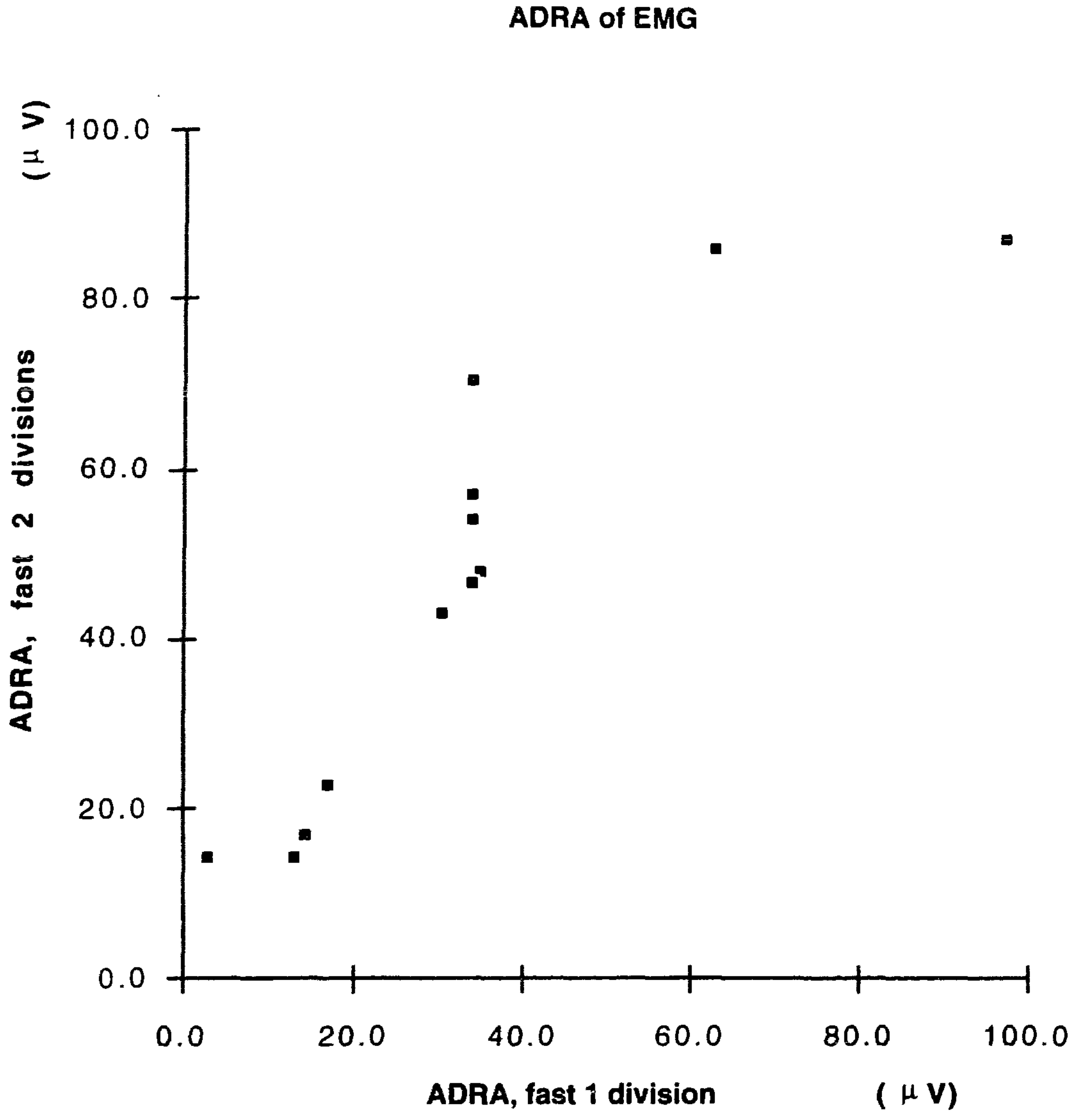

Fig. 11. Absolute Dynamic Response Amplitude (ADRA) of EMG in fast 1 division and fast 2 division contractions. The contraction speed of fast 2 division was 1.9 times as large as that of the fast 1 division contraction. As the result, the mean ADRA of EMG in fast 1 division is smaller than that in fast 2 division. Paired t-test shows a significant difference with p value of 0.0046.

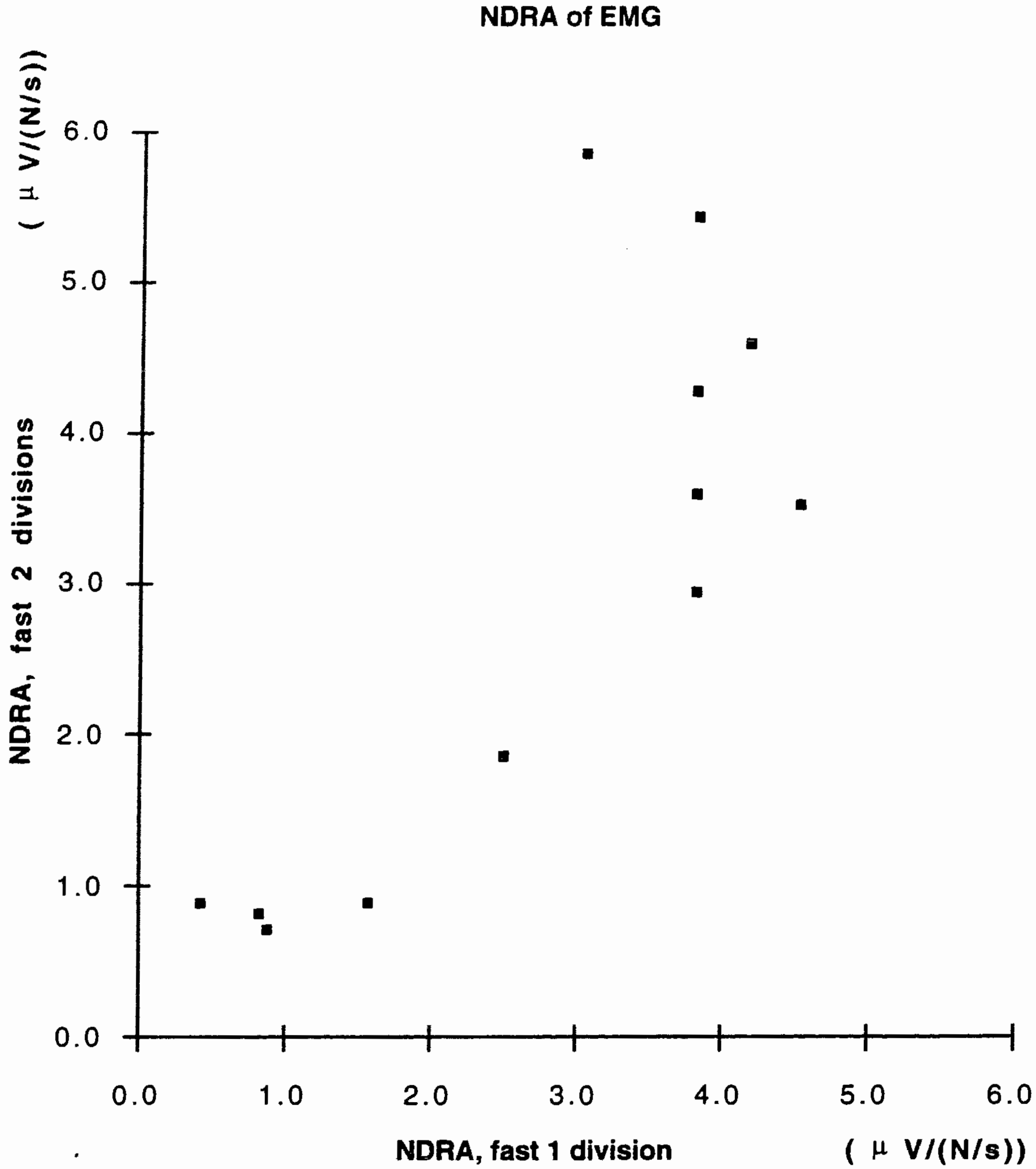

Fig. 12. Normalized Dynamic Response Amplitude (NDRA) of EMG in fast 1 division and fast 2 division contractions. No significant difference was observed in the data (paired t-test, p=0.64).

of our experiments, the contraction speed increased linearly with the amplitude of contraction during "as fast as possible" contractions. To test the relation between the dynamic activity of EMG and amplitude, ADRA of surface EMG was divided by amplitude of contraction. When the values in F[0-1] and those in F[0-2] were compared, no significant difference was observed. The results were shown in Fig. 13.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of average rectified surface EMG in F[0-1] contractions ranged from 0.7 μV/N to 9.0 μV/N with a mean of 5.05 μV/N. The SSRA of EMG in F[0-2] contractions ranged from 1.0 μV/N to 10.6 μV/N with a mean of 4.29 μV/N. Paired t-test showed that the mean SSRA of F[0-1] contractions was not significantly different from that in F[0-2] contractions at level of $p \geq 0.13$. This result supports the result that the static activity of motoneuron pool is not related to the contraction speed but only to the amplitude of contraction. Further more, it also indicates that for FCR muscle at the low force level, the static activity of motoneuron pool is linearly related to the contraction amplitudes. The results are shown in Fig. 14.

III. Single Motor Unit Firing Patterns

Overall, when muscle contracted at high speed, the SMU activity showed a large overshoot in its activity. The peak of SMU activity appeared around the start of force trajectory (see Fig. 15). When muscle contracted at slow speed with the same amplitude, the SMU activity showed the same activity during the steady state. In the dynamic phase, however, the overshoot was much smaller or even hard to detect (Fig. 16.). Two methods can be used to quantify SMU activity. The first was using Peri-Stimulus Time Histogram (PSTH). It was difficult to observe the peak in PSTH. The problem was more serious in slow contraction conditions. The second method was to construct the average response histogram (ARH) of instantaneous firing rate of the SMU. Usually, the histogram was clear enough after 20 sweeps (Fig. 15.). Furthermore, ARHs of instantaneous firing rate

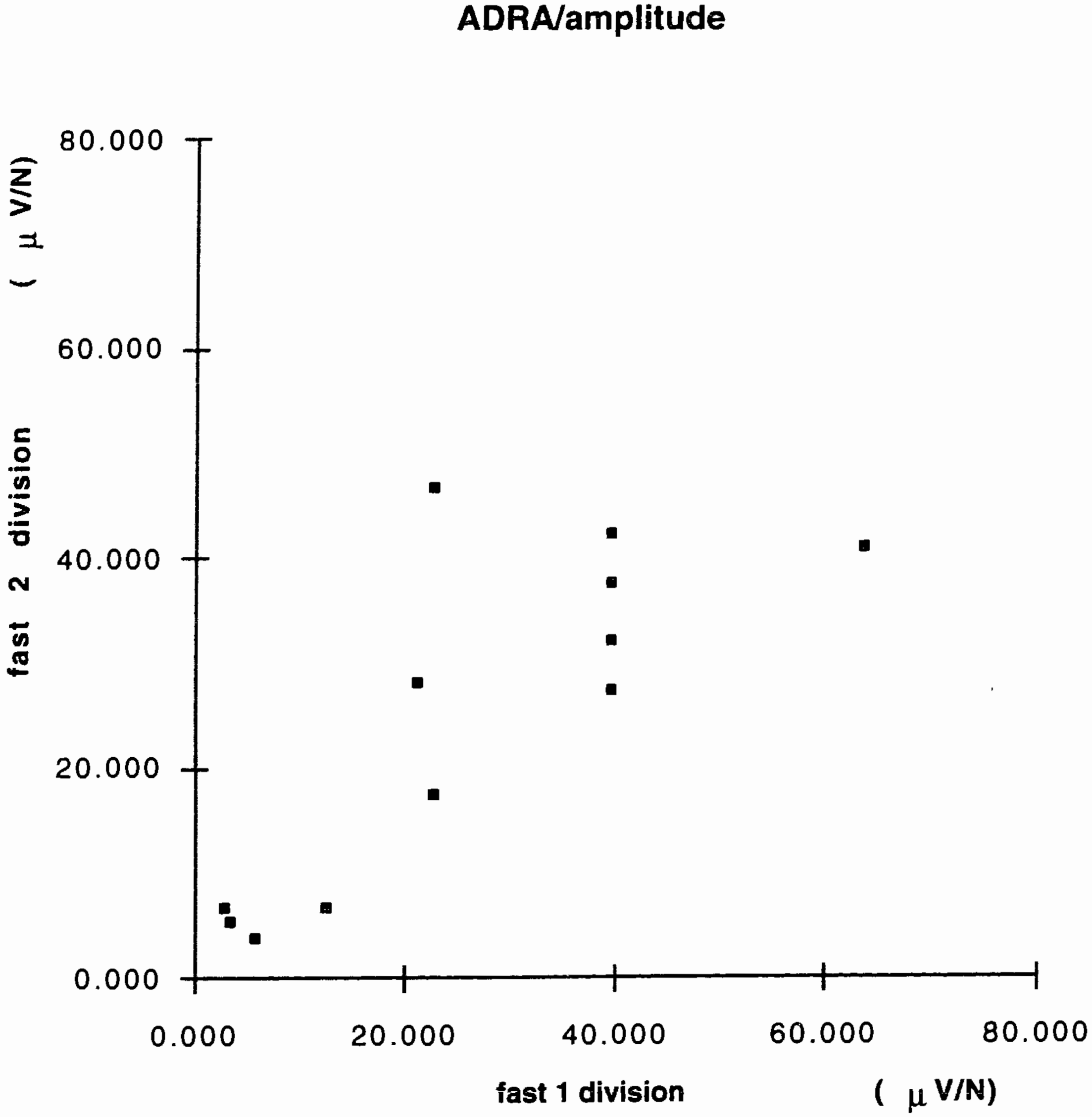

Fig. 13. Absolute Dynamic Response Amplitude divided by contraction amplitude. The results were quite similar to the comparison of NDRA in F[0-1] and F[0-2].

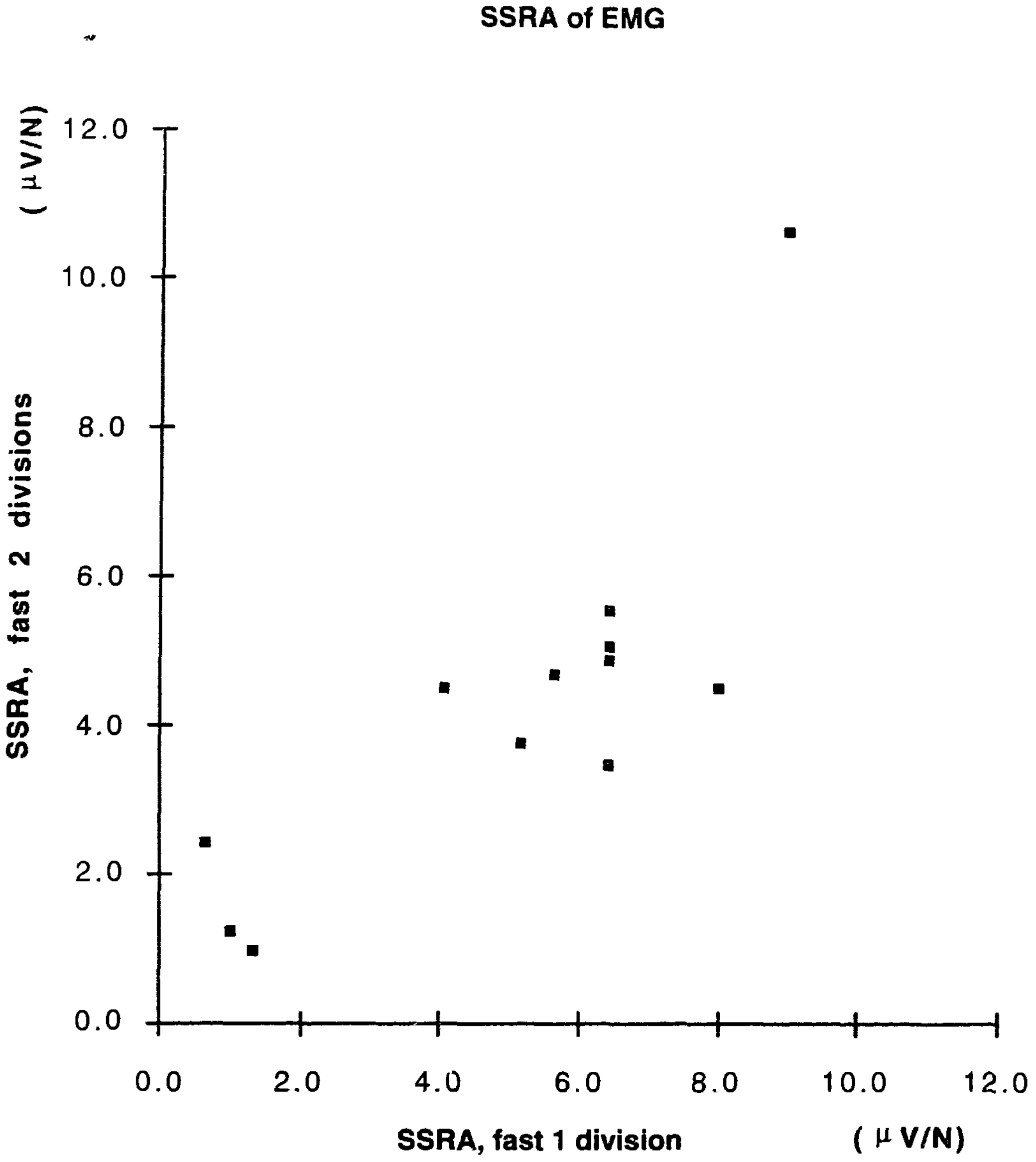

Fig. 14 Steady State Response Amplitude (SSRA) of EMG in fast 1 division and fast 2 division contractions. There is no significant difference between the SSRA of EMG in fast 1 division contraction and that in fast 2 division contraction paired t-test, p=0.13).

