

# Discharge Properties of Primate Forearm Motor Units During Isometric Muscle Activity

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## SUMMARY AND CONCLUSIONS

1. Activity of single motor units (MUs) was recorded in forelimb muscles of rhesus macaques while they generated isometric ramp-and-hold torques about the wrist. Multiunit electromyographic (EMG) activity was recorded from 10–12 identified flexor and extensor muscles of the wrist and digits with implanted EMG wire electrodes. Single MUs from these muscles were recorded with a remotely controlled tripolar microelectrode array. The parent muscle of each MU was determined by compiling MU-triggered averages of multiunit EMGs.

2. The MU firing patterns during the isometric task were determined from response histograms aligned with change in torque. At moderate torque levels, MUs ( $n = 86$ ) exhibited four types of discharge patterns during the ramp-and-hold trajectory: phasic-tonic (23%), tonic (33%), decrementing (39%), and phasic (5%). 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.

3. The relation between MU firing rate and torque was investigated as the monkeys generated responses of different levels of static torque during the hold period. Mean firing rate during the hold was found to be proportional to static torque up to moderate torque levels, where it reached a maximum. In the linear range, the mean rate-torque slope was  $3.4 \pm 1.9$  imp/s per  $10^5$  dyn · cm ( $n = 9$ ).

## INTRODUCTION

Properties of single motor units (MUs) have been studied extensively in acute experiments in cats, and during isometric responses in humans (see Refs. 6, 9, and 23 for reviews). The twitch tension of human MUs was found to be inversely proportional to contraction time (36) and directly proportional to recruitment threshold (17, 36). MUs were recruited into action in the order of the relative amplitude of their intramuscular action potentials (45) and their contribution to the surface-recorded EMG (38, 44). The *firing pattern* of human MUs was found to be related to axonal conduction velocity and to muscle fiber histochemistry; continuously firing MUs were associated with slow axonal conduction velocities and oxidative muscle fibers, whereas intermittently firing MUs had fast axonal conduction velocities and glycolytic muscle fibers (3, 4, 29).

Relatively few studies have dealt with the physiological properties of MUs in nonhuman primates. The twitch tensions and contraction times of forearm MUs have been documented for extensor digitorum communis (EDC) MUs in baboons (18) and for forearm flexor and extensor muscles in the macaque (32). Histochemical analysis indicated that forearm muscles in monkeys contain both oxidative and glycolytic fiber types (35). Like human forelimb MUs, jaw muscle MUs of the monkey had contraction times and action-potential amplitudes proportional to recruitment threshold, and their twitch tensions were inversely proportional to recruitment threshold (14).

The firing patterns of single forearm MUs in monkeys performing isometric ramp-and-

hold responses have not been examined heretofore. In the present study, forearm MUs were identified by 1) their firing patterns during ramp-and-hold torque trajectories, 2) their MU signatures obtained from MU-triggered averages (MU-TAs) of parent EMG, and 3) the time of their firing onset relative to the beginning of the ramp-and-hold isometric contraction. MU firing patterns were compared with the discharge patterns under identical behavioral conditions of corticomotoneuronal (CM) cells that facilitate forearm muscles (12).

We also observed the firing frequency of single MUs as a function of static torque, and obtained results that were consistent with previous findings in humans, i.e., MU firing rates increased with increases in static and dynamic muscle force (8, 25, 30). Investigators have studied the relative contribution of firing rate versus recruitment toward muscle force at different force levels in humans (2, 34, 37). For monkey forearm MUs, changes in firing rate appeared to be important at low to moderate torque levels, since firing rates stabilized at high torque levels. The rate-torque relation of MUs was compared with that obtained for CM cells that facilitate forearm muscle activity (12). Preliminary reports of some of these results have been presented elsewhere (42).

## METHODS

### *Training of monkeys*

Four male rhesus macaques (*Macaca mulatta*) were trained to exert alternate flexor and extensor isometric force about the wrist joint, as described previously (12, 22). They sat in a primate chair inside a sound-attenuating booth (model 100, Industrial Acoustics, New York) with their right arm constrained in a manipulandum designed to quantify torque about the wrist. The manipulandum consisted of a styrofoam-lined, stainless steel cylinder, which held the forearm (Fig. 1). The hand was held securely in a semiprone position, with the fingers extended in a styrofoam-lined metal cylinder attached to the axis of a wheel located below the wrist. The rim of the wheel was clamped to preclude any wrist movement, thus rendering muscle contractions isometric. The absence of movement was confirmed by direct observation and by a potentiometer that would have recorded any rotation of the manipulandum.

Four strain gauges were attached to the spokes of the wheel and were connected in a bridge circuit

to register the active torque exerted about the wrist joint. The strain gauges were calibrated for isometric torque by hanging weights on the locked manipulandum at a designated distance from the hub of the wheel. Torque was defined as the product of force and distance, i.e.,  $T = F \cdot d = m \cdot a \cdot d$ , where  $T$  is torque,  $F$  is force,  $d$  is distance from the hub of the wheel to the position from which the weights were hung for calibration,  $m$  is mass of the suspended weights, and  $a$  is acceleration of gravity ( $980 \text{ cm/s}^2$ ). The strain gauge sensitivity was  $0.26 \mu\text{V}$  per  $\text{dyn} \cdot \text{cm}$ .

Isometric wrist torques with a ramp-and-hold time course and alternating between flexion and extension zones were rewarded on a variable-ratio schedule with a small amount of banana or applesauce disbursed by a syringe feeder pump. A digital logic circuit (BRS Electronics, Beltsville, MD) detected successful isometric contractions: a dynamic torque ramp from the flexion to extension zone (or vice versa), followed by a 1-s static hold within a torque zone.