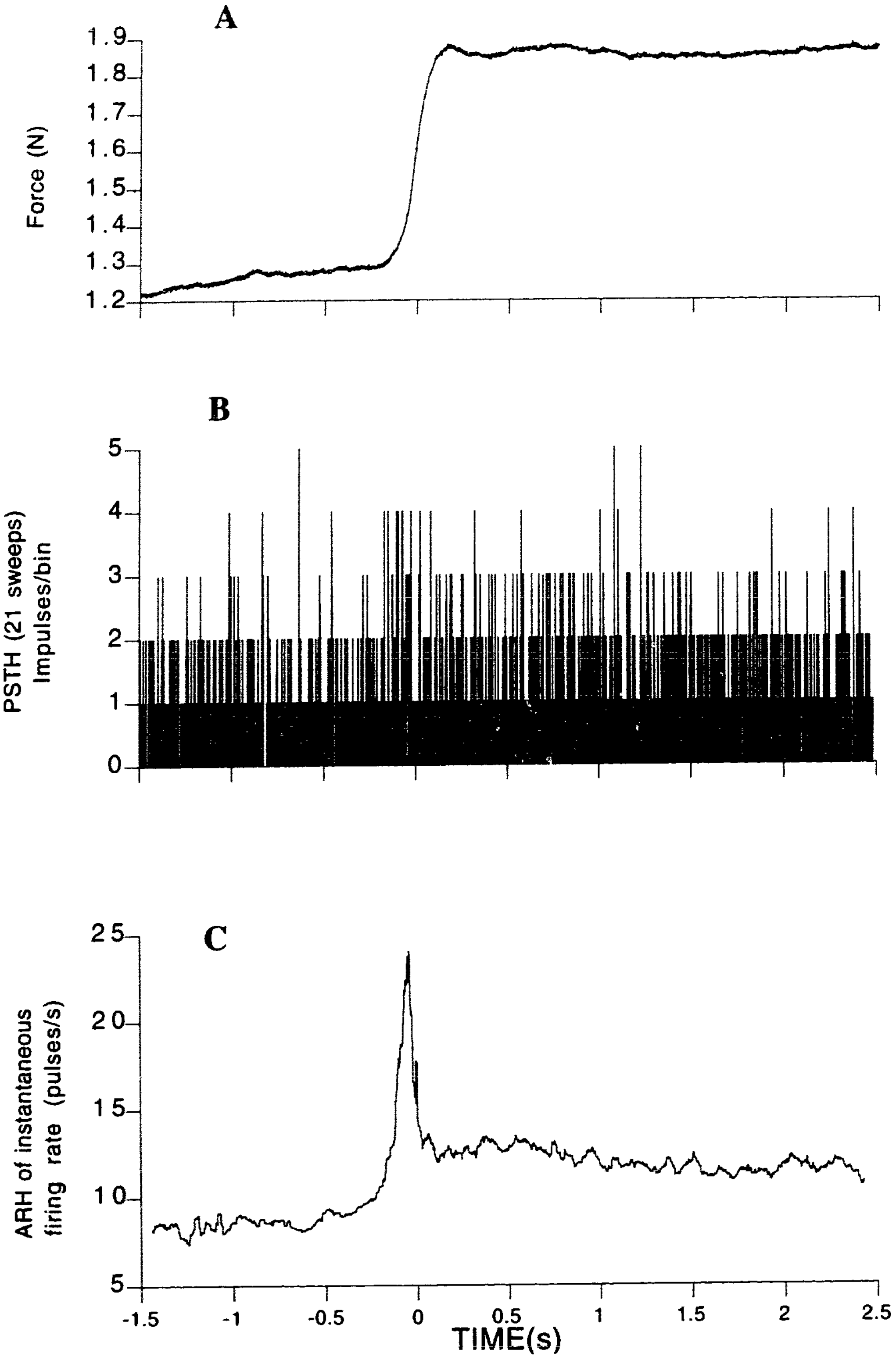

Fig. 15. A, B, C represent the average fast force trajectory, corresponding PSTH and ARH of instantaneous firing rate of a single motor unit, respective. Number of sweeps =21. Subject TR,.

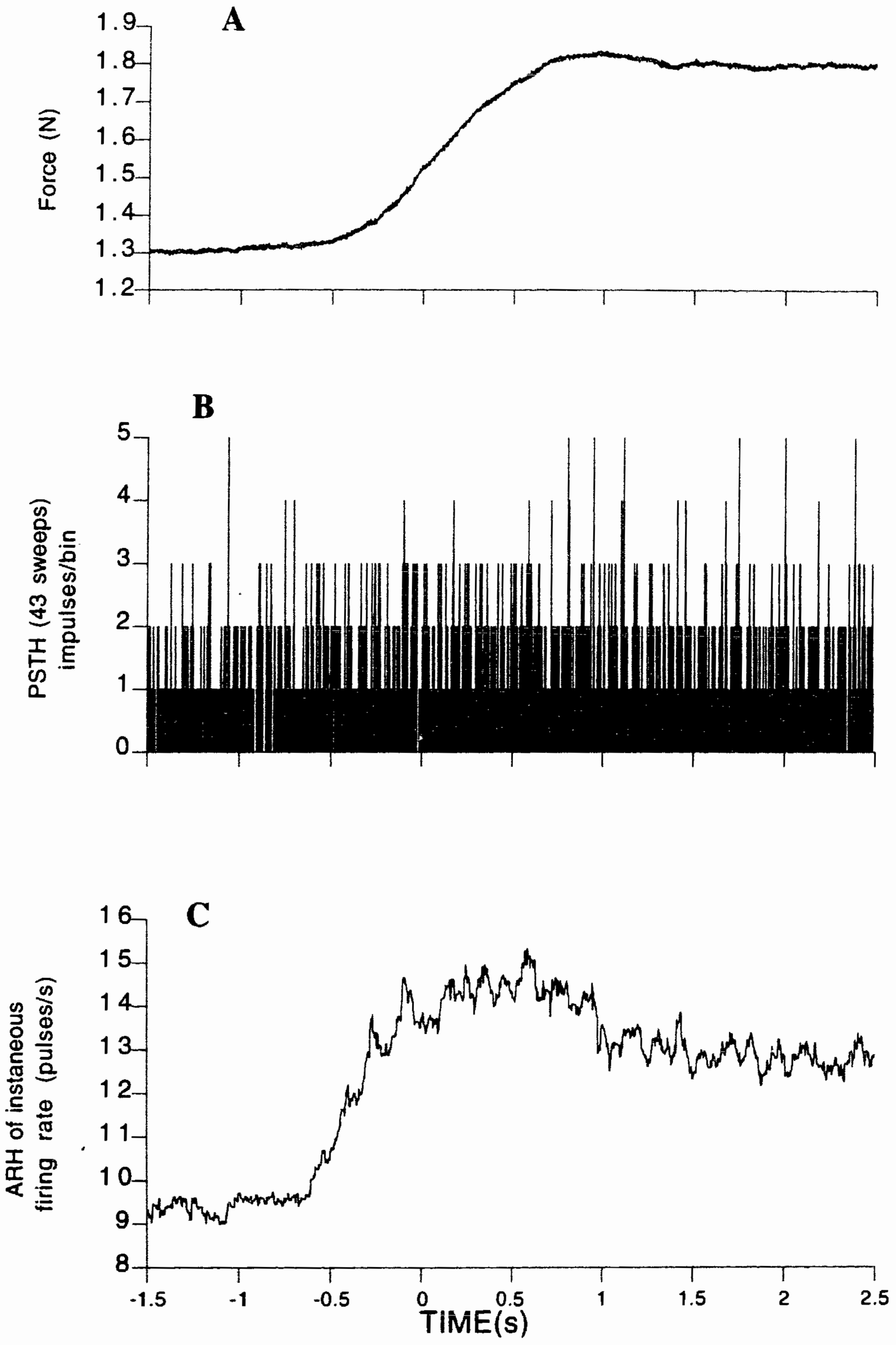

Fig. 16. A, B, C represent the average slow force trajectory, corresponding PSTH and ARH of instantaneous firing rate of a single motor unit, respective. Number of sweeps =21. Subject: TR.

are more appropriate for the interpretation of the data, and for comparison with the animal work. Therefore, ARH of SMU instantaneous firing rate was used to quantify the SMU activities.

Most of the phasically firing units (units with zero background firing) recorded were recruited during the rising phase of force and continued to fire during the steady state, except one which fired only during the rising phase. However, the units which fired only during the rising phase of force were observed very often during the experiments and data processing. These units fired several spikes during the ramp phase of force. The mean steady state firing rate of phasically firing units in fast 1 division contractions was 10.8 imp/sec while in fast 2 division contractions was 11.3 imp/sec. The means of averaged peak firing rates were 22.9 imp/sec and 27.1 imp/sec respectively. However, the data only represented the phasic units which kept firing during steady state.

The mean steady state firing rate of tonically firing units in fast 1 division contractions was 11.4 imp/sec while in fast 2 division contractions was 11.6 imp/sec. The mean of averaged peak firing rates were 21.5 imp/sec and 22.7 imp/sec respectively.

The background SMU activity was calculated by averaging the relative steady activity in background of ARH, usually over 1.0 to 2.0 seconds according to the data available. The steady state SMU activities were calculated by averaging the steady state activity, usually over 1.5 to 3 seconds according to the data available. The peaks were obtained by visual observation combined with automatic detection in SPIKE2.

a) SMU activities in slow and fast contractions

A total of 18 pairs of SMUs were used for these comparisons. The Absolute Dynamic Response Amplitude, Normalized Dynamic Response Amplitude and Steady State Response Amplitude of each SMU were calculated and compared. Paired t-tests were carried out for each set of comparisons.

Absolute Dynamic Response Amplitude. The Absolute Dynamic Response Amplitude (ADRA) of SMUs in fast contractions ranged from 4.8 imp/s to 20.6 imp/s with a mean of 9.98 imp/s. The ADRA of SMU in slow contractions ranged from 1.3 imp/s to 4.8 imp/s with a mean of 2.86 imp/s. The mean ADRA of SMU in fast contraction was significantly larger than that in slow contraction. The paired t-test shows that the difference was significant by p<=2.11E-6. This result indicates that the dynamic activity of SMU increases with increasing contraction speed. The higher the contraction speed, the higher the dynamic activity of SMU. The results are shown in Fig. 17.

Normalized Dynamic Response Amplitude. The Normalized Dynamic Response Amplitude (NDRA) of SMUs in fast contractions ranged from 0.4 (imp/s)/(N/s) to 8.8 (imp/s)/(N/s) with a mean of 1.74 (imp/s)/(N/s). The NDRA of SMU in slow contraction ranged from 0.7 (imp/s)/(N/s) to 8.9 (imp/s)/(N/s) with a mean of 3.17 (imp/s)/(N/s). The mean NDRA in fast contractions was significantly smaller than that in slow contractions. The paired t-test shows that the difference was significant by p<=0.00032. This result indicates that the dynamic activity of SMU increases with the increase of contraction speed. However, NDRA, which equals ADRA divided by contraction speed, was larger in slow contraction than that in fast contraction. This implies that SMU dynamic activity was not linearly related to the contraction speed. The NDRA of SMU data for the comparison between the fast and slow contractions were are plotted in Fig. 18.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of SMUs in fast contractions ranged from 0.6 (imp/s)/N to 10.0 (imp/s)/N with a mean of 3.00 (imp/s)/N. The SSRA of SMU in slow contractions ranged from 1.1 (imp/s)/N to 11.4 (imp/s)/N with a mean of 2.93 (imp/s)/N. The SSRA of SMUs in fast contractions was not significantly different from that in slow contractions. The paired t-test shows no significance with p=0.702. The SSRA in fast contractions and that in the slow

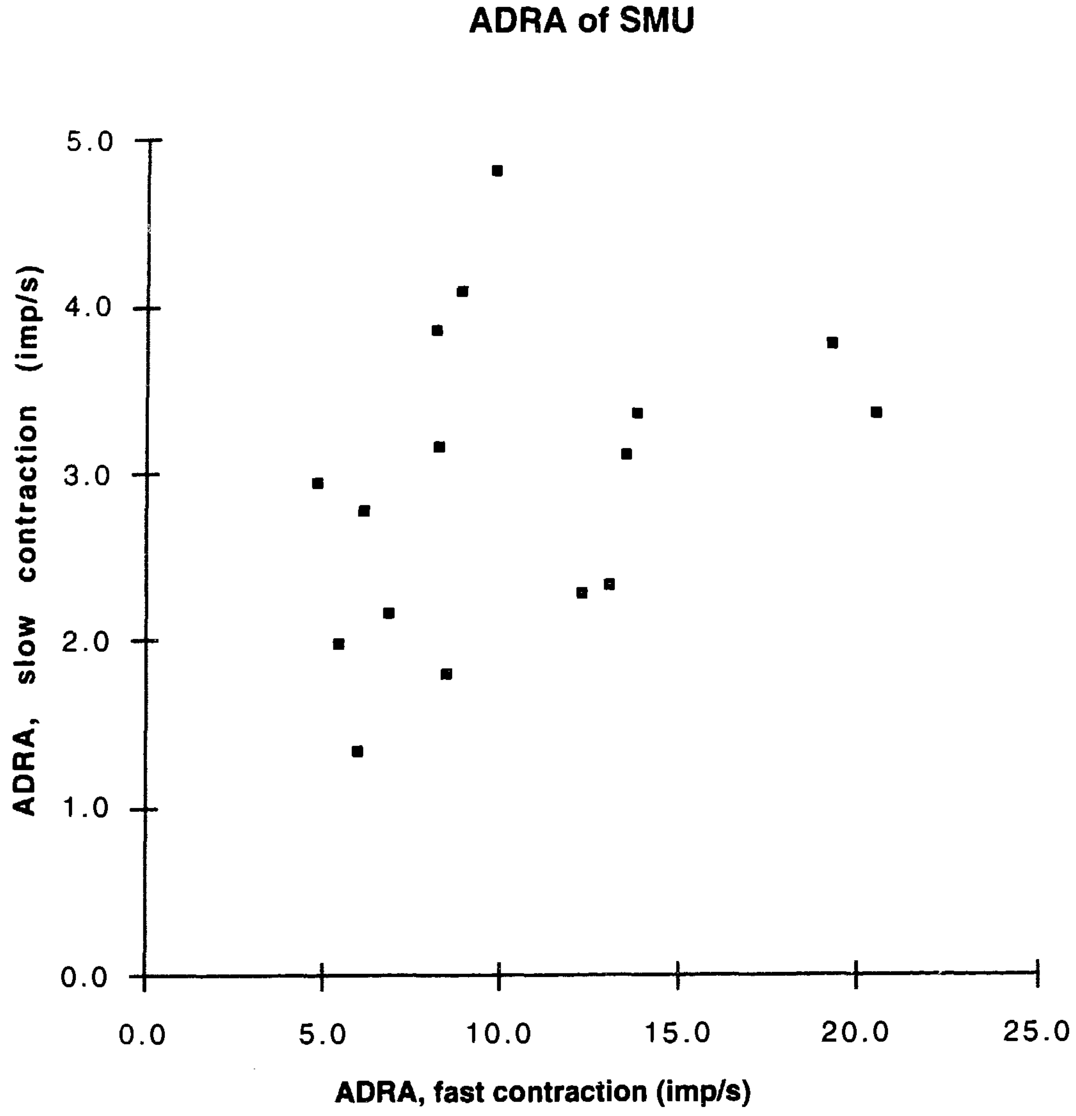

Fig. 17. Absolute Dynamic Response Amplitude (ADRA) of SMU in slow and fast contractions. In the figure, the difference between the ADRA of SMU in fast contraction and that in slow contraction is obvious. The former is much larger than the later.

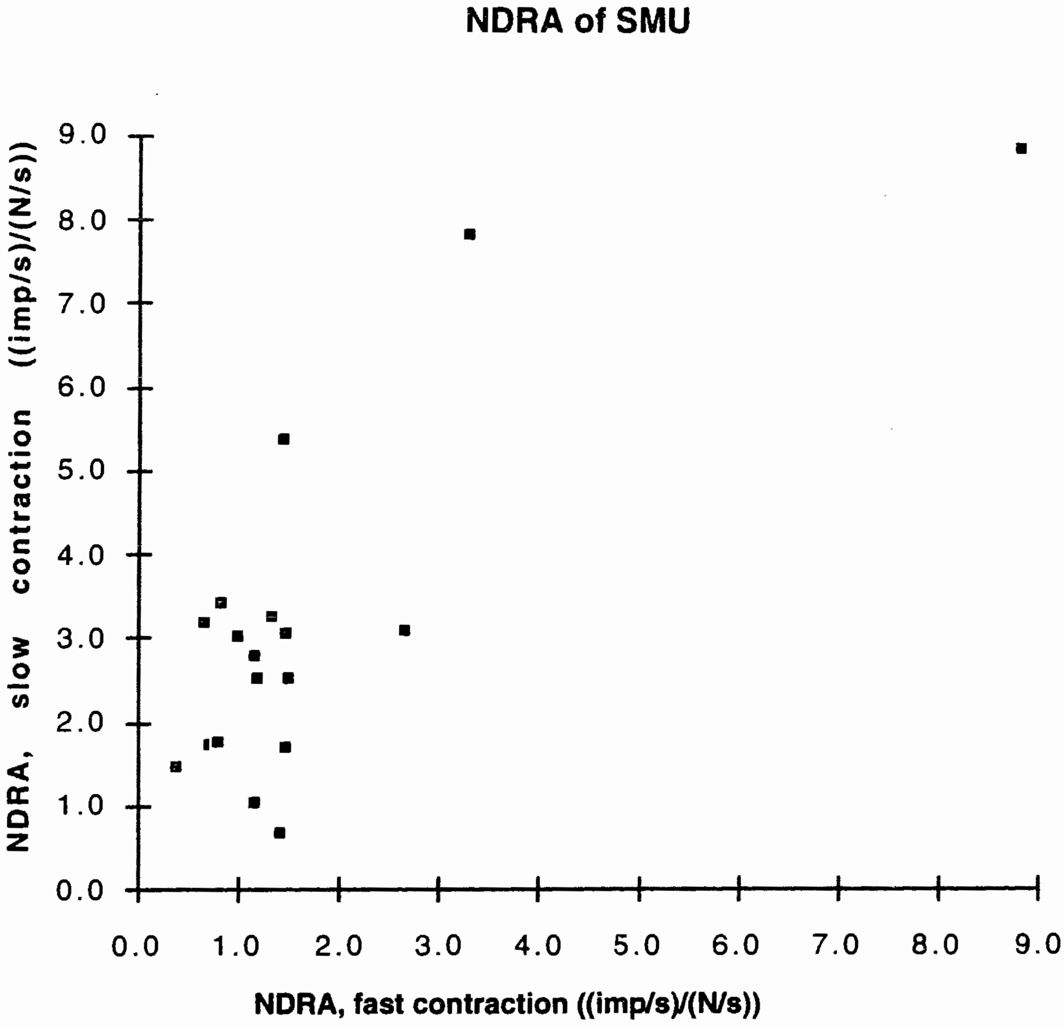

Fig. 18. Normalized Dynamic Response Amplitude (NDRA) of SMU in slow and fast contractions. NDRA of SMU in slow contraction is significantly larger than that of the fast contraction. This indicates that the dynamic activity of SMU is not linearly related to the contraction speed.

contractions was highly correlated (r=0.95). This result indicates that the steady state activity of SMU is not related to the contraction speed but only the amplitude of contraction. For similar force levels, the Steady State Response Amplitude of SMUs is the same for both fast and slow contractions. The results are shown in Fig. 19.

b) SMU activities in F[0-1] and F[0-2] contraction

As mentioned before, on average, the contraction speeds of F[0-2] contractions were 1.9 times as large as that of F[0-1] contractions. Therefore, the results could further support the results obtained from the comparison of slow and fast contractions. At the same time, the effects of amplitudes on the steady state properties could be assessed. A total of 18 pairs of SMUs were used for comparison. Absolute Dynamic Response Amplitude, Normalized Dynamic Response Amplitude and Steady State Response Amplitude of SMU were calculated and compared.

Absolute Dynamic Response Amplitude. The Absolute Dynamic Response Amplitude (ADRA) of SMUs in F[0-1] contractions ranged from 2.0 imp/s to 20.6 imp/s with a mean of 11.44 imp/s. The ADRA of SMU in F[0-2] contractions ranged from 2.7 imp/s to 18.7 imp/s with a mean of 13.36 imp/s. The mean ADRA of SMU in F[0-1] contraction was significantly smaller than that in F[0-2] contraction. The paired t-test shows that the difference was significant by $p<=0.021$. This result indicates that the dynamic activity of SMU increases with the increase of contraction speed. The higher the contraction speed, the higher the dynamic activity of SMU. The relationship to contraction speed will be assessed by normalizing with speed. The results are shown in Fig. 20.

Normalized Dynamic Response Amplitude. The Normalized Dynamic Response Amplitude (NDRA) of SMU in F[0-1] contractions ranged from 0.14 (imp/s)/(N/s) to 3.31 (imp/s)/(N/s) with a mean of 1.35 (imp/s)/(N/s). The NDRA of SMU in F[0-2] contractions ranged from 0.11 (imp/s)/(N/s) to 2.46 (imp/s)/(N/s) with a mean of

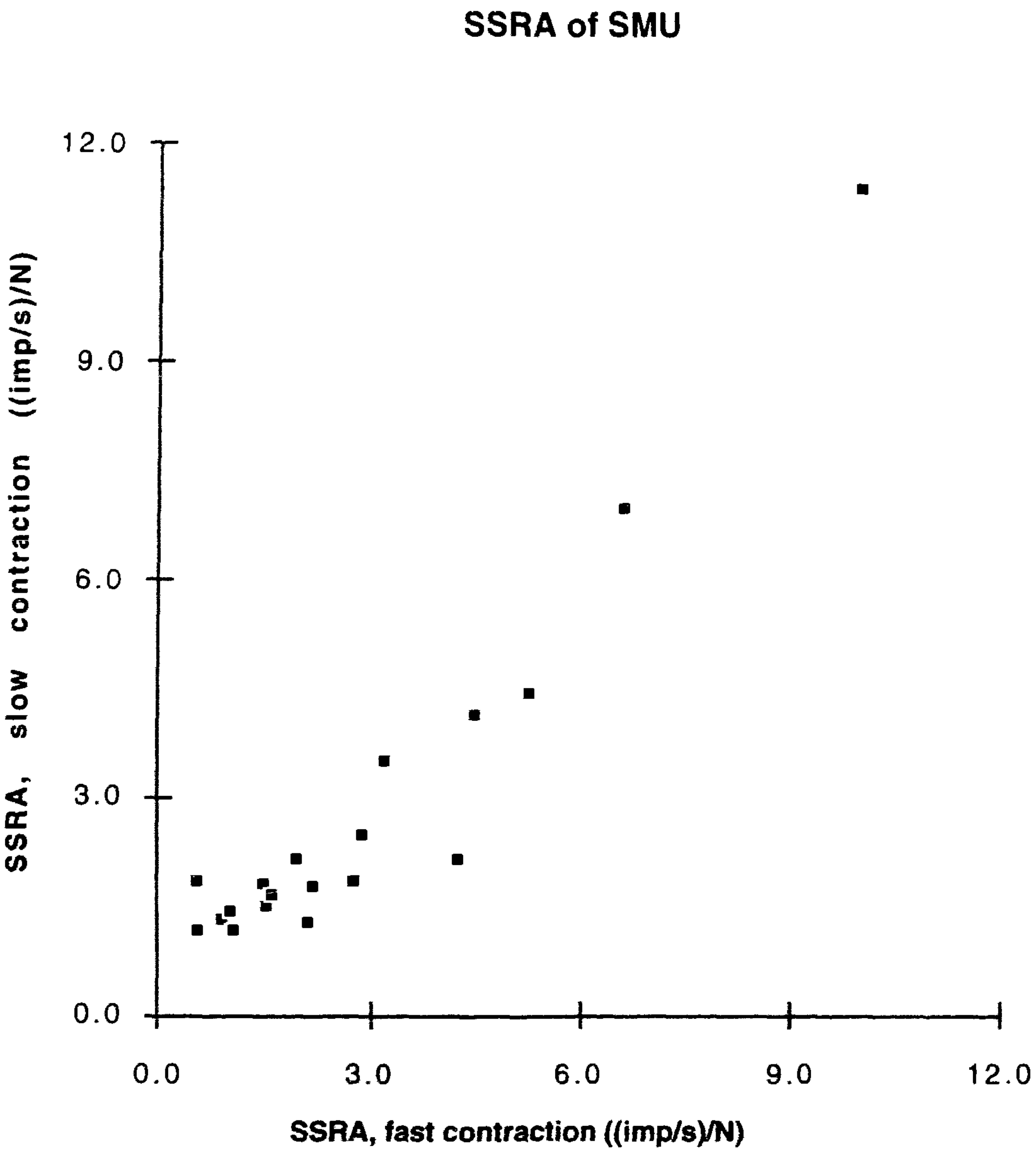

Fig. 19. Steady State Response Amplitude (SSRA) of SMU in slow and fast contractions. The data are highly correlated (r=0.94). There is no significant difference between the SSRA of EMG in slow contraction and that in fast contraction (p=0.704). Steady properties of SMU was not controlled by the factors controlling SMU dynamic activities.

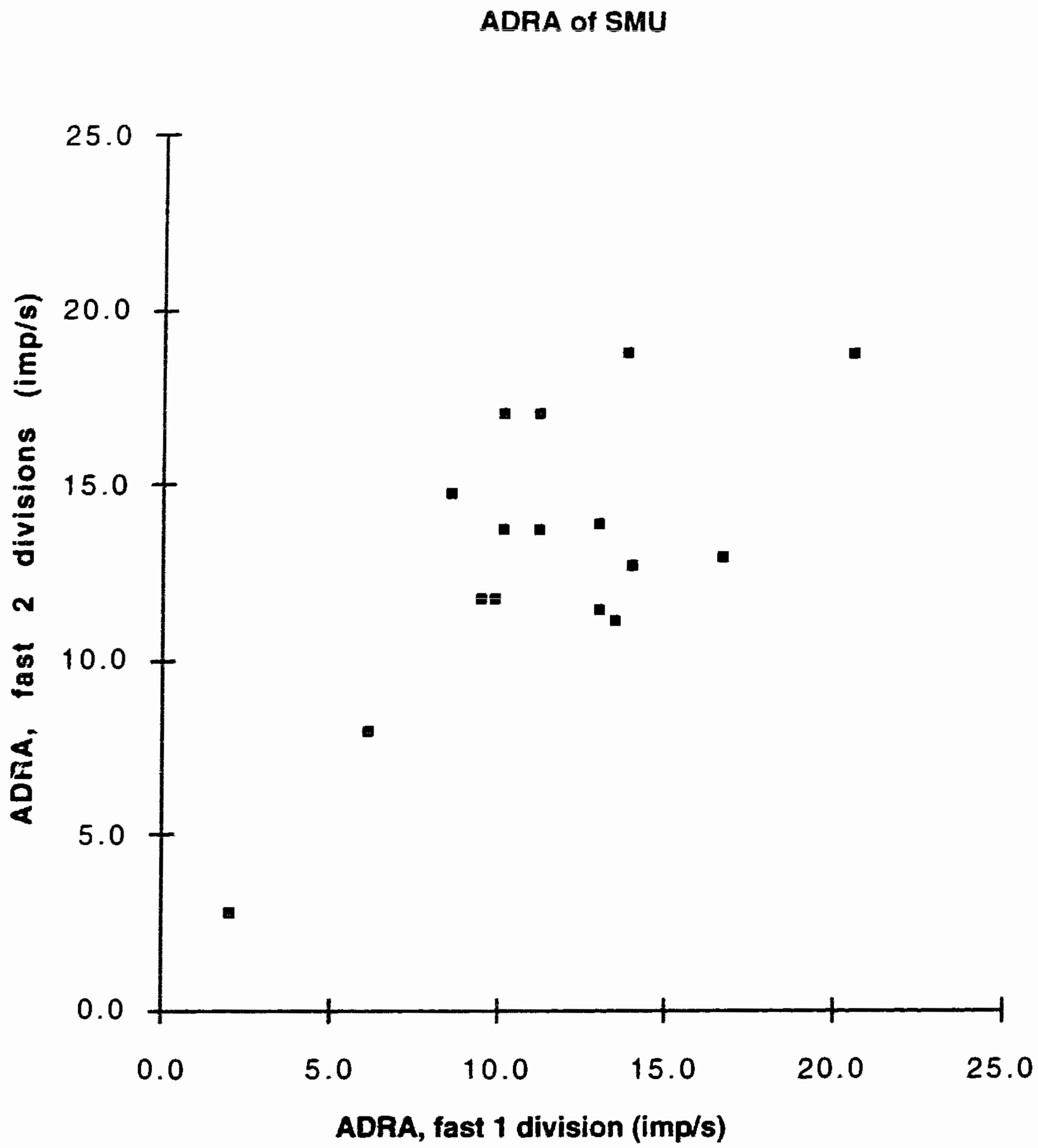

Fig. 20. Absolute Dynamic Response Amplitude (ADRA) of SMU in fast 1 division and fast 2 division contractions. The mean ADRA in fast 1 division contraction is smaller than that in fast 2 division contraction. The difference is small compare to the change in the contraction speeds, a sign of non linearity.

0.87 (imp/s)/(N/s). The mean NDRA of SMU in F[0-1] contraction was significantly larger than that in F[0-2] contraction. The paired t-test shows that the difference was significant by $p<=6.4E-7$. This result supports the results from the comparison of slow and fast contractions. When the contraction speed is high, the increase of SMU dynamic activity decreases with the same change in contraction speed. The results are shown in Fig. 21.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of SMU in F[0-1] contractions ranged from 0.6 (imp/s)/N to 6.6 (imp/s)/N with a mean of 2.68 (imp/s)/N. The SSRA of SMU in F[0-2] contractions ranged from 0.6 (imp/s)/N to 3.3 (imp/s)/N with a mean of 1.93 (imp/s)/N. The mean SSRA in F[0-1] contraction was significantly larger than that in F[0-2] contraction. The paired t-test shows a significance with $p=0.007$. This result indicates that the steady activity of SMU was not linearly related to the force. The SSRA of SMU decreases when force increases. The results are shown in Fig. 22.

c) Same SMU responses at different background firing rates

The following results were obtained from comparisons between the responses of same SMU with two different background firing rates. The force used in this condition was a fast contraction to have a clear dynamic phase of SMU activity. A total of 11 pairs were used. The lower background firing rates ranged from 3.2 imp/sec to 10.7 imp/sec while the higher firing rates ranged from 7.2 to 11.7 imp/sec. The mean background firing rate for lower rates was 7.5 ± 1.8 (mean±S.D.) while for higher rates it was 9.7 ± 1.4 (mean±S.D.) imp/sec. The two background firing rates was significantly different at the level of $p\leq0.0005$. Only Normalized Dynamic Response Amplitude and Steady State Response Amplitude of SMU were used for the comparisons. After the direct comparisons between the SMU activities with two different firing rates, the difference between the SMU activities will be compared to the difference of background firing rates.

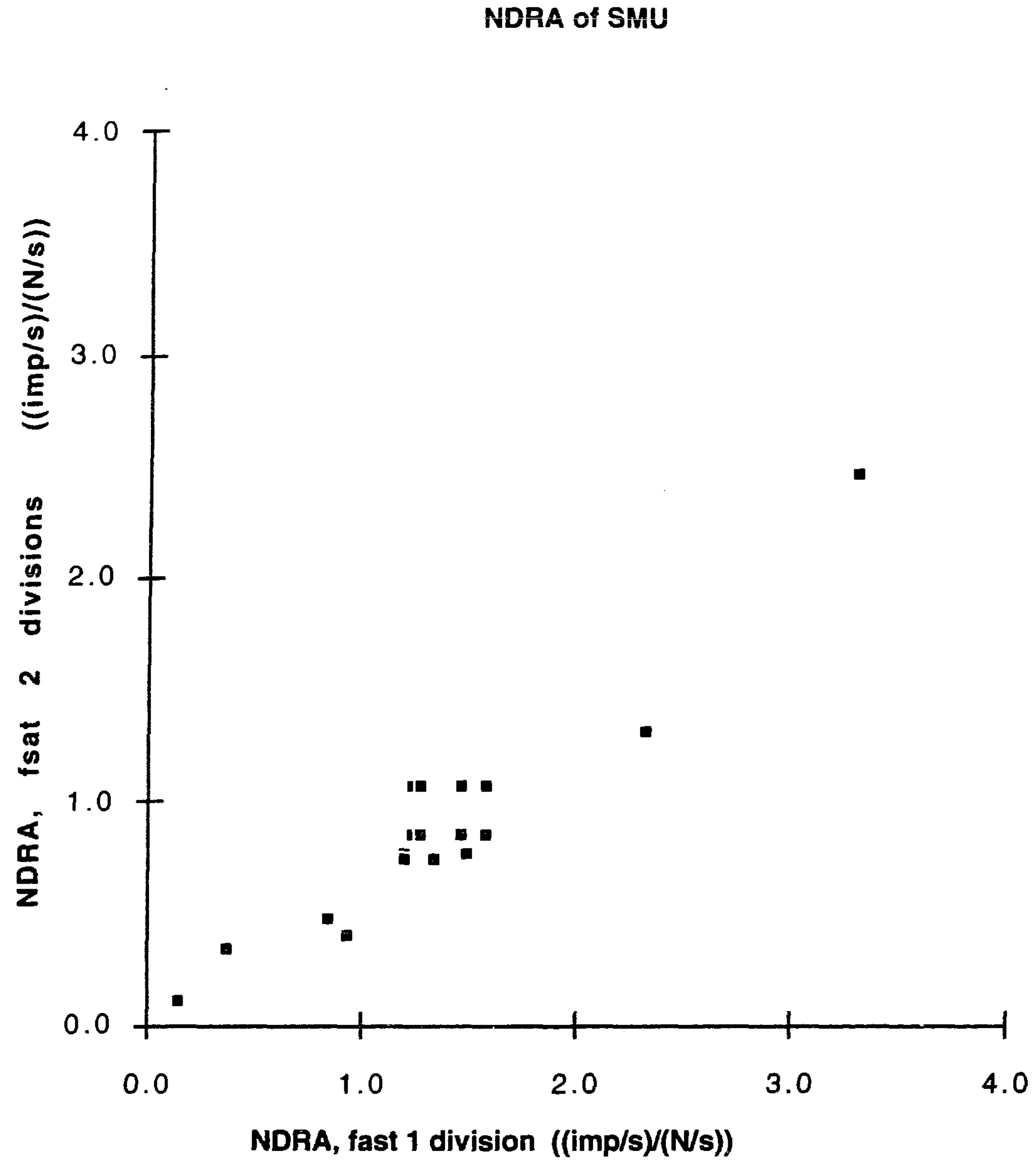

Fig. 21. Normalized Dynamic Response Amplitude (NDRA) of SMU in fast 1 division and fast 2 division contractions. Mean NDRA of SMU in fast 1 division contraction is significantly larger than that in fast 2 division contraction. This supports the result that the dynamic activity was not linearly related to the contraction speed.