Monkeys usually were required to work at moderate torque levels of  $8\text{--}15 \times 10^5 \text{ dyn} \cdot \text{cm}$ . To study MU firing as a function of torque, we also required the monkeys to generate different levels of static torque in zones of 6–9, 8–12, 9–15, 15–22, and  $23\text{--}34 \times 10^5 \text{ dyn} \cdot \text{cm}$ . The ranges of the hold zone were widened in proportion to the mean torque level required. Torque levels above  $15 \times 10^5 \text{ dyn} \cdot \text{cm}$  were considered high. Since the monkeys did not reliably sustain torque levels  $>34 \times 10^5 \text{ dyn} \cdot \text{cm}$ , this level was defined as the maximal behavioral contraction (MBC). Defined in percentage of MBC the required torque zones were 17–26, 24–35, 26–44, 44–64, and 67–100% MBC.

When MU discharge was studied as a function of torque level, many units became active at torque levels  $>6 \times 10^5 \text{ dyn} \cdot \text{cm}$  (cf. Fig. 10). The six ranges of torque zones were chosen to encompass recruitment levels of most MUs of the active muscles and still maintain reliable isometric responses. Previous investigations of human MU recruitment during low to maximal voluntary isometric contractions have shown that most MUs are recruited at less than one-half the maximum voluntary contraction (24, 26, 34, 36, 45). A systematic study of MUs recruited at the highest torque levels, where MU isolation becomes difficult, was not attempted in this investigation.

Visual and auditory cues provided the monkey with feedback concerning its behavior. When the active torque exceeded the maximum required level, a yellow light came on. When the torque was in the correct range, a green light signaled extension torques, and a red light signaled flexion. A tone sounded throughout holding in the correct range, and a beep signaled the completion of a correct response.

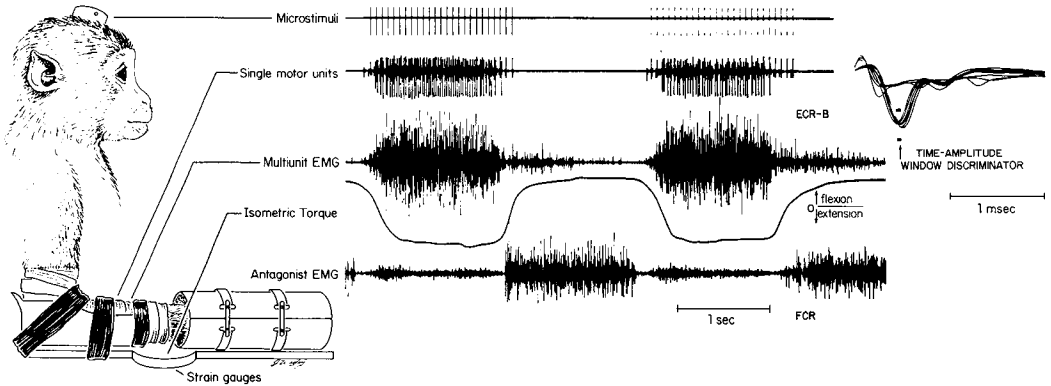


FIG. 1. Experimental paradigm. The monkey generated isometric torque response about the wrist joint alternating between flexion and extension zones. Strain gauges in the locked wheel transduced torque. A single MU recorded with the microelectrodes shown on a fast sweep at *right*, to illustrate window of discriminator that generated acceptance pulses from a single MU. (This record also shows stimulus artifacts coincident with intracortical microstimuli.) Multiunit EMG was recorded with implanted wire electrodes. The figure also illustrates intracortical microstimuli (ICMS) used in the subsequent study (39); the results in this report were obtained in the absence of ICMS.

Daily recording sessions lasted 4–6 h. The monkeys typically performed 3,000–10,000 correct responses, and consumed 15–28 oz of banana or applesauce in a session.

### EMG implant and MU recording

EMG activity of up to 12 forelimb muscles was recorded differentially from pairs of multistranded, stainless steel wires (AS 632 Bioflex insulated wire, Cooner Sales, Chatsworth, CA), inserted transcutaneously as described previously (20–22). During surgery, the stimulus thresholds and movements observed for each muscle were recorded carefully and compared with anatomical information about the forearm muscles of rhesus macaques (31). The EMG wires were taped along the arm and led to a terminal connector at the upper arm. The terminal connector, constructed of ITT Cannon Centi-Loc strip connectors, was attached to another connector strip with wires leading to preamplifiers.

We recorded from six extensor and six flexor muscles: extensor digitorum 2 and 3 (ED2,3) extensor digitorum 4 and 5 (ED4,5), extensor carpi ulnaris (ECU), extensor digitorum communis (EDC), extensor carpi radialis brevis (ECR-B), extensor carpi radialis longus (ECR-L), flexor digitorum sublimis (FDS), flexor digitorum profundus (FDP), flexor carpi ulnaris (FCU), palmaris longus (PL), flexor carpi radialis (FCR), and pronator teres (PT). Their relative locations in the arm have been illustrated previously (Fig. 1 in Ref. 22). Synergists refer to muscles that are coactivated to produce a movement, either extension or flexion. The six extensor muscles were considered “antagonists” of the flexor muscles, and vice versa. The EMG electrodes were implanted in the forearm muscles several days before the experimental sessions, and the sessions

for each implant lasted 2–3 wk. The monkey remained in the primate chair during this period, and a Plexiglas divider prevented access to the EMG wires by the contralateral arm.

The MU microelectrode was made from three insulated tungsten wires, 0.005 in. in diameter and 4.5 in. long, bonded together and insulated with Epoxylite. The tip of this triad was ground to a bevelled surface on a corborundum glass-filled rotary wheel. The exposed tips were then reinsulated with Epoxylite, and carefully nicked with a 30-gauge hypodermic needle to expose a minimal area. Impedances of the microelectrodes were 100 k $\Omega$  to 5 M $\Omega$ , measured at 1 kHz.