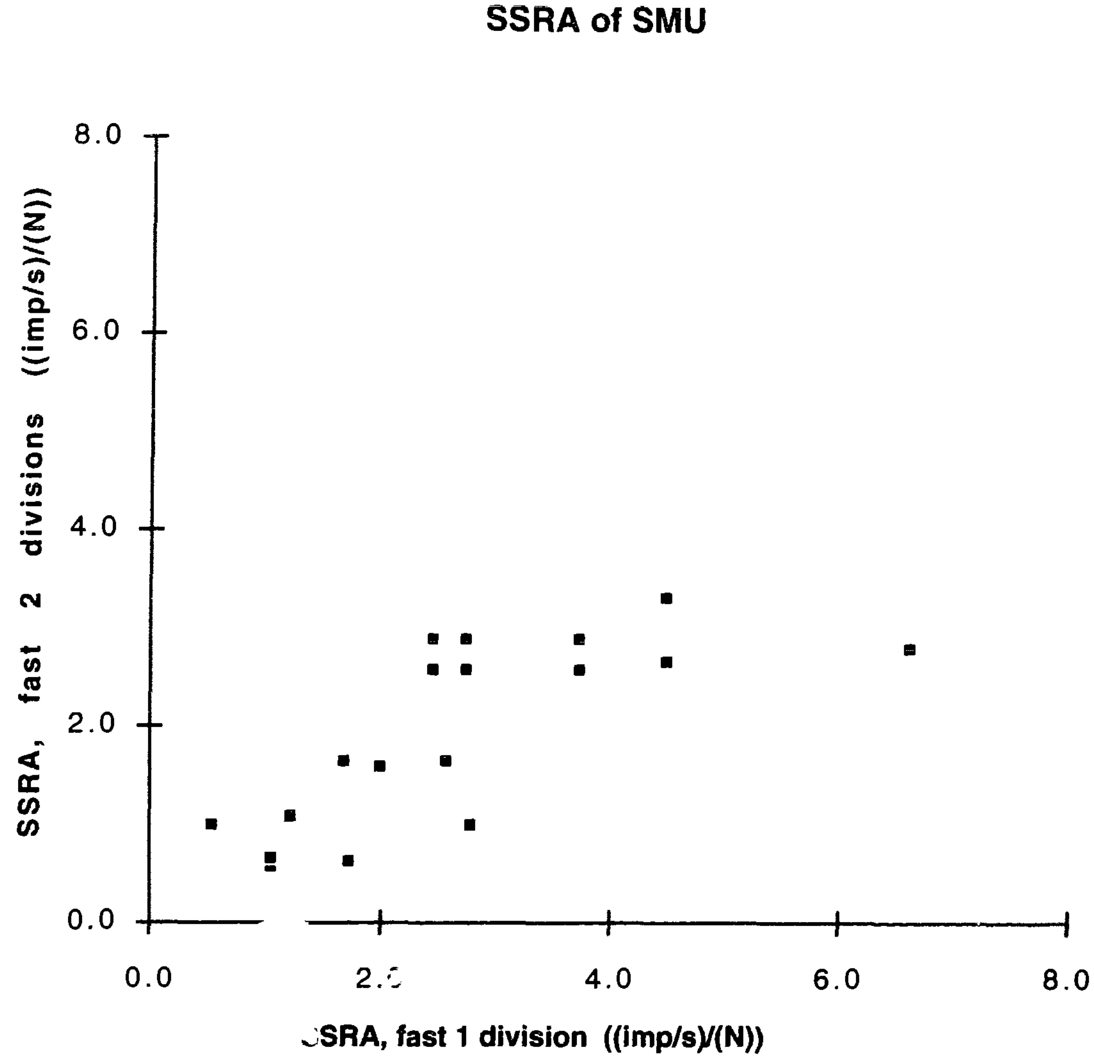

Fig. 22. Steady State Response Amplitude (SSRA) of SMU in fast 1 division and fast 2 division contractions. The SSRA in fast 1 division contraction was larger than that in fast 2 division contraction, a sign of non linearity in the steady state activities of SMU.

Normalized Dynamic Response Amplitude. The Normalized Dynamic Response Amplitude (NDRA) of SMU at lower background firing rates ranged from 0.4 (imp/s)/(N/s) to 2.0 (imp/s)/(N/s) with a mean of 1.37 (imp/s)/(N/s). The NDRA of SMU at higher background firing rates ranged from 0.3 (imp/s)/(N/s) to 1.3 (imp/s)/(N/s) with a mean of 1.02 (imp/s)/(N/s). The mean NDRA of SMU at lower background firing rates was significantly larger than that of SMU at higher background firing rates. The paired t-test shows that the difference was significant by $p<=0.011$. This result indicates that SMU dynamic activity is influenced by its background firing rate. The higher its background firing rate, the lower its dynamic response. The results are shown in Fig. 23.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of SMU at lower background firing rates ranged from 2.3 (imp/s)/N to 4.0 (imp/s)/N with a mean of 2.98 (imp/s)/N. The SSRA of SMU at higher background firing rates ranged from 0.6 (imp/s)/N to 4.3 (imp/s)/N with a mean of 2.22 (imp/s)/N. The mean SSRA of SMU at lower background firing rates was significantly larger than that of same SMU at higher background firing rates. The paired t-test shows a significance with $p=0.012$. This result indicates that the steady state activity of SMU was affected to the background firing rate of SMU. The higher the background firing rate, the lower the SSRA of SMU. The results are shown in Fig. 24.

Difference between the firing rates versus the difference between various indices activities of SMU. To further investigate the effect of firing rate on the dynamic and steady state activities of SMU, the above data were reorganized to show the relation between the firing rate and SMU activities. The difference of the background firing rate is calculated by subtracting the lower rate from the higher rate. The difference of NDRA and SSRA was calculated by subtracting the NDRA and SSRA of SMU at higher rate from those of the same SMU at lower rate. From Fig. 25 and Fig. 26, the difference between the activities of SMU increases when the difference between the firing rates of

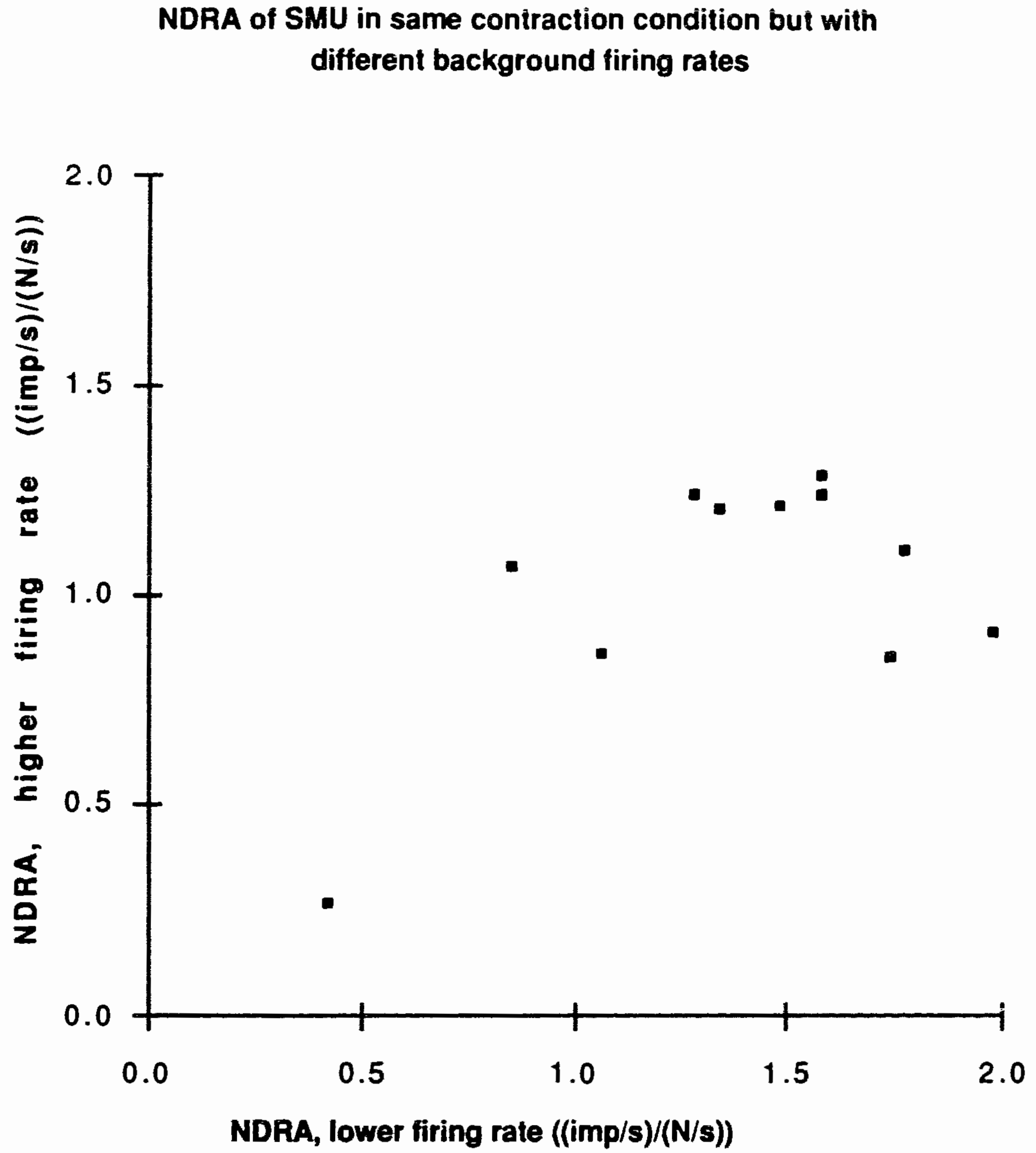

Fig. 23. Normalized Dynamic Response Amplitude (NDRA) of SMU at higher and lower background firing rates. The NDRA of SMU at lower background firing rate is smaller than that of the same SMU at higher background firing rate.

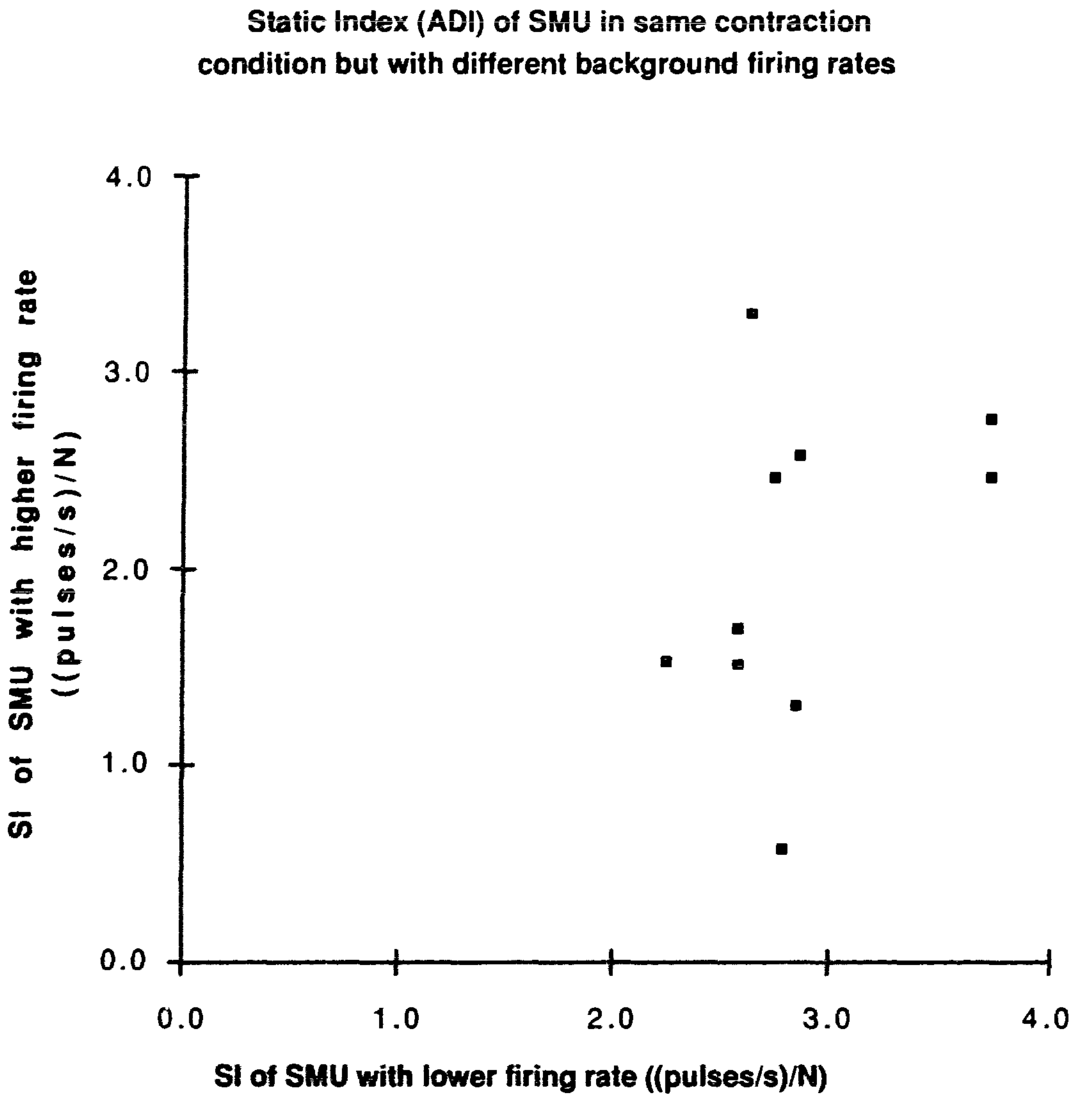

Fig. 24. The Steady State Response Amplitude (SSRA) of SMU at higher and lower background firing rates. The SSRA of SMU at lower background firing rate is smaller than that of the same SMU at higher background firing rate.