Single MUs were recorded differentially between the optimal pairs of the tripolar microelectrode. Bipolar recordings insured a good signal-to-noise ratio. To prevent damaging their tips during penetration of the skin, the microelectrodes were held in a 21-gauge hypodermic needle; after placement in the arm, the needle was retracted from the arm, leaving only the microelectrode in the muscle. Some monkeys did not react when the microelectrode was inserted, whereas others required brief (2-min) anesthesia (5% halothane). The microelectrode was held in a hydraulic microdrive, remotely controlled by a micromanipulator, allowing the microelectrode to be repositioned in the muscles while the monkey was performing the task. Isometric fixation of the forearm provided sufficient stability to record a single MU for up to 2 h.

The MU microelectrode was connected via high-impedance probes to Grass P511 preamplifiers with 30-Hz to 10-kHz (one-half amplitude) cutoff frequencies (5). Sometimes MU recordings were filtered with a 60-Hz band-reject filter. Amplification of MU action potentials was about 1,000–50,000

and was adjusted for optimal tape recording of each MU. Because this optimal amplification varied for each MU, the amplitudes of MU potentials from different sessions could not be compared. When measured, the absolute amplitudes of MU action potentials were about 0.5–1.5 mV.

Isolation of single MUs was verified by observing 1) action potentials of approximately the same shape, including duration, amplitude, and form, and 2) firing of the MU with regular interspike intervals (15). Further criteria are discussed below.

In a recording of several MUs, pulses could be triggered from a single MU with a BAK time-amplitude window discriminator (model DIS-1, BAK Electronics). To trigger an acceptance pulse, the waveform had to cross a threshold voltage level and then, after a specified time delay, reach a value within a specified voltage window. The waveforms of discriminated units were photographed from the oscilloscope screen with a Tektronix C-5 camera. The frequency of acceptance pulses was monitored occasionally by a frequency calculator (1–100 Hz) to confirm that discrimination was of only a single MU. When more than one MU generates acceptance pulses, the frequency monitor typically shows abnormally short interpulse intervals (19). The isolation of a single MU potential was confirmed further by displaying the delayed MU waveforms on a storage oscilloscope triggered from the acceptance pulses. In some cases, more precise selection criteria were implemented by cascading two window discriminators.

Data were recorded on a Honeywell 101 tape recorder with one direct channel (bandwidth: 0.1–37.5 kHz at 7.5 ips) and 15 FM wideband channels (bandwidth: 0–5 kHz at 7.5 ips). Recorded data included intracortical microstimulation pulses (39), EMG activity of 12 muscles, torque, and differential recordings of MUs.

### Data analysis

MU-TAs. Cross-correlations of the single MU with EMG activity from different forearm muscles were used to identify the muscle to which the MU belonged. The MU discriminator acceptance pulses were used to trigger averages of rectified and unrectified multiunit EMG from synergist muscles. Usually such MU-TAs were flat for all but one muscle (the parent muscle), indicating negligible cross talk in the averages from other muscles.

The MU-TA of multiunit EMG of the parent muscle had a characteristic shape (number of phases, duration, amplitude) that served as a “signature” of the particular MU. The MU action potential, recorded with the tripolar microelectrode, varied in shape as a function of electrode position, and occasionally decreased over time (perhaps due to fluid accumulation around the tip of the microelectrode). The MU action potentials differed con-

siderably in amplitude and number of phases for different MUs, as well as for the same MU recorded at different sites in the muscle. To control for the possibility of recording the same MU more than once, the microelectrode was assumed to be recording the same MU, even when recordings at different sites in the muscle showed different action potentials, if the MU signatures were identical.

RESPONSE AVERAGES. “Response averages” of MU firing, rectified EMG, and torque during the behavioral ramp-and-hold responses were compiled on the PDP-8/e computer. The response averages were triggered from the ramp change in active torque, as described previously (20–22). The response averages were 2,500 ms in duration (500 ms before and 2 s after the trigger), divided into 250 bins of 10-ms bin width. Response averages usually included 35–70 responses. The temporal derivative of the torque ( $dT/dt$ ) was calculated, and both torque and  $dT/dt$  were compared with the firing pattern of the MU. Time histograms of MU firing were used to determine the firing frequency and firing pattern of single MUs during the isometric contraction.

The mean tonic firing frequency of single MUs during the hold period was usually determined by calculating the mean firing frequency between 400 and 650 ms after the termination of the ramp phase. The static torque level during the hold period was determined as the mean torque in the same interval. A statistics program written for the PDP/8e computer calculated mean counts per bin over selected intervals, and exhibited a “base-line level” (in this case, the mean tonic level) as well as the level of any multiple of the standard deviation (SD) away from base line. The algorithm for SD was

$$SD = \sqrt{\frac{\sum_{i=1}^n (X_i - \bar{x})^2}{(n-1)}} \quad (1)$$

Some MUs exhibited a phasic component of firing during the ramp phase. The phasic firing frequency during the ramp was determined by calculating the mean firing frequency of all bins in the ramp phase that were between the earliest and latest bins  $>1$  SD above the mean tonic level.

Response histograms of some single MUs revealed a steadily decremting firing frequency during the static hold period. For these “decremting” MUs, the mean firing frequency during the hold period was quantified as the mean firing rate between 200 and 800 ms after the end of the ramp.

Response histograms also were used to investigate changes in firing frequency and pattern with changes in torque levels. The slope of the relation between firing rate and static torque was determined by linear regression analysis. Response histograms and av-

erages were smoothed for display only, using the following algorithm

$$s_i = (n_{i-1} + 2n_i + n_{i+1})/4 \quad (2)$$

where  $n_i$  is the original content of  $i$ th bin, and  $s_i$  is content of  $i$ th smoothed bin. Smoothing reduces the variance by averaging adjacent bin values. However, all statistical analyses were calculated using unsmoothed values.