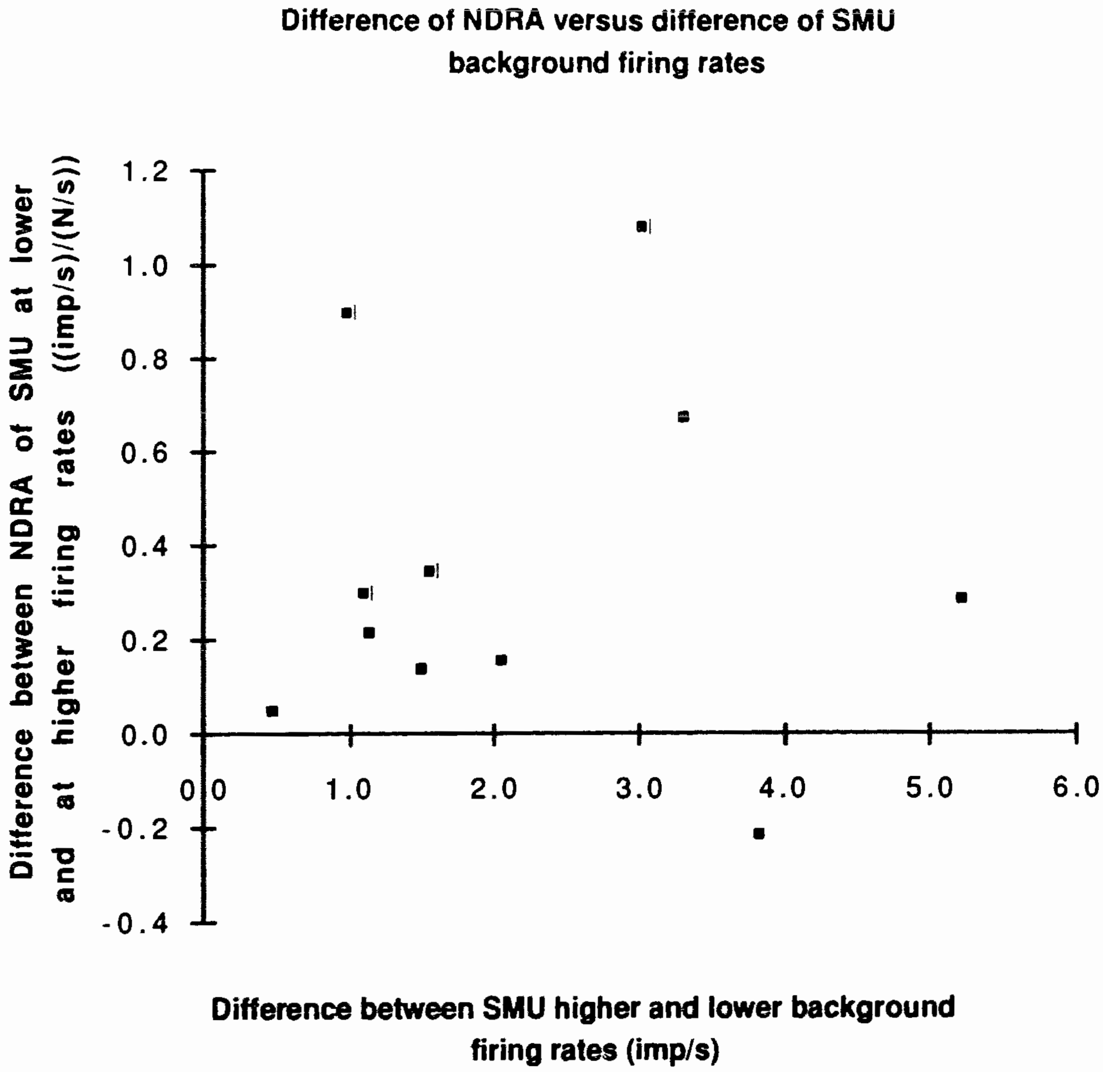

Fig. 25. Difference of NDRA versus difference of background firing rates of the same SMU. An increase in the difference between NDRA of SMU can be observed with the increase of difference in firing rates. The relatively scattered data were caused by the individual difference among subjects.

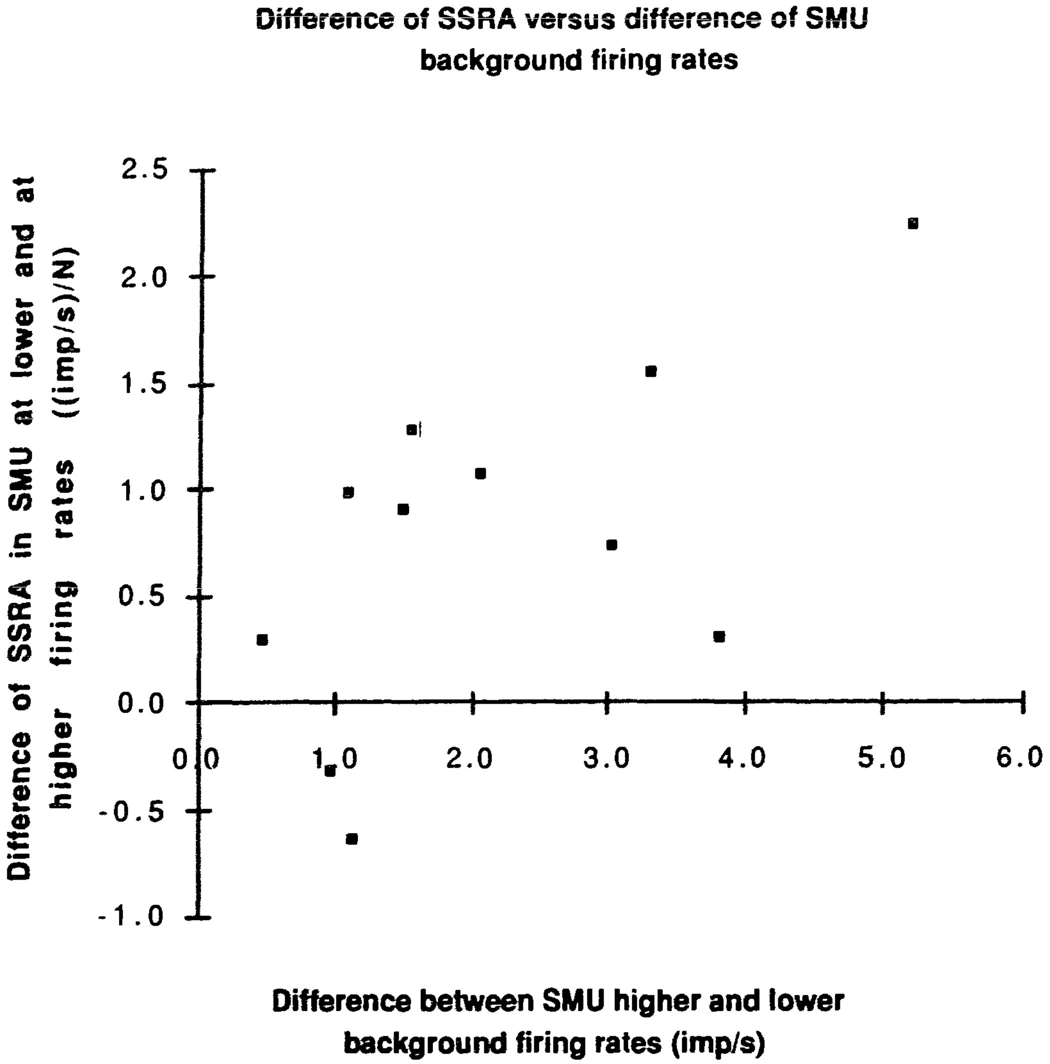

Fig. 26. Difference of SSRA versus difference of SMU background firing rates. An increase in the difference between SSRA of SMU can be observed with the increase of difference in firing rates. The relatively scattered data were caused by the individual difference among subjects.

SMU increases. A positive relationship was observed in both of the figures i.e. difference of NDRA versus difference of firing rate ($r = 0.12$) and difference of SSRA versus difference of firing rat ($r = 0.62$). The relatively scattered data were caused by the individual differences among subjects. For example, the same force amplitude represents different relative forces for each subject because of the differences in the amplitudes of their maximal voluntary contractions. Further more, the same difference of firing rates could be made by different background rates, for example a difference of 3 imp/s could be made by 6 and 9 imp/s or 9 and 12 imp/s,.

d). Same SMU responses at zero (phasic) and nonzero background (tonic) firing rates

The following results were obtained from comparisons between the responses of same SMU with phasic and tonic firing patterns. A total of 14 pairs of SMUs were used. Only Normalized Dynamic Response Amplitude and Steady State Response Amplitude of SMU were used for the comparisons.

Normalized Dynamic Response Amplitude. The Normalized Dynamic Response Amplitude (NDRA) of SMU with phasic firing pattern ranged from 0.16 (pulses/s)/(N/s) to 3.21 (pulses/s)/(N/s) with a mean of 1.41 (pulses/s)/(N/s). The NDRA of SMU with tonic firing pattern ranged from 0.34 (pulses/s)/(N/s) to 2.33 (pulses/s)/(N/s) with a mean of 1.07 (pulses/s)/(N/s). The mean NDRA of SMU with phasic firing pattern was significantly larger than that of SMU with tonic firing pattern. The paired t-test shows that the difference was significant by $p \leq 0.034$. The results are shown in Fig. 27.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of SMU with phasic firing pattern ranged from 2.27 (pulses/s)/N to 18.2 (pulses/s)/N with a mean of 7.61 (pulses/s)/N. The SSRA of SMU with tonic firing pattern ranged from 0.57 (pulses/s)/N to 6.12 (pulses/s)/N with a mean of 2.56 (pulses/s)/N. The

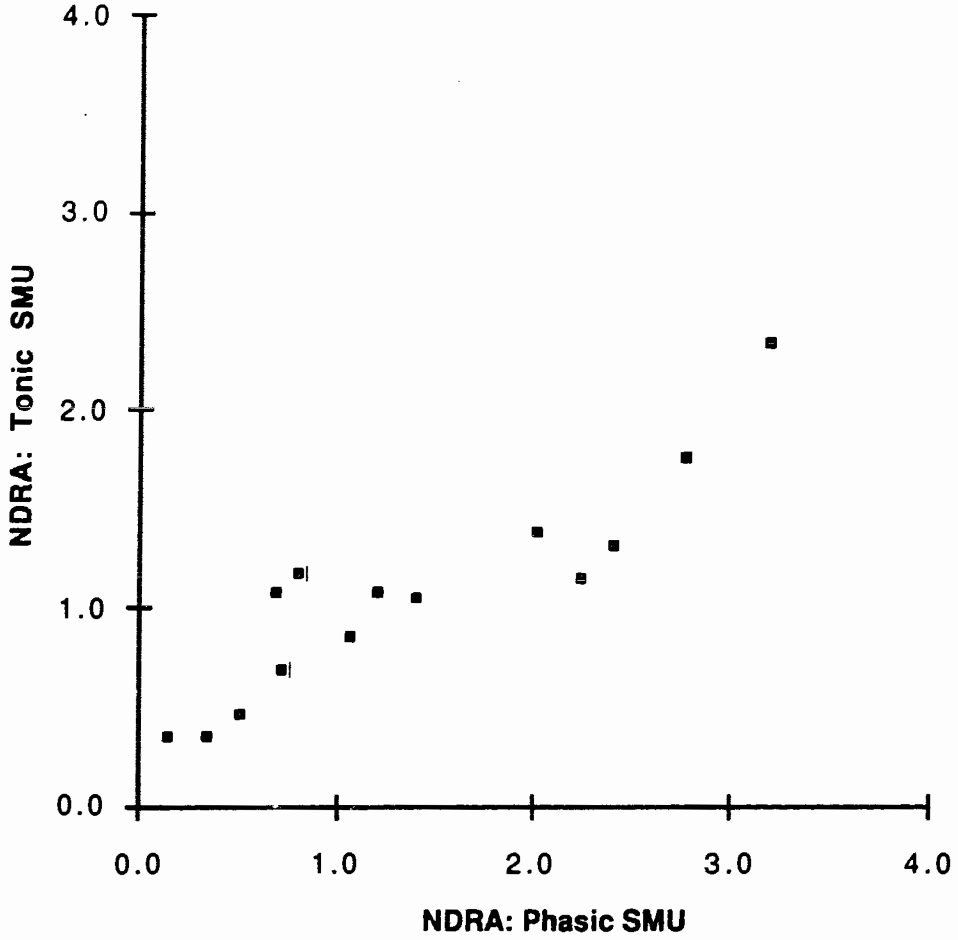

Fig. 27. The Normalized Dynamic Response Amplitude in SMU firing at phasic and tonic patterns. The NDRA of phasic firing SMU were significantly larger than that of the same SMU firing tonically.

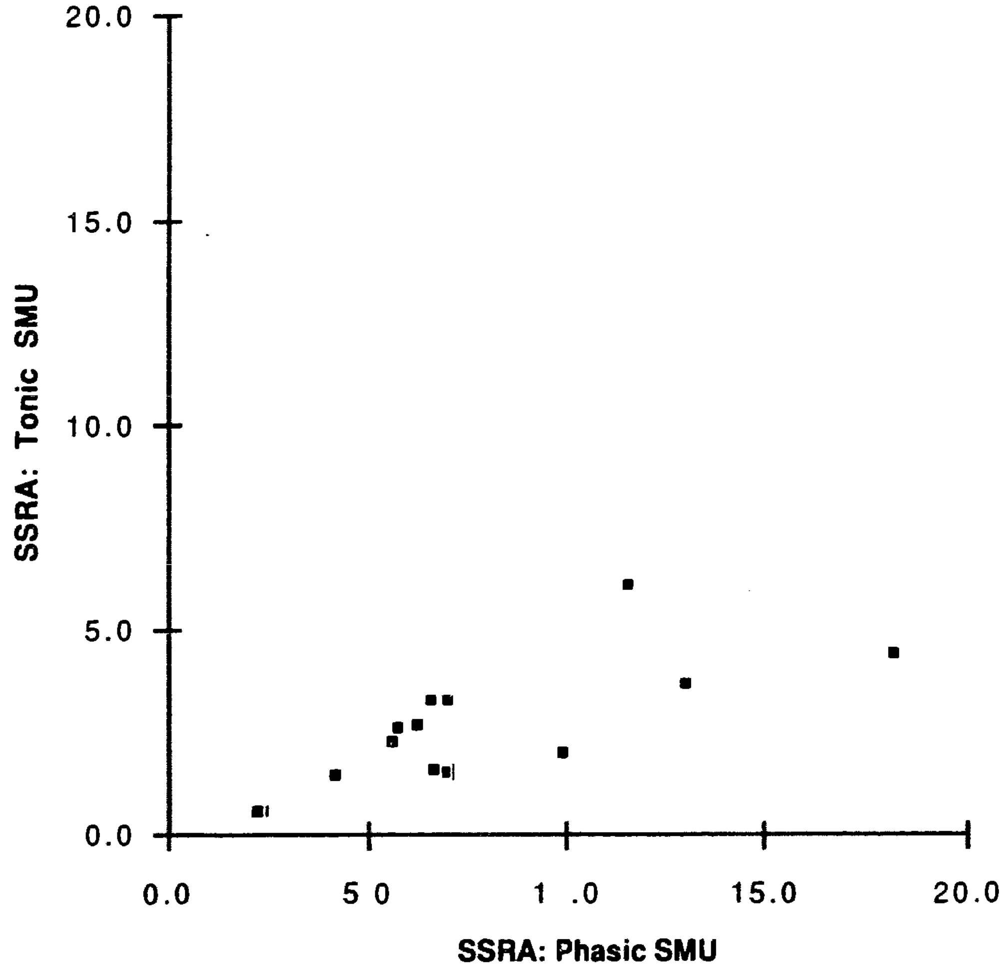

Fig. 28 The Steady State Response Amplitude in SMU firing at phasic and tonic patterns. The SSRA of phasic firing SMU were significantly larger than that of the same SMU firing tonically.

mean SSRA of SMU with phasic firing pattern was significantly larger than that of same SMU with tonic firing pattern. The paired t-test shows a significance with $p \leq 8E-5$. The results are shown in Fig. 28.

e) SMU activities of two motor units firing simultaneously

The following results were from comparisons between the two simultaneously recorded SMU. A total of 9 pairs of SMUs were used for comparisons. Only Normalized Dynamic Response Amplitude and Steady State Response Amplitude of SMU were calculated and compared. When two SMUs with different threshold were recruited, the lower threshold SMU were likely to fire at higher firing rate (Monster and Chan, 1977). This was confirmed by our data. The lower threshold SMUs had background firing rates ranged from 8.38 imp/sec to 11.7 imp/sec. The higher threshold SMUs had background firing rates ranged from 6.34 to 10.1 imp/sec. The mean background firing rate for lower threshold of SMU (9.656±1.27 imp/s) was significantly larger than that for higher threshold SMU (7.919±1.28 imp/s) ($p=0.022$). As indicated above, the difference in the background firing rate will cause the difference in the SMU dynamic and steady state responses. Therefore, after the direct comparison between activities of two simultaneously recorded SMUs, the difference of the SMU activities will be compared to the difference in background firing rates. The results will be compared to the results from comparisons of the same SMU at different background firing rates.