The onset of MU firing relative to attainment of zero torque was determined as the difference between the time when the torque ramp reached zero in the torque average and the time of onset of MU firing in the response histogram. Zero torque was achieved during the ramp transition from one hold zone to the other. The onset of MU firing was determined to be the first of at least three consecutive bins in the response histogram with values  $> 0$  imp/s.

**STATISTICAL ANALYSIS.** For statistical analyses, we used the group comparison  $t$  test (47). In one analysis we compared mean phasic and tonic firing rates of MUs, and in another we compared mean firing rates during different 200-ms intervals during the hold period to determine whether MUs had a significant decrement in firing rate during the static hold. The statistics program calculated the mean, SD, variance,  $t$  value, and degrees of freedom for different intervals of the response histograms of MU firing. The computer also calculated a modified degree-of-freedom value to compensate for unequal variances in determining statistical significance (46).

Using the group comparison  $t$  test, we also tested for a difference in the relative onset times of MU firing for MUs of different firing patterns. Finally, we used the  $t$  test to determine the statistical significance of differences in the slopes of the rate-torque relation for different MUs.

## RESULTS

### Identification of parent muscles

The action potentials and signatures of different MUs varied in form from diphasic to multiphasic waveforms. The MU signatures (obtained from MU-TAs of multiunit EMG recorded via wire electrodes) had durations of 6–20 ms; these were invariably longer than durations of the MU action potentials recorded via a microelectrode ( $\sim 2$ –6 ms). The signature of a given MU remained unchanged over hours of recording, whereas signatures of different MUs differed in amplitude and number of components. Thus, the MU signature in the parent muscle could be used to identify the same MU, even when the microelectrode recorded a different action-potential waveform as it moved through the muscle.

Figure 2 illustrates the records of a MU in ECR-B. The MU signature (in the MU-TA of ECR-B) was a triphasic waveform of 6-ms duration (trace 3). MU-TAs of the other synergist muscles were essentially flat (traces 5–8). The MU action potential recorded by the microelectrode was triphasic, and had a duration of 2 ms (trace 1).

### MU firing frequency and patterns

Figure 3 illustrates the firing pattern of this ECR-B MU during the extensor ramp-and-hold contraction. This MU had a phasic-tonic

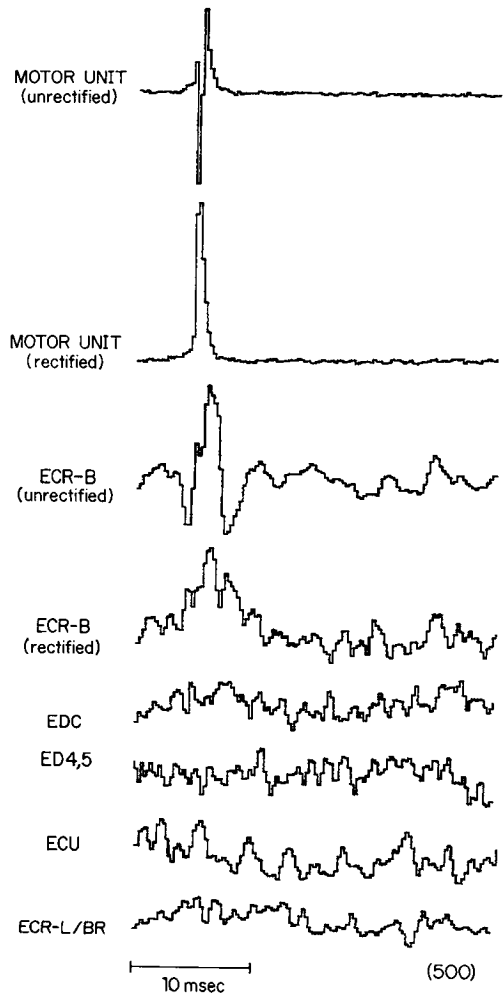


FIG. 2. MU-TAs of the single MU record (unrectified and rectified), of EMG from ECR-B (the parent muscle), and of rectified EMG of synergist muscles. The MU-TA of unrectified EMG from ECR-B was this MU's signature. In this and subsequent figures, the number of samples in the averages is given in *parentheses* at bottom right.

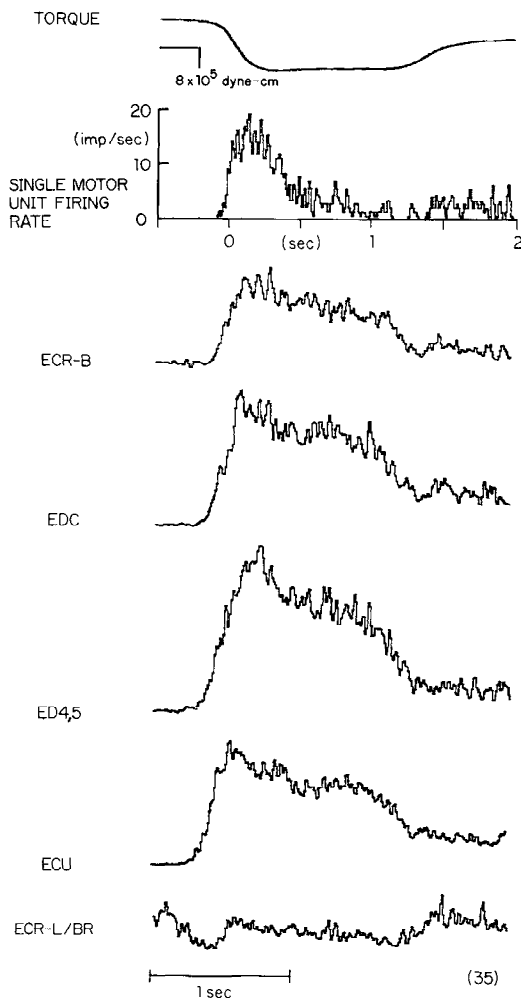


FIG. 3. Response pattern of a single MU belonging to ECR-B (cf. Fig. 2). Response averages shown from *top to bottom*: isometric torque, histogram of MU discharge, and rectified EMG of extensor muscles. The record from ECR-L/BR shows some flexion-related EMG, probably due to a contribution from brachioradialis (BR). In this and subsequent figures, zero torque level is indicated by the *horizontal calibration bar*, and flexion torque is positive.

firing pattern, with peak firing frequency occurring nearer to maximum  $dT/dt$  ( $dT/dt_{max}$ ) than to  $T_{max}$ . The firing frequency was substantially higher during the initial ramp phase than during the subsequent hold period. The average of the rectified EMG of ECR-B also showed a phasic-tonic firing pattern; however, the EMG during the hold period was almost as great as that during the ramp phase, presumably due to contributions from tonic firing of other MUs.

On the basis of their activity during the ramp-and-hold torques, the firing patterns of MUs could be grouped into four types: *phasic-tonic*, *tonic*, *phasic*, and *decrementing*. These MU firing patterns were distinguished on the basis of quantitative measures of the changes in firing rate associated with the ramp-and-hold torque trajectory ( $T$ ) and its derivative ( $dT/dt$ ).

MUs with a *tonic* firing pattern exhibited an approximately constant firing frequency throughout the static hold period (Fig. 4). There was no statistically significant difference in their firing rate during any 200-ms interval selected during the hold period from 0 to 800 ms after the end of the ramp. Tonic MUs attained their maximum firing rate closer to the end of the ramp (when torque also attained its maximum value) than to the time of maximum  $dT/dt$ .

MUs with a *phasic-tonic* firing pattern exhibited a phasic discharge during the ramp phase that was significantly higher ( $P < 0.05$ ) than the tonic firing frequency during the hold period. The maximum firing rate of phasic-tonic MUs was attained closer to  $dT/dt_{max}$  than to the end of the ramp. Figure 4 illustrates an extensor phasic-tonic MU with a mean phasic firing frequency of 39.7 imp/s and a mean tonic firing rate of 27.1 imp/s. The dynamic index of phasic-tonic MUs was calculated as the drop in firing rate from the peak phasic discharge to the mean tonic firing rate. For 20 phasic-tonic MUs, the dynamic index ranged from 12.8 to 42.8 imp/s, with a mean of  $22.5 \pm 8.8$  imp/s.

MUs with a *phasic* firing pattern exhibited a phasic discharge during the torque ramp and negligible firing during the hold period; they attained their maximum firing rate near  $dT/dt_{max}$  (Fig. 5). The maximum firing rate of the phasic MU illustrated in Fig. 5 was 42 imp/s.

Many MUs showed a *decrementing* firing pattern characterized by a steadily decreasing firing rate during the hold period. Comparing the firing rates during two different 200-ms intervals of the hold period showed a statistically significant decrease in firing rate, which exceeded any possible decrease in torque. (Torque typically did not decrease more than 6% during the hold.) Usually, mean rates during intervals of 100–300 ms and 400–600 ms after the end of the ramp were compared using the statistics program. The maximum firing