Normalized Dynamic Response Amplitude. The Normalized Dynamic Response Amplitude (NDRA) of lower threshold SMUs ranged from 0.26 (imp/s)/(N/s) to 1.84 (imp/s)/(N/s) with a mean of 1.00 (imp/s)/(N/s). The NDRA of higher threshold SMUs ranged from 0.34 (imp/s)/(N/s) to 1.76 (imp/s)/(N/s) with a mean of 1.15 (imp/s)/(N/s). The mean NDRA of lower threshold SMUs was significantly smaller than that of higher threshold SMUs. The paired t-test shows that the difference was significant by $p<=0.012$. Since SMU activities are influenced by firing rate, different threshold SMUs

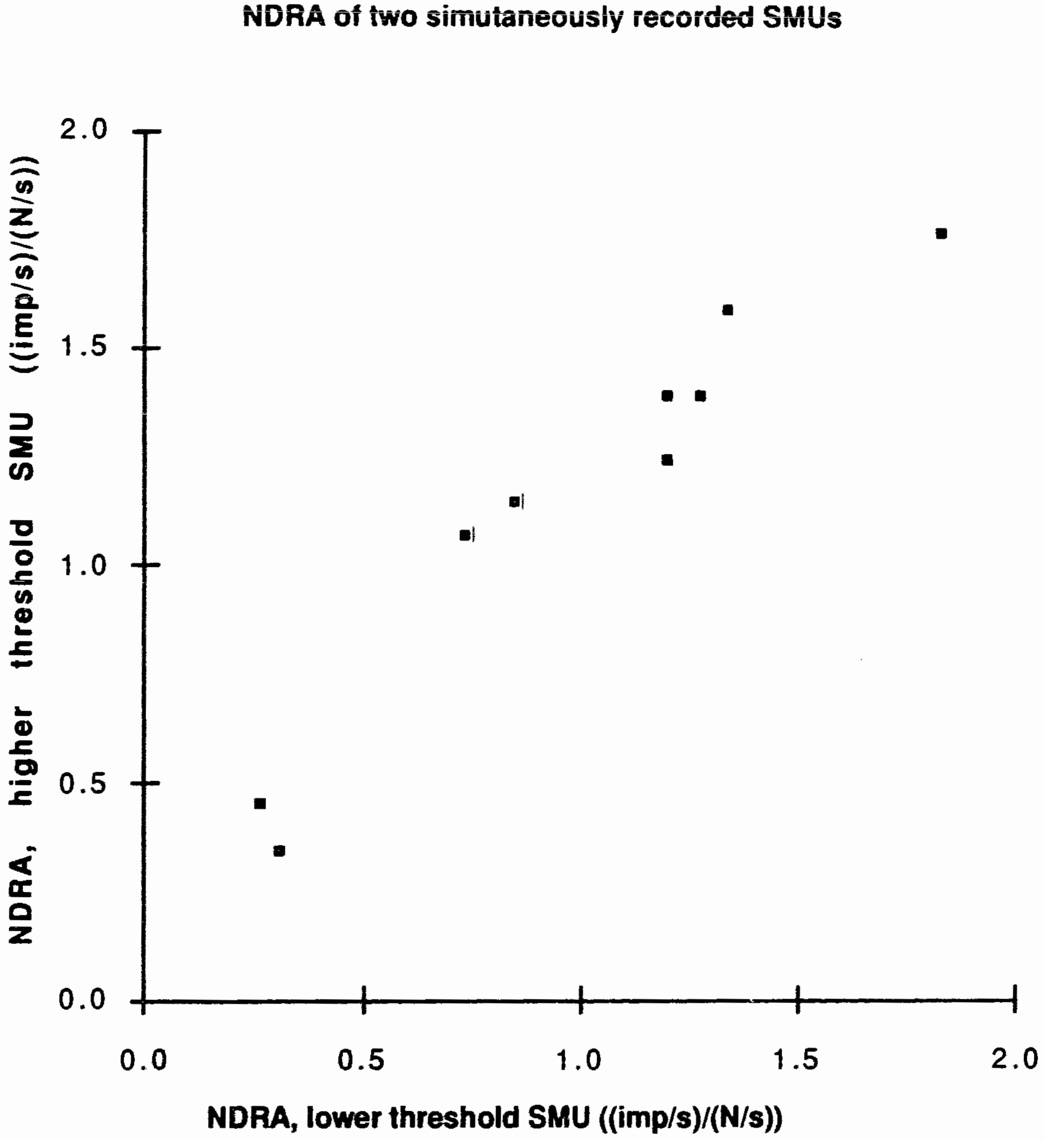

Fig. 29. The Normalized Dynamic Response Amplitude (NDRA) of SMU of higher and lower thresholds. The NDRA of a lower threshold SMU is smaller than that of the higher threshold SMU.

have different dynamic activity can not be concluded yet. Further comparison is needed. The results are shown in Fig. 29.

Steady State Response Amplitude. The Steady State Response Amplitude (SSRA) of lower threshold SMUs ranged from 0.56 (imp/s)/N to 4.34 (imp/s)/N with a mean of 2.21 (imp/s)/N. The SSRA of higher threshold SMUs ranged from 0.57 (imp/s)/N to 6.12 (imp/s)/N with a mean of 3.12 (imp/s)/N. The mean SSRA of lower threshold SMUs was significantly larger than that of higher threshold SMUs. The paired t-test shows a significance with p=0.002. For the same reason as above, the conclusion of different threshold SMU having different steady state property can not be taken yet. Further comparison is conducted. The results are shown in Fig. 30.

Difference between the firing rates versus the difference between the activities of SMU. To further investigate whether the effect of firing rate on the dynamic and steady state activities of SMU causes the difference in lower and higher threshold SMUs activities, the above data was reorganized to show the relation between the firing rate and SMU responses. The difference of the background firing rate was calculated by subtracting the firing rate of higher threshold SMU from the firing rate of lower threshold SMU. The difference of NDRA and SSRA was calculated by subtracting the NDRA and SSRA of SMUs in lower thresholds from those of SMUs at higher thresholds. From Fig. 31 and Fig. 32, the difference between the activities of SMU increase when the difference between the firing rates of SMU increase. When Fig. 31. is compared to Fig. 25. and Fig. 32. is compared to Fig. 26, the similarity of both pairs of figures is obvious. From the data for the difference of NDRA versus difference of firing rates, a positive relationship was observed (r=0.48). Similar relationship was seen from the data for the difference of NDRA versus difference of firing rates (r=0.55). Therefore, the difference in the activities of SMUs with different thresholds is more likely to be caused by the difference in the background firing rates than by the property of motoneuron.

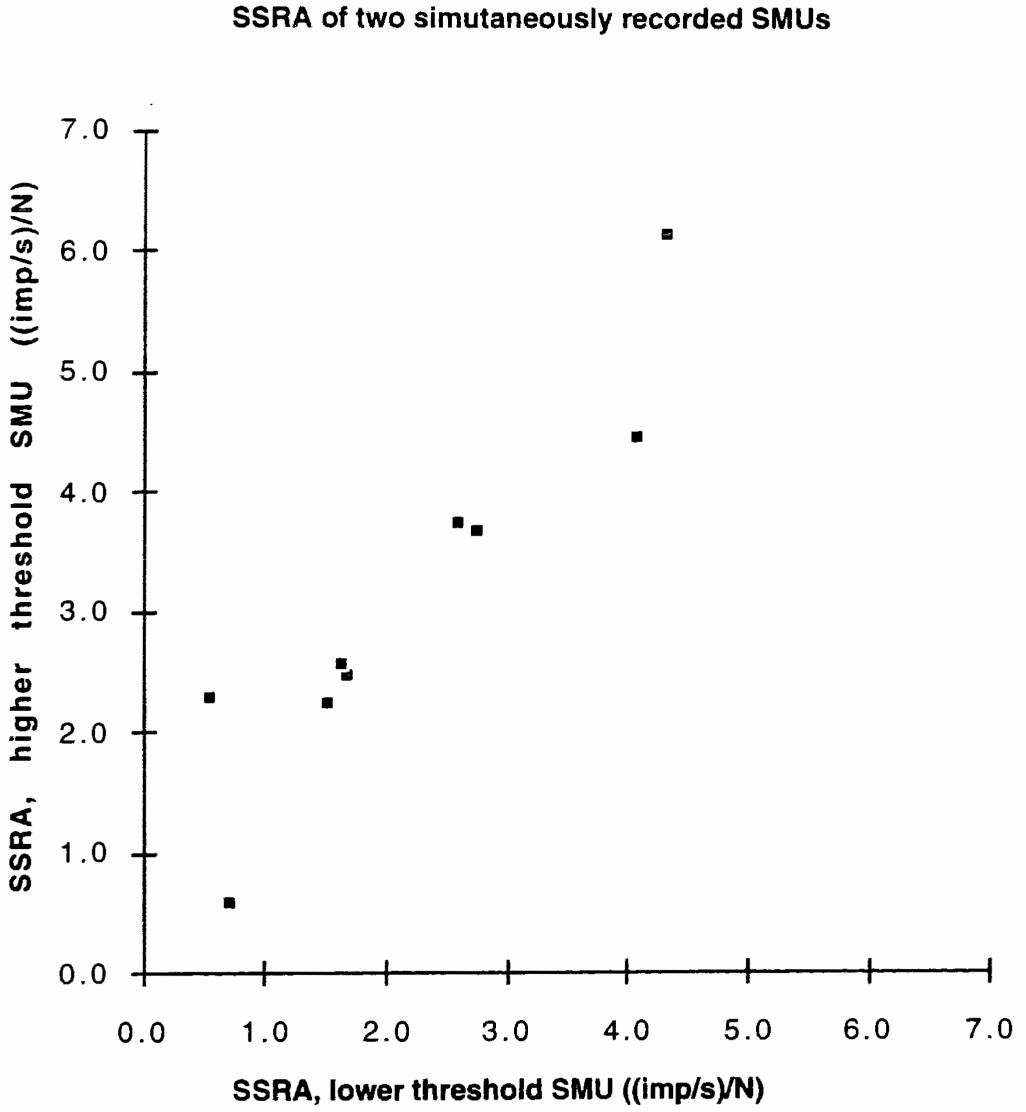

Fig. 30. The Steady State Response Amplitude (SSRA) of higher and lower threshold SMUs. The SSRAs of lower threshold SMUs are smaller than those of the higher threshold SMUs.

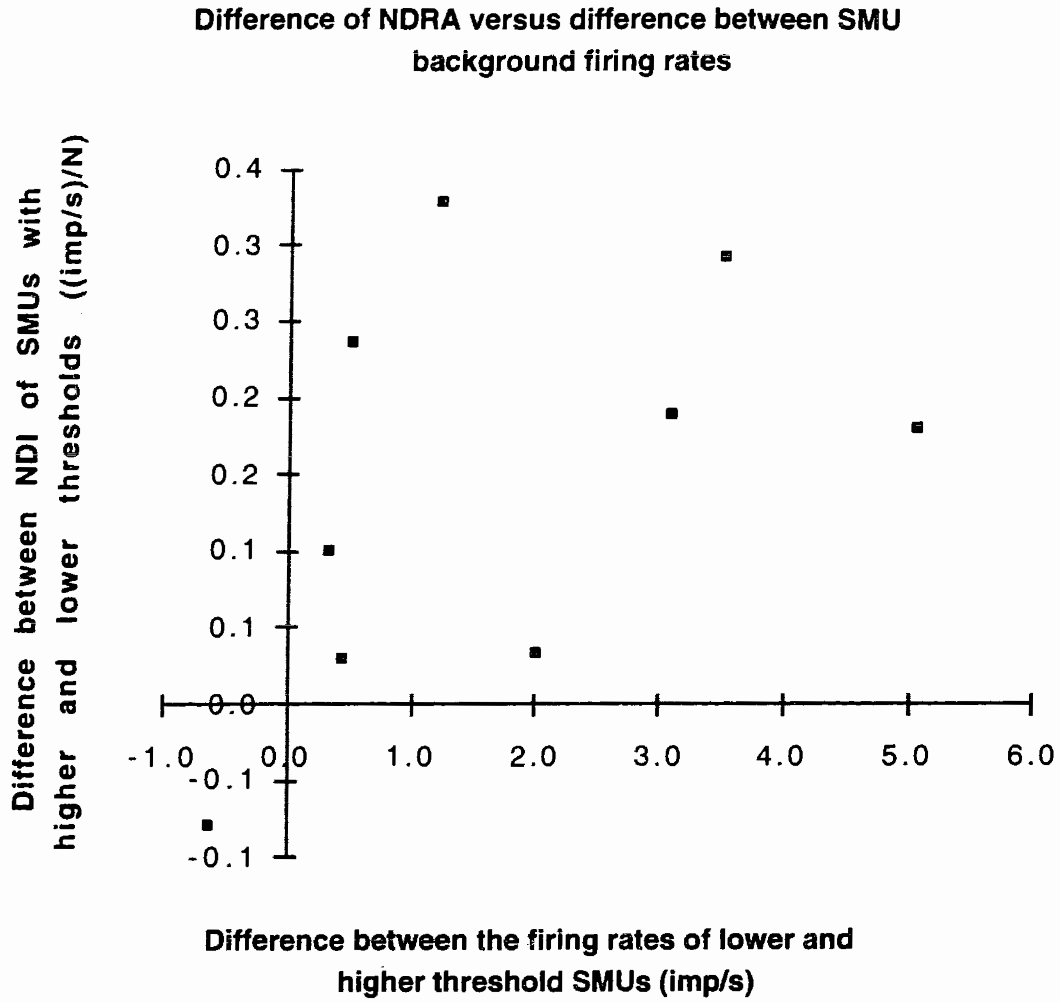

Fig. 31. Difference of NDRA versus difference of SMU background firing rates. The data were obtained from experiments of recording two SMUs simultaneously. Similar to Fig. 15., an increase in the difference between NDRA of SMU can be observed with the increase of difference in firing rates.

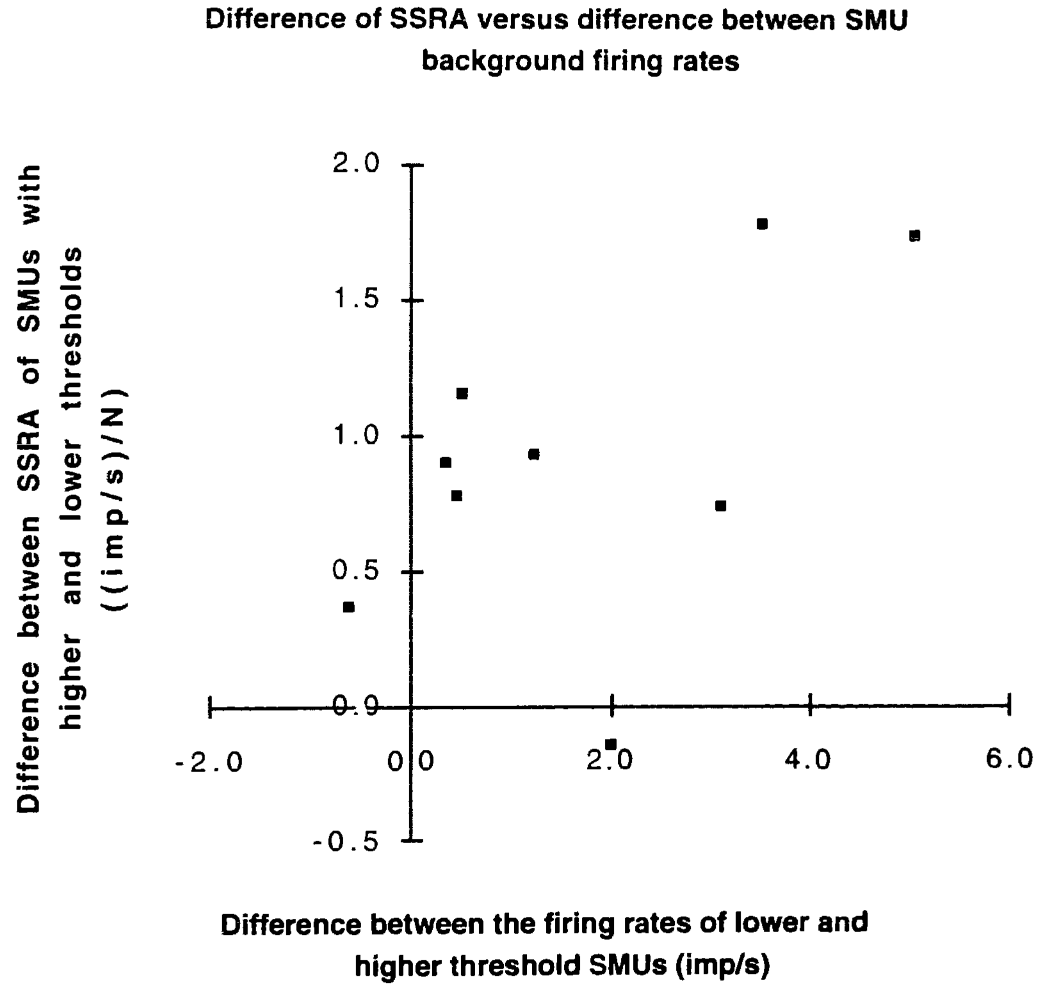

Fig. 32. Difference of SSRA versus difference of SMU background firing rates. The data were obtained from experiments of recording two SMU simultaneously. Similar to that in Fig. 15, an increase in the difference between SSRA of SMU can be observed with the increase of difference in firing rates.

DISCUSSION

The results of this study show that the dynamic activity of surface EMG and SMU is affected by the speed of isometric contraction. SMU dynamic activity is also affected by the background firing rate. For two SMUs with different thresholds, the difference between the dynamic activities of these two SMUs is more likely to be caused by the difference in their background firing rates, though the possibility of different threshold SMUs having different firing properties cannot be eliminated.

The results show that the dynamic response of surface EMG is linearly related to the contraction speed while the dynamic activity of SMU has a nonlinear relationship. The steady state activity of surface EMG is linearly related to the amplitude of contraction while the relation between the steady state activity of SMU and force amplitude is nonlinear. The following discussion will focus on the possible mechanisms and control of dynamic and steady state phases of surface EMG and SMU. The surface EMG activity will be discussed first.

I. Surface EMG Activity

In this study, surface EMG was recorded from the wrist flexors in proximity of the flexor carpi radialis (FCR) muscle. During wrist flexion, other muscles, such as the palmaris longus and flexor carpi ulnaris, are also activated. Therefore, the recorded EMG received contribution from several muscles activated in the task of flexion, though a large part of it was from FCR muscle. The measured force also resulted by the contraction of all these muscles. The SMU activity was collected only from FCR, which was one of muscles activated during flexion. Motor unit activity from FCR was compared with the EMG activity of this task.

The linear relationship between surface EMG and force in the dynamic phase of an isometric contraction observed in the present study has been shown previously by Bigland and Lippold (1954), and, Brown and Cooke (1981). The details of this relationship have been discussed by Milner-Brown and Stein (1975).