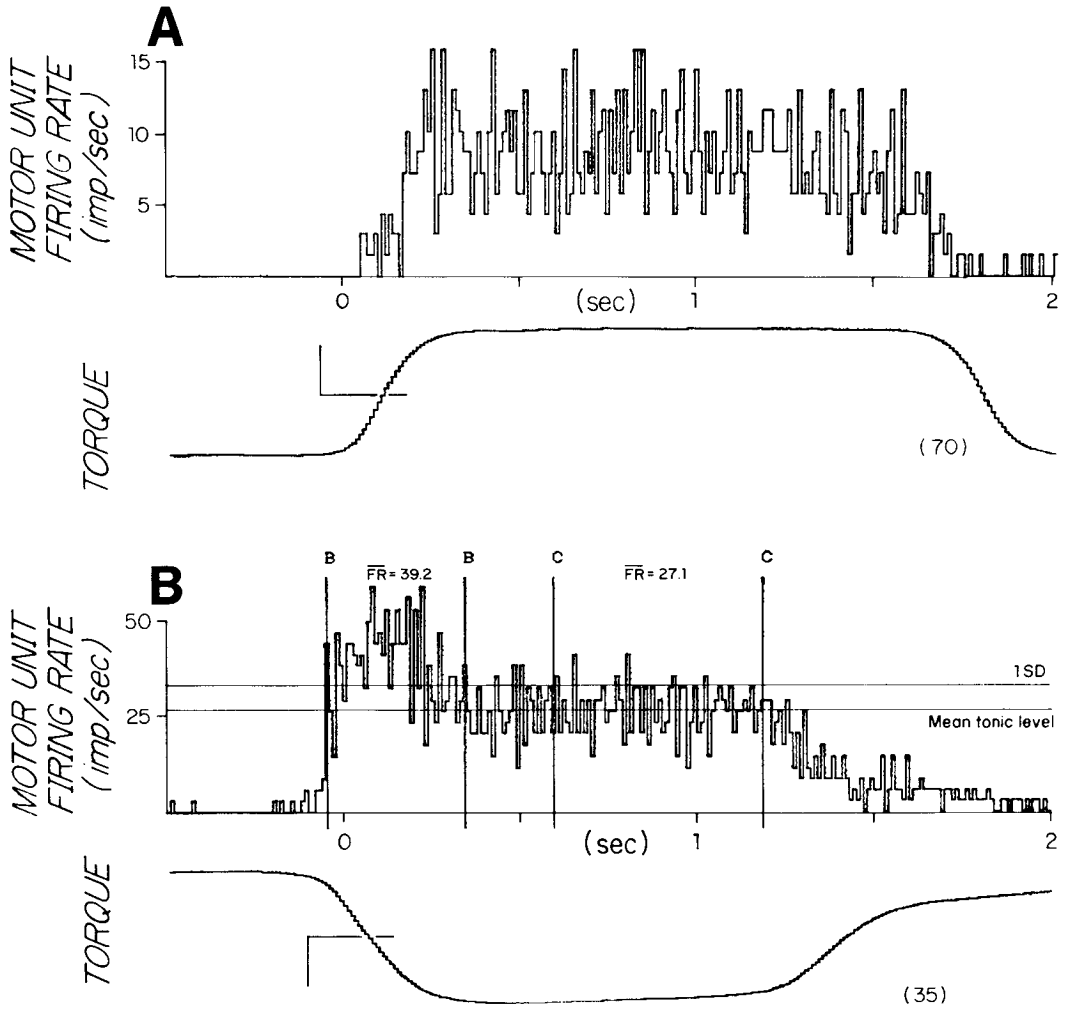


FIG. 4. Response histograms of *A*: tonic (flexor) and *B*: phasic-tonic (extensor) MU, with corresponding response averages of torque. For the phasic-tonic MU, the phasic (*B*) group included all bins during the ramp that were between the first and last bin that exceeded the comparison (*C*) group by more than 1 SD. The comparison (*C*) group included bins from 200 to 800 ms after the end of the ramp. The mean phasic (*B*) and mean tonic (*C*) firing frequencies were significantly different ( $P < 0.001$ ). Torque calibration is  $6 \times 10^5$  dyn · cm.

rate of decrementing MUs was attained closer to the end of the ramp (near  $T_{\max}$ ) than to  $dT/dt_{\max}$ .

The rate at which firing frequency dropped differed substantially for different decrementing MUs. The firing rate of some decrementing units fell to 0 imp/s toward the end of the hold period. Some decrementing MUs showed a decrement to 0 imp/s at low torque levels, but not at higher torque levels. Figure 6 illustrates two representative decrementing MUs. The extensor MU (upper records) showed a dec-

rement in rate of 31% ( $26.2 - 18.1 = 8.1$  imp/s,  $8.1/26.2 = 31\%$ ) from the interval 100–300 ms to 400–600 ms after the end of the ramp. The flexor MU (lower records) showed a decrement of 77% during these same intervals; its firing rate dropped to 0 imp/s at  $\sim 650$  ms after the end of the ramp.

The discharge patterns of 86 forelimb MUs were documented at a single torque level, usually at a moderate torque level. Of these, 23% had a phasic-tonic firing pattern, 33% were tonic, 39% were decrementing, and 5% were

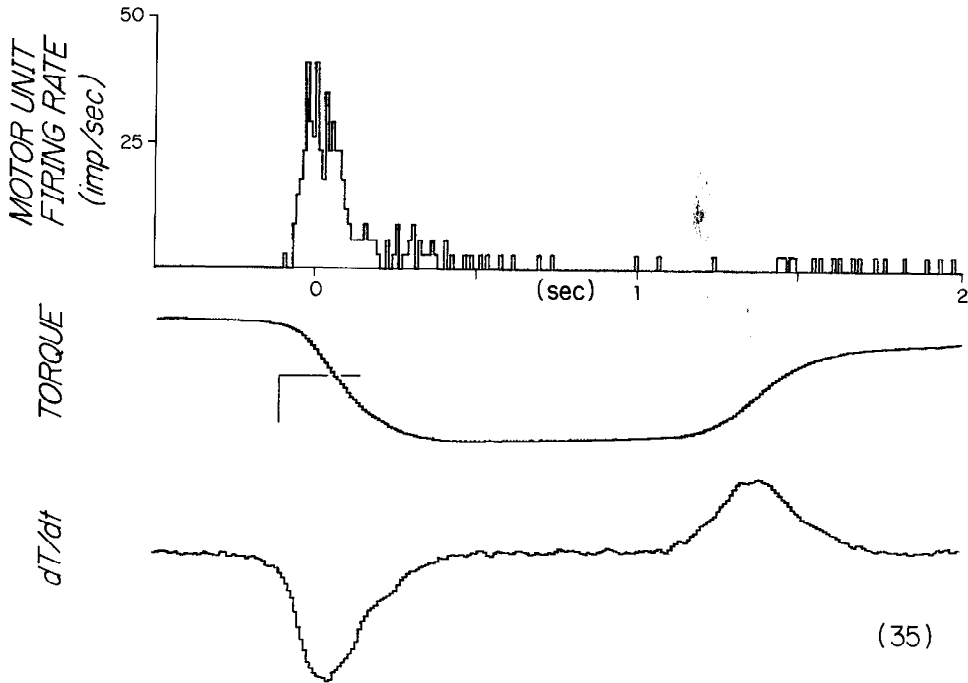


FIG. 5. Example of a phasically firing MU. *Top*: histogram of MU discharge; *middle*: isometric torque ( $T$ ); *bottom*: rate of change of torque ( $dT/dt$ ). Torque calibration is  $6 \times 10^5$  dyn  $\cdot$  cm. Note that MU reached maximum firing rate close to peak of  $dT/dt$ .

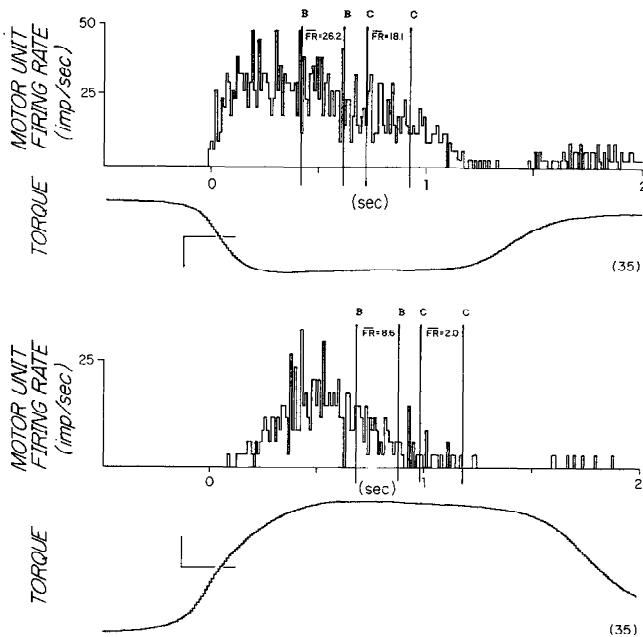


FIG. 6. Two decrementing MUs. Mean firing rate is given for the intervals at 100–300 (B) and 400–600 (C) ms after the end of the ramp of the isometric response; the difference in rate was highly significant ( $P < 0.01$ ). Torque calibration is  $6 \times 10^5$  dyn  $\cdot$  cm.



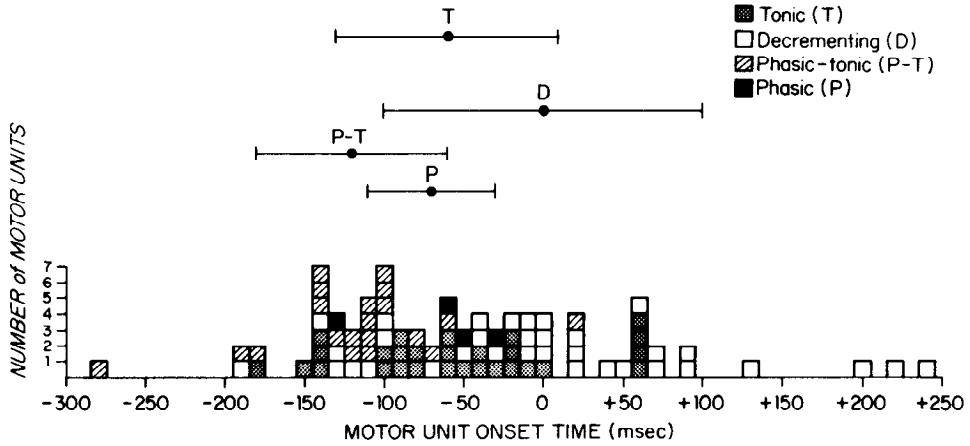


FIG. 7. Onset times of MU firing relative to attainment of zero torque. MU firing pattern is indicated separately for each. Bars over frequency distribution summarize the mean (center dot) and SD of onset times for each group.

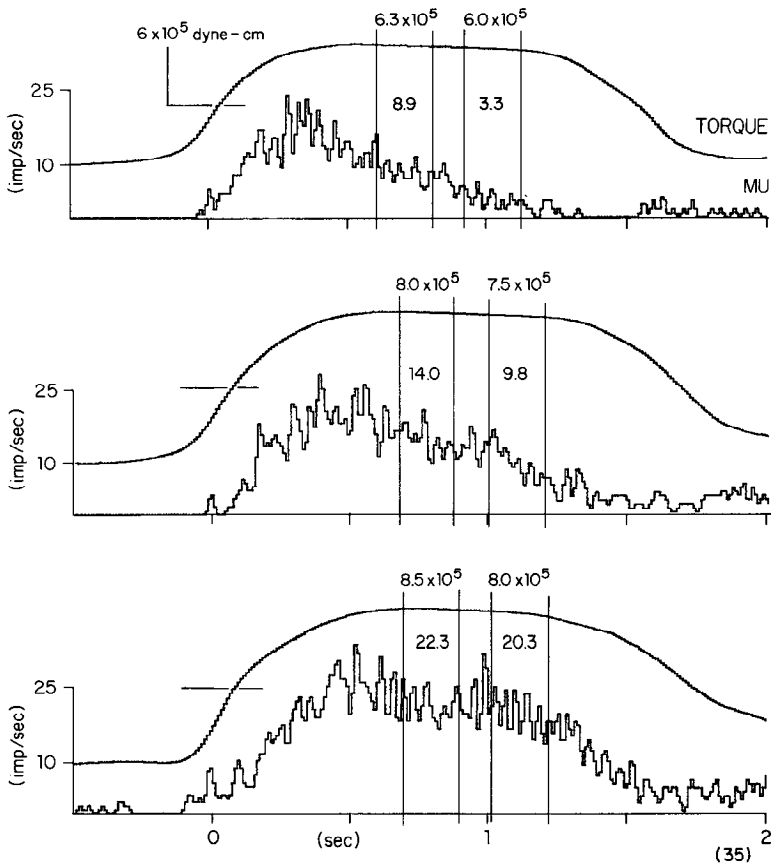


FIG. 8. Response histograms of a decrementing MU at 3 different torque levels. The mean firing rate (imp/s) and torque (dyn · cm) calculated for the indicated intervals are given. Intervals chosen were 100–300 and 450–650 ms after the end of the ramp. The percent decrement in firing rate during the hold period became less at higher torque levels.

phasic. Sixteen of the 86 MUs were recorded at high torque levels ( $>15 \times 10^5$  dyn · cm); of these, only two had tonic firing patterns. Five of the 16 were recruited at the *highest* torque zone at which the monkey worked reliably; two of these were phasic-tonic, two were decrementing, and one was phasic.

Most MUs fell clearly into one of the four firing pattern categories, and only a few showed intermediate patterns. Three MUs attained their maximum firing rate closer to  $dT/dt_{\max}$  than to  $T_{\max}$ , but they exhibited an essentially steady firing rate throughout the hold period and had no statistically significant phasic discharge; their behavior was classified as tonic. Some tonic MUs showed a slight decrement in firing rate during the hold period, which was not statistically significant.