During the dynamic phase, since the relation of force and SMU responses is not linear, the linearity of surface EMG is suggested to arise from phasic contribution of additional motor units. This pattern was observed many times. While the tonically firing unit was studied, additional units fired a few action potentials during the dynamic phase. Phasic responses of motor units have also been reported by Palmer and Fetz (1985). These phasic responses were seen mostly during fast contractions when higher dynamic responses were required. For slow speed contractions, when dynamic phase of EMG was small, recruitment of additional SMUs was rarely observed.

No difference was observed between the Steady State Response Amplitude of surface EMG in slow and that in fast contractions when force amplitudes of the two conditions were equal. The steady state activity of EMG, which is the difference of EMG in hold period and background, showed a linear relationship to the force amplitudes. This proportional relationship between EMG and force output has been reported previously by Bigland and Lippold (1954), and, Milner-Brown and Stein (1975).

As shown in the results, the steady state activity of SMU, which is the difference of SMU firing rates between the hold period and background, has a non-linear relationship with the force amplitude. Therefore, for the same reason given in the discussion of dynamic properties of EMG, the contribution of changes in firing rates of tonically firing motor units was not enough to establish a linear relationship between the steady state activity of EMG and the force amplitude. There must be contribution from SMUs which were not recruited during the background but fired phasically during the steady state. The recruitment of new SMUs was observed very often in our experiments and by others (Taji and Kato, 1972; Freund, 1983). These newly recruited SMUs contribute to the linearity of surface EMG-force relation in the steady state.

II. Single Motor Unit Activity

The results show that single motor units are able to fire with different patterns during ramp-and-hold force output. The same single motor unit can fire tonically throughout the whole of ramp-and-hold force output or fire phasically only during the hold period of force or fire phasically during the rising phase of force. Most of the motoneurons are able to fire with different patterns depending on the force trajectory and threshold of the motoneurons. To recruit a motoneuron tonically throughout the ramp-and-hold force trajectory, the background force level should be larger than the tonic threshold of the motor unit. To recruit a motoneuron phasically during the ramp and continue during the hold period, the background force level should be lower than the tonic threshold of the motor unit while the hold force level should be higher than the threshold. The tonic firing rate of a given motoneuron during the background and hold periods is only related to the steady state level of force output but not contraction speed. However, to recruit a motoneuron only during the rising phase of force output, contraction speed should be considered. First, both of the background and hold forces should be lower than the tonic thresholds of these motor units. Then, increasing contraction speed could increase the number of SMUs recruited during the dynamic phase. The motoneuron being recruited or not during the phasic phase of force output depends on how large the contraction speed is. The higher the contraction speed, the more likely the motoneuron will be recruited during the rising phase of force trajectories. The conclusion was also made by others (Freund, 1983; Person and Kudina, 1972).

The underlying mechanisms for the dynamic phase of SMU firing are not very clear. Accommodation, after-hyperpolarization and recruitment will be discussed in this section. The inputs to the motoneuron, which was believed to be very important in the control of its dynamic activity (Palmer and Fetz, 1985), will be discussed in a separate section.

Accommodation is the phenomenon of increase in rheobase of motoneuron when a slow increase of current is injected into the soma. It may have influence on the dynamic phase of the firing patterns during the slow force contraction. Sasaki and Otani (1961) showed that large motoneurons were easier to accommodate than small motoneurons. The force needed in our experiments were low. The motoneuron recruited were believed to be small motoneurons. The effect of accommodation on them may not be prominent.

Baldissera et al. (1982) established a model of membrane conductance accumulation during afterhyperpolarization (AHP). They suggested that the accumulation of the AHP conductance during repetitive firing should be the main reason for adaptation. With the increase in AHP conductance, the input needed to generate the next spike increases. If the increase of synaptic or injected current is faster than the increase of AHP conductance, the interspike interval decreases, otherwise, it increases. The firing patterns of SMUs, therefore, are highly related to the inputs to the motoneuron. The higher the increase of synaptic inputs, the higher the peak firing rate (Baldissera et al., 1982).

Baldissera et al. (1982) showed that the peak firing rate in cat motoneurons was linearly related to the rising ramp slope of injected current. The force slope of a motor unit is linearly related to the slope of the inputs to motoneuron (Baldissera, 1987). From cat work, one would infer linearity between the speed of contraction and peak firing rate. In this study, saturation of motoneuron firing is prominent in high speed contractions. Saturation of peak firing rate is also seen by increasing background firing rate. Therefore, the nonlinearity observed in the present experiment between the peak firing rate and speed of contraction of wrist flexors may result from inhibitory feedback.

The steady state firing patterns of SMUs showed an increase in steady state firing rate with the increase of force. The increase of firing rate, however, was nonlinearly related to the force output. The saturation of firing rate was observed by many authors (Bigland and Lippold, 1954; Milner-Brown et al., 1973b). For the same SMU at different background firing rates, the responses decreased with increasing firing rate. In cat work, Kernell (1965) showed that when injected currents increased step by step, the repetitive firing rate of SMUs and the instantaneous firing rate for the first interspike intervals were linearly related to the injected current. Therefore, the saturation of firing rates in both of the cases implies that the effects of inhibitory inputs to the motoneuron increase with increasing firing rate. Renshaw cell and Ib inhibition, decrease in Ia feedback and saturation of synaptic currents could be possible candidates for the nonlinearities observed.

Comparison of two simultaneously recorded SMUs shows that the dynamic activities and steady state activities of different threshold SMUs are significantly different. The lower threshold SMUs had lower dynamic and steady state activity. However, the firing rates of the lower threshold SMUs were significantly higher than those of the higher threshold SMUs. Therefore, the difference could be either caused by the difference in background firing rates or the difference in the threshold.

Baldissera et al. (1987) observed that the smaller cat motoneurons had greater dynamic sensitivity than larger motoneurons. Therefore, if the inputs to the motoneuron pool are evenly distributed, then the smaller motoneurons should have larger dynamic firing rates than larger motoneurons if the background firing rates are zero. In voluntary contractions, if two motoneurons are recruited, there is a difference in the background firing rates. Further more, most of the motor units in our experiments are lower threshold motor units. The difference in the thresholds is not very large. As a results, the effect of background firing rates may have larger effect on the firing patterns of SMU.

III. Functional Importance

Tanji and Kato (1972) observed the shortest interspike interval during the dynamic phase was around 10ms. Short interspike intervals in the beginning of a spike train enhance the force output and the rate of force output (Burke, 1972). It was shown that initial interspike interval of 10ms was optimal for force production (Zajac and Young, 1978). Further shortening of interspike intervals did not improve the output force. The cat results have shown that the interspike intervals during the dynamic phase can shorten to 4-5 ms (Kernell, 1965; Baldissera et al., 1987). While increasing the slope of 'ramp and hold current' injected into motoneuron, the rate of force output of motor unit saturates even the peak firing rate of its motoneuron keeps rising (Baldissera et al., 1987). In behaving animals or man, inhibitory feedback probably limits the shortest interspike intervals to 10 ms since any further shortening does not improve the speed of force output.

The nonlinear responses during the steady state contractions are also of functional significance. There is a narrow range of firing rates within which the tension production is very sensitive to the change in firing rate (Rack and Westbury, 1969). Further increases in firing rates produce very small changes in tension. The same trend was observed in cats (Baldissera and Parmiggiani, 1975). Therefore, for the muscle to work in an efficient range for greater economy and sensitivity, it is better to recruit new units rather than to keep increasing the firing rate of the already recruited units. This is what our results show. It has been shown that in some muscles, more than 50% of motor units are recruited within 30% of maximal voluntary contraction (Milner-Brown et al. 1973a, b, c; Freund, 1983). In the present experiments, the forces used were relatively small. The contribution of recruitment to force output must be prominent. The observations for ramp-and-hold contractions support the mechanisms of rate coding and recruitment of motor units to increase force and the rate of change of force.

IV. Inputs To The Motoneuron Pool

The combined inputs to the motoneuron pool discussed here are the combination of inputs from all sources to the motoneuron pool such as the inputs from descending pathways, interneurons, Renshaw cells and peripheral afferents. It is obvious that the inputs include a dynamic phase and a steady state phase during ramp and hold force output. When the contraction speed increases, the slope of inputs to the motoneuron pool increases. During the dynamic phase while the slope of inputs increase, there are two possible cases, one is a ramp and hold input without an overshoot and the other with an overshoot just like the dynamic phase of SMU firing. For the first case, because of the dynamic properties of motoneuron (Kernell, 1965a; Baldissera, 1982), the firing of SMU should show an overshoot in its dynamic phase. And if the input currents during the hold period are higher than rheobase but lower than the threshold for repetitive firing for some motoneurons, these motoneurons will fire briefly and not repetitively (Granit et al., 1963; Kernell, 1965a). In the latter case, of course, the phasic firing of some motoneurons will be observed.

In the present experiments, we observed quite a few motor units firing phasically during the ramp period only in fast contractions but not in slow contractions with the same amplitudes. The steady state magnitudes of motoneuron responses and EMG in fast contractions were not different from those in slow contraction with the same amplitudes. This implies that the combined inputs in the hold periods to the motoneuron pool and motoneuron were the same during the hold period in fast and slow contractions with same amplitudes. As being discussed before, the accommodation effects in our case is small. Therefore, if the combined input in the hold period is larger than the rheobase of the motoneuron but smaller than the threshold of repetitive firing, the motoneuron should fire briefly in both fast and slow contractions. Since it is not the case, then, this is most likely that during in fast contraction, there is an overshoot in the phasic phase of the combined inputs. This overshoot will recruited more motoneurons during the fast contraction than those in slow contraction during the ramp period.

One of the excitatory inputs to motoneuron pool is from the monosynaptic corticomotoneuronal pathway. Palmer and Fetz (1985) suggested that corticomotoneurons with different firing patterns could affect the dynamic phase of motoneuron firing. Palmer (1982) observed four kinds of motoneuron firing patterns in the corticomotoneuron, namely, phasic, tonic, phasic tonic and decrementing. The phasic and phasic tonic firing corticomotoneuron have a clear dynamic phase of firing, an overshoot. The overshoot, if large enough, can cause an overshoot in the combined synaptic input to the motoneuron pool in fast contractions. In slow contractions, on the other hand, the number of the phasic and phasic tonic firing corticomotoneuron may not be large enough to generate an overshoot in the synaptic current during the dynamic phase.

Renshaw cells are inhibitory interneurons which are excited by motoneuron itself and feedback onto the motoneuron. The recurrent inhibition from Renshaw cells are believed to be fast enough to control all phases of the motoneuronal firing pattern (Eccles et al., 1961). The negative feedback from Renshaw cells could decrease the effective excitatory inputs to the motoneurons. The Ib afferent feedback also offers inhibitory inputs to motoneuron. The distance from the spinal cord to the FCR muscle is about 0.5 meter. The average conduction speed of the motoneuron axon is about 50 m/s. It will take approximately 20 ms for feedback and action potential to travel along the Ib axon and come back along α-motoneuron axon. Adding up the time for the synaptic connections, it will take at least 30 ms for the Ib loop to react on the dynamic phase. Ib inhibition will provide effective inhibition during the steady state phase but may not during the dynamic phase of the fast contractions. Furthermore, during contraction the spindles may unload leading to the decreased spindle afferent feedback.

V. Conclusions

This work shows that single motor unit activity has a nonlinear relationship to the force output during both the dynamic and the steady state phases. The linear relationship of EMG and force is attributed to rate coding of tonically firing motoneurons and phasic recruitment of additional motoneurons during the dynamic and steady state phases. The nonlinear behaviour of motor units operate in its most effective range of force-firing rate relationship.

APPENDICES: DATA TABLES

EMG DATA: Slow versus Fast Contractions

Fast Contractions					Slow Contractions				
filename	dF/dt	ADRA	NDRA	SSRA	filename	dF/dt	ADRA	NDRA	SSRA
units	N/s	uV	uV/(N/s)	uV/N	units	N/s	uV	uV/(N/s)	uV/N
F13T3AFU	11.69	10.849	0.9281	0.662	F13T3ASC	1.41	1.153	0.815	0.584
A05T3CF1	16.01	14.352	0.8962	1.343	A05T3CS	1.88	1.463	0.778	0.973
E02T1AF1	13.82	62.873	4.5494	0.669	E02T1AS	1.33	10.518	7.895	0.765
E02T2AF	13.67	60.038	4.3927	6.872	E02T2AS	5.50	1.132	0.206	6.140
F14T1AFC	7.16	7.098	0.9907	4.478	F14T1ASC	0.93	0.943	1.016	4.153
F14T1BFC	6.81	8.758	1.2861	2.258	F14T1BSC	1.13	1.219	1.076	1.969
F21T1AF	8.22	6.680	0.8124	2.140	F21T1AS	1.28	0.680	0.531	2.030
F21T1BF	5.17	6.213	1.2020	2.482	F21T1BS	0.67	0.306	0.460	2.230
F21T2AF	6.17	7.630	1.2362	1.511	F21T2AS	0.76	0.620	0.816	1.663
F12T1AF	6.12	5.725	0.9354	1.287	F12T1AS	1.17	0.670	0.574	2.533
F12T2BF	3.75	4.960	1.3226	1.990	F12T2BS	0.87	0.748	0.856	3.060
F12T3AF	4.07	4.656	1.1435	1.863	F12T3AS	0.85	0.557	0.652	1.276

EMG DATA: F[0-1] versus F(0-2] Contractions

F(0-1) Contractions					F(0-2) Contractions				
filename	**dF/dt**	**ADRA**	**NDRA**	**SSRA**	**filename**	**dF/dt**	**ADRA**	**NDRA**	**SSRA**
units	**N/s**	**uV**	**uV/(N/s)**	**uV/N**	**units**	**N/s**	**uV**	**uV/(N/s)**	**uV/N**
A05T1AF2	15.00	87.435	5.830	4.683	**A05T1AF3**	31.95	97.512	3.052	5.660
A05T3CF1	16.01	14.352	0.896	1.343	**A05T3CF2**	23.31	16.612	0.713	0.966
A05P3CF1	20.23	17.005	0.840	1.020	**A05P3CF2**	28.07	22.584	0.805	1.215
E01T3AF1	13.93	34.988	2.511	5.154	**E01T3AF2**	26.06	47.915	1.839	3.744
E02T1AF1	13.82	62.873	4.549	0.669	**E02T1AF2**	24.50	86.120	3.516	2.406
E02T3AF1	8.91	34.148	3.834	6.430	**E02T3AF2**	13.00	70.452	5.419	5.033
E02T3AF1	8.91	34.148	3.834	6.430	**E02T3AF4**	13.38	56.977	4.259	3.433
E02T3AF1	8.91	34.148	3.834	6.430	**E02P3AF2**	15.11	54.041	3.578	5.514
E02T3AF1	8.91	34.148	3.834	6.430	**E02P3AF4**	15.82	46.393	2.932	4.872
E06T1AF1	7.25	30.480	4.203	8.994	**E06P1AF2**	9.35	42.846	4.581	10.626
O05TF1	7.05	3.075	0.436	7.996	**O05TF2**	15.95	14.092	0.884	4.474
O05TF3	8.20	13.021	1.588	4.062	**O05TF2**	15.95	14.092	0.884	4.474

SMU DATA: Slow versus Fast Contractions

		Fast Contractions					Slow Contractions		
filename	**dF/dt**	**ADRA**	**NDRA**	**SSRA**	**filename**	**dF/dt**	**ADRA**	**NDRA**	**SSRA**
units	**N/s**	**imp/s**	**(imp/s)/(N/s)**	**(imp/s)/N**	**units**	**N/s**	**imp/s**	**(imp/s)/(N/s)**	**(imp/s)/N**
F13T3AF	11.69	9.782	0.837	0.927	**F13T3AS**	1.41	4.814	3.406	1.293
O20T2BF	1.39	12.321	8.839	9.991	**O20T2BS**	0.26	2.275	8.852	11.416
M15T1AF	4.10	13.550	3.307	6.615	**M15T1AS**	0.40	3.105	7.811	6.996
P05T3CF1	16.01	6.133	0.383	1.067	**P05T3CS**	1.88	2.778	1.476	1.147
E02T1AF1	13.82	20.554	1.487	2.791	**E02T1AS**	1.33	3.346	2.512	1.843
E02T1AF3	11.51	13.868	1.205	0.555	**E02T1AS**	1.33	3.346	2.512	1.843
E02T2AF	13.67	19.262	1.409	4.256	**E02T2AS**	5.50	3.762	0.684	2.127
E02T3AF1	8.91	13.038	1.464	4.493	**E02T3AS**	0.77	2.324	3.034	4.130
E06T1AF	7.25	8.472	1.168	1.496	**E06T1AS**	1.75	1.789	1.025	1.783
O27T2AF	11.52	8.221	0.714	1.965	**O27T2AS**	1.84	3.146	1.709	2.146
N10T3AF	4.03	5.976	1.482	2.921	**N10T3AS**	0.78	1.335	1.702	2.460
F14T1AFC	7.16	4.832	0.674	2.218	**F14T1ASC**	0.93	2.937	3.167	1.758
F14T1BFC	6.81	5.472	0.804	1.533	**F14T1BSC**	1.13	1.979	1.746	1.483
F21T1AF	8.22	8.149	0.991	1.629	**F21T1AS**	1.28	3.847	3.003	1.661
F21T1BF	5.17	6.849	1.325	1.023	**F21T1BS**	0.67	2.163	3.249	1.402
F21T2AF	6.17	8.887	1.440	2.118	**F21T2AS**	0.76	4.082	5.376	1.286
O27T2AF	7.06	8.221	1.165	3.209	**O27T2AS**	1.13	3.146	2.790	3.504
N10T3AF	2.23	5.976	2.675	5.273	**N10T3AS**	0.43	1.335	3.073	4.441

SMU DATA: F[0-1] versus F(0-2] Contractions

F(0-1) Contractions						F(0-2) Contractions				
filename	dF/dt	ADRA	NDRA	SSRA		filename	dF/dt	ADRA	NDRA	SSRA
units	N/s	imp/s	(imp/s)/(N/s)	(imp/s)/N		units	N/s	imp/s	(imp/s)/(N/s)	(imp/s)/N
M15T1AF	4.10	13.550	3.307	6.615		M15T1AF2	4.52	11.109	2.459	2.782
P05T1AF3	15.00	14.022	0.935	1.725		P05T1AF4	31.95	12.672	0.397	0.625
P05T3CF1	16.01	6.133	0.383	1.067		P05T3CF2	23.31	7.953	0.341	0.572
E01T3AF1	13.93	2.020	0.145	1.063		E01T3AF2	26.06	2.747	0.105	0.650
E02T1AF1	13.82	20.554	1.487	2.791		E02T1AF2	24.50	18.718	0.764	0.971
E02T1AF3	11.51	13.868	1.205	0.555		E02T1AF2	24.50	18.718	0.764	0.971
E02T3AF1	8.91	13.038	1.464	4.493		E02T3AF2	13.00	13.872	1.067	2.641
E02T3AF1	8.91	13.038	1.464	4.493		E02T3AF4	13.38	11.417	0.853	3.281
A27T2BF1	7.19	16.745	2.329	1.988		A27T2BF2	9.91	12.932	1.306	1.586
S07T2AF1	10.18	8.603	0.845	1.218		S07T2AF2	31.02	14.743	0.475	1.076
O05T1AF1	7.05	9.475	1.344	2.583		O05T1AF2	15.95	11.751	0.737	1.638
O05T1BF1	7.05	11.135	1.580	3.732		O05T1BF2	15.95	16.985	1.065	2.568
O05T1AF3	8.20	9.881	1.205	1.688		O05T1AF2	15.95	11.751	0.737	1.638
O05T1BF3	8.20	10.126	1.235	2.459		O05T1BF2	15.95	16.985	1.065	2.568
O05T1BF5	8.74	11.209	1.282	2.752		O05T1BF2	15.95	16.985	1.065	2.568
O05T1BF1	7.05	11.135	1.580	3.732		O05T1BF7	16.15	13.718	0.849	2.871
O05T1BF3	8.20	10.126	1.235	2.459		O05T1BF7	16.15	13.718	0.849	2.871
O05T1BF5	8.74	11.209	1.282	2.752		O05T1BF7	16.15	13.718	0.849	2.871

SMU DATA: lower versus higher background firing rate

Lower background firing rate						Higher background firing rate				
filename	Rate	ADRA	NDRA	SSRA		filename	Rate	ADRA	NDRA	SSRA
units	imp/s	imp/s	(imp/s)/(N/s)	(imp/s)/N		units	imp/s	imp/s	(imp/s)/(N/s)	(imp/s)/N
E01T1AF1	10.7	8.751	1.742	4.016		E01T1AF3	11.7	8.785	0.848	4.340
E02T1AF1	6.3	20.554	1.487	2.791		E02T1AF3	11.5	13.868	1.205	0.555
E02T3AF2	6.6	13.872	1.067	2.641		E02T3AF4	7.7	11.417	0.853	3.281
A27T4AF1	8.1	4.827	0.420	2.583		A27T4AF3	10.2	3.420	0.264	1.509
O05T3AF1	6.4	17.225	1.981	2.255		O05T3AF3	9.5	12.103	0.905	1.519
O05T1AF1	8.4	9.475	1.344	2.583		O05T1AF3	9.9	9.881	1.205	1.688
O05T1BF1	7.9	11.135	1.580	3.732		O05T1BF3	9.4	10.126	1.235	2.459
O05T1BF1	7.9	11.135	1.580	3.732		O05T1BF5	9.0	11.209	1.282	2.752
O05T1BF5	9.0	11.209	1.282	2.752		O05T1BF3	9.4	10.126	1.235	2.459
O05T1BF7	3.4	13.718	0.849	2.871		O05T1BF2	7.2	16.985	1.065	2.568
N23T1AF1	7.4	14.223	1.776	2.853		N23T1AF3	10.8	8.856	1.106	1.302

SMU DATA: zero (phasic) versus nonzero (tonic) background firing rate

Phasic firing						Tonic firing				
filename	Rate	ADRA	NDRA	SSRA		filename	Rate	ADRA	NDRA	SSRA
units	imp/s	imp/s	(imp/s)/(N/s)	(imp/s)/N		units	imp/s	imp/s	(imp/s)/(N/s)	(imp/s)/N
P05P2BF	0.1	8.800	0.725	4.177		P05T2BF	6.4	7.896	0.686	1.433
P05P3CF2	0.0	3.159	0.156	2.391		P05T3CF2	8.4	7.953	0.341	0.572
P05P3CF4	0.0	9.892	0.352	2.272		P05T3CF2	8.4	7.953	0.341	0.572
E01P1BF	0.8	11.334	2.256	11.586		E01T1BF	8.1	11.811	1.139	6.117
E01P4BF	0.8	12.370	1.417	7.031		E01T4AF	8.4	9.153	1.049	3.263
E02P3AF2	0.0	10.476	0.694	6.284		E02T3AF2	6.6	13.872	1.067	2.641
E02P3AF4	0.2	17.151	1.084	6.638		E02T3AF4	7.7	11.417	0.853	3.281
E06P1AF	0.0	7.563	0.809	6.962		E06T1AF	8.5	8.472	1.168	1.496
A27P2BF1	0.0	19.447	3.212	9.895		A27T2BF1	10.3	16.745	2.329	1.988
A27P2BF2	0.0	18.979	2.417	6.646		A27T2BF2	9.8	12.932	1.306	1.586
A27P4BF1	0.0	5.960	0.519	5.662		A27T4BF3	7.0	5.852	0.452	2.244
O05P4BF3	0.0	18.244	2.790	18.200		O05T4BF1	10.1	8.389	1.757	4.445
O05P1BF4	0.1	14.974	1.212	5.761		O05T1BF2	7.2	16.985	1.065	2.568
O05P1CF3	0.0	16.522	2.029	13.065		O05T1CF5	8.6	12.085	1.382	3.652

SMU DATA: lower versus higher threshold motoneurons

Lower threshold motoneuron					Higher threshold motoneuron				
filename	Rate	ADRA	NDRA	SSRA	filename	Rate	ADRA	NDRA	SSRA
units	imp/s	imp/s	(imp/s)/(N/s)	(imp/s)/N	units	imp/s	imp/s	(imp/s)/(N/s)	(imp/s)/N
P05T3BF2	8.4	7.180	0.308	0.724	P05T3CF2	6.4	7.953	0.341	0.572
E01T1AF3	11.7	8.785	0.848	4.340	E01T1BF	8.1	11.811	1.139	6.117
E02T1AF3	11.5	13.868	1.205	0.555	E02T1BF3	6.4	15.930	1.385	2.288
A27T4AF3	10.2	3.420	0.264	1.509	A27T4BF3	7.0	5.852	0.452	2.244
O05T4AF1	9.4	8.765	1.835	4.084	O05T4BF1	10.1	8.389	1.757	4.445
O05T1AF1	8.4	9.475	1.344	2.583	O05T1BF1	7.9	11.135	1.580	3.732
O05T1AF3	9.9	9.881	1.205	1.688	O05T1BF3	9.4	10.126	1.235	2.459
O05T1AF2	8.5	11.751	0.737	1.638	O05T1BF2	7.2	16.985	1.065	2.568
O05T1BF5	9.0	11.209	1.282	2.752	O05T1CF5	8.6	12.085	1.382	3.652

SMU Results Table

TYPE OF COMPARISON	TYPE OF RESPONSE	RANGE OF RESPONSE VALUES	MEAN VALUES	n	t	p
<u>SAME UNIT</u> S(0-1) vs F(0-1)	ADRA	1.3 -4.8 vs 4.8 - 20.6 imp/s	2.86 < 9.98	18	7.01	0.000002
	NDRA	0.7 - 8.9 vs 0.4 - 8.8 (imp/s)/(N/s)	3.17 > 1.74	18	4.48	0.0003
	SSRA	1.1 - 11.4 vs 0.6 - 10.0 (imp/s)/N	2.93 ≈ 3.00	18	0.39	0.7
<u>SAME UNIT</u> F(0-1) vs F(0-2)	ADRA	2.0 -20.6 vs 2.7 - 18.7 imp/s	11.4 < 13.36	18	2.53	0.02
	NDRA	0.14 - 3.31 vs 0.11 - 2.46 (imp/s)/(N/s)	1.35 > 0.87	18	7.68	0.000006
	SSRA	0.6 - 6.6 vs 0.6 - 3.3 (imp/s)/N	2.68 > 1.93	18	3.07	0.007
<u>SAME UNIT</u> SLOW FIRING RATE vs FAST FIRING RATE	NDRA	0.4 - 2.0 vs 0.3 - 1.3 (imp/s)/(N/s)	1.37 > 1.02	11	3.10	0.01
	SSRA	2.3 - 4.0 vs 0.6 - 4.3 (imp/s)/N	2.98 > 2.22	11	3.07	0.01
<u>SAME UNIT</u> PHASIC vs TONIC	NDRA	0.16 - 3.21 vs 0.34 - 2.3 (imp/s)/(N/s)	1.41 > 1.07	14	2.38	0.03
	SSRA	2.3 - 18.2 vs 0.57 - 6.12 (imp/s)/N	7.61 > 2.56	14	5.70	0.00008
<u>TWO UNITS</u> LOWER THRESHOLD vs HIGHER THRESHOLD	NDRA	0.26 - 1.84 vs 0.34 - 1.76 (imp/s)/(N/s)	1.00 < 1.15	9	3.25	0.01
	SSRA	0.56 - 4.34 vs 0.57 - 6.12 (imp/s)/N	2.21 < 3.12	9	4.49	0.002
<u>TWO UNITS</u> SLOW FIRING RATE vs FAST FIRING RATE	NDRA	0.34 - 1.84 vs 0.26 - 1.76 (imp/s)/(N/s)	1.16 > 0.99	9	4.46	0.002
	SSRA	0.57 - 6.12 vs 0.56 - 4.46 (imp/s)/N	3.08 > 2.25	9	3.43	0.009

REFERENCES

Araki T. and Otani T. (1959) Accommodation and local response in motoneurons of toad's spinal cord. Jap. J. Physiol. 9: 69-83

Baldissera F. and Parmiggiani F. (1975) Relevance of motoneuronal firing adaptation to tension development in the motor unit. Brain Res. 91: 315-320

Baldissera F., Campadelli P. and Piccinelli L. (1982) Neural encoding of input transients investigated by intracellular injection of ramp currents on cat a-motoneurones. J. Physiol. 328:73-86.

Baldissera F., Campadelli P. and Piccinelli L. (1984) The Dynamic Response of Cat a-Motoneurons Investigated by Injection of Sinusoidal Currents. Exp Brain Res 54: 275-282

Baldissera F., Campadelli P. and Piccinelli L. (1987) the dynamic response of cat gastrocnemius motor units investigated by ramp-current injection into their motoneurones. J. Physiol. 387:317-33

Bigland B. and Lippold O. (1954) Motor unit activity in the voluntary contraction of human muscle. J Physiol. 125: 322-335.

Borg J. et al. (1978) Axonal conduction velocity and voluntary discharge properties of individual short toe extensor motor units in man. J. Physiol. 277: 143-152.

Brown, S.H.C. and Cooke, J.D. Amplitude-and instruction-dependent modulation of movement-related electromyoram activity in humans. J. Physiol. Lond. 316: 97-107, 1981.

Burke, R.E., Rudomin P. and Zajac F.E. (1970) Catch properties in single mammalian motor units. Science 168:122-124.

Calancie, B. and Bawa, P. (1985) Firing patterns of human carpi radialis motor units during the stretch reflex. J. Neurophysiol. 53: 1179-1193.

Cheney P.D. and Fetz E.E. (1980) functional classes of primate corticomotoneuronal cells and their relation to active force. J. Neurophysiol. 44: 773-791.

Deluca C.J. (1979) Physiology and mathematics of myoelectric signals. Trans. Biomed. E. 26:313-325.

Deluca C.J. (1985) Control properties of motor units. J. Exp. Biol. 115: 125-136.

Deluca C.J., Lefever R.S., Mccue M.P. and Xenakis A.P. (1982a) Behavior of human motor units in different muscles during linearly varying contractions.

Deluca C.J., Lefever R.S., Mccue M.P. and Xenakis A.P. (1982b) Control scheme governing concurrently active human motor units during voluntary contractions. J. Physiol. 329: 113-128

Eccles J.C., Eccles R.M. and Lundberg A. (1958) The action potentials of the alpha motoneurones supplying fast and slow muscles. J. Physiol. 142: 275-291.

Eccles J.C., Eccles R.M., Iggo A. and Lundberg A. (1961) Electrophysiological investigation on Renshaw cells. J. Physiology 159: 461-478

Freund H.-J. Budingen H.J. and Dietz V. (1975) Activity of single motor units from human forearm muscle during voluntary isometric contractions. J. Neurophysiol. 38: 933-946.

Freund H.J. (1983) Motor unit and muscle activity in voluntary motor control. Physiol. Rev. 63: 387-436

Ghez C. and Gordon J. (1987) Trajectory control in targeted force impulses. I. Role of opposing muscles. Exp. Brain Res. 67: 225-240.

Gillies J. D. (1972) Motor unit discharge patterns during isometric contraction in man. J. Physiol. 223: 36p-37p.

Granit R., Kernell D. and Shortess R. (1963) Quantitative aspects of repetitive firing of mammalian motoneurons, caused by injected currents. J. Physiol. 168: 911-931.

Grimby L. and Hannerz J. (1977) Firing rate and recruitment order of toe extensor motor units in different modes of voluntary contraction J. Physiol. 264: 865-879.

Kandel E. R. and Schwartz J. H.(1985) In Principle of neural science (2nd edition) by Elsevier science publishers B.V. pp: 49-86.

Kernell D. (1965a) the adaptation and the relation between discharge frequency and current strength of cat lumbosacral motoneurones stimulated by long-lasting injected currents. Acta Physiol. Scand. 65:65-73.

Kernell D. (1965b) High-frequency repetitive firing of cat lumbosacral motoneurones stimulated by long-lasting injected currents. Acta Physiol. Scand. 65: 74-86.

Kernell D. (1965c) The limits of firing frequency in cat lumbosacral motoneurones possessing different time course of afterhyperpolarization. Acta Physiol. Scand. 65:87-100

Kernell D. (1972) The early phase of adaptation in repetitive impulse discharge of cat spinal motoneurons. Brain Research 41: 184-186.

Lawrence J.H. and Deluca C.J. (1983) Myoelectric signal versus force relationship in different human muscles. J Appl. Physiol. 54: 1653-1659.

Milner-Brown H.S. and Stein R.B. (1975) The relation between the surface electromyogram and muscular force. J. Physiol. 246:549-569

Milner-Brown H.S., Stein R.B. and Yemm R. (1973a) The orderly recruitment of human motor units during voluntary isometric contraction. J. Physiol. 230:359-370

Milner-Brown H.S., Stein R.B. and Yemm R. (1973b) Changes in firing rate of human motor units during linearly changing voluntary contractions. J. Physiol. 230: 371-390

Milner-Brown H.S., Stein R.B. and Yemm R. (1973c) The contractile properties of human motor units during voluntary isometric contractions. J. Physiol. 228: 285-306.

Monster A.W. (1979) Firing rate behavior of human motor units during isometric voluntary contraction: relation to unit size. Brain Res. 171: 349-354.

Monster A.W. and Chan H. (1977) Isometric force production by motor units of extensor digitorum communis muscle in man. J. Neurophysiol. 40:1432-1443.

Palmer S.S. and Fetz E.E. (1985) Discharge properties of primate forearm motor units during isometric muscle activity. J Neurophysiol. 54: 1178-1193.

Person R.S. and Kudina L.P. (1972) Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. Electroencephalograghy and Clinical Neurophysiol. 32: 471-483.

Rack, P.M.H. and Westbury, D.R. The effects of length and stimulus rate on tension in the isometric cat soleus muscle. J. Physiol. Lond. 204: 443-460, 1969.

Sasaki K. and Otani T. (1961) Accommodation in spinal motoneurons of the cat. Jap. J. Physiol. 11: 443-456.

Tanji J. and Kato M. (1973) Firing rate of individual motor units in voluntary contraction of abductor digiti minimi muscle in man. Exp. Neurology 40: 771-783.

Tanji J. and Kato M. (1981) Activity of low- and high- threshold motor units of abductor digiti quinti in slow and fast voluntary contractions. In: Progress in clinical neurophysiology, edited by J.E. Desmedt. Vol. 9: 137-144.