MUs in extensor and flexor muscles showed about the same proportion of the four firing patterns ( $\sim 60\%$  of the MUs were in extensor

muscles and 40% in flexors). Thus, MU firing patterns were not related to differences in the flexion and extension response.

#### *MU firing onset relative to torque trajectory*

Motor units usually began firing before attainment of zero torque during the ramp. In Figs. 4–6, zero torque level is indicated by the broken line crossing the torque ramp. The distribution of onset times of MUs with different firing patterns is illustrated in Fig. 7. The phasic-tonic MUs had significantly earlier onset times ( $P < 0.001$ ) than the tonic and decrementing MUs. The mean onset time relative to zero torque was  $-120 \pm 60$  ms for phasic-tonic MUs ( $n = 20$ ),  $-55 \pm 70$  ms for tonic MUs ( $n = 28$ ), and  $0 \pm 100$  ms for decrementing MUs ( $n = 34$ ). The mean onset time for phasic MUs was  $-70 \pm 40$  ms ( $n = 4$ ), and their onset times were not statistically different from the other groups. Within each firing-pat-

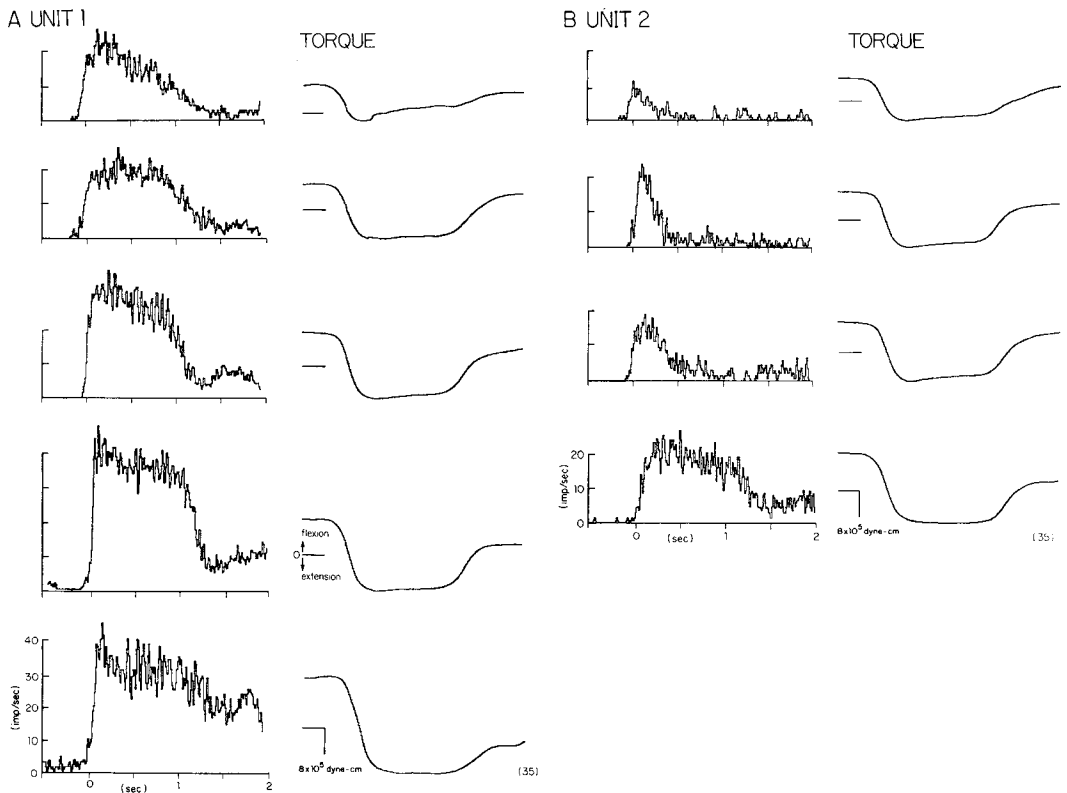


FIG. 9. Response histograms of 2 MUs at different torque levels. For MU 1 (53PAS4; cf. Table 1), static torques were, from *top to bottom*, about 6, 7.5, 10, 11, and  $16 \times 10^5$  dyn · cm. For MU 1, changes in firing frequency approximated the torque trajectory; this MU was classified as tonic. For MU 2 (53PAS1), torques were about 6, 7, 8, and  $10 \times 10^5$  dyn · cm; this MU was classified as phasic-tonic.

tern category there was no statistically significant difference in the onset times of extension and flexion MUs.

#### Relation of MU firing frequency and static torque

The firing patterns of single MUs during isometric contraction reflect their contribution to generation of active force. As the monkeys generated different static torque levels, the firing frequency and sometimes the discharge pattern of single MUs changed as a function of torque.

Fifteen MUs were studied at different torque levels; eight (53%) were decremting, four (27%) were phasic-tonic, and three (20%) were tonic (at the intermediate torque level). Figure 8 illustrates the discharge patterns of a typical decremting MU at three different torque levels. Its firing frequency decremmented less rapidly at high torque levels. Of eight decremting MUs studied as a function of torque, four attained essentially tonic firing frequencies at the highest torque levels, i.e., their mean firing rates during different 200-ms intervals in the hold period were not statistically different at the highest torque level.

Figure 9 illustrates the behavior of two representative MUs with different ramp-and-hold

torque trajectories. At most levels, MU 1 showed the maximum firing frequency when maximum static torque was attained. MU 1 had an essentially *tonic* firing pattern, i.e., its firing frequency followed the torque trajectory, except at the highest levels, where it exhibited evidence of a phasic peak. At the lowest torque level, the decrease in firing frequency during the hold period did not exceed the decrease in the average torque trajectory. (The static torque during the hold period was steadiest at moderate torque levels, which were most frequently performed.)

In contrast to MU 1, MU 2 fired maximally during the ramp phase of the torque trajectory at most torque levels, attaining its highest firing frequency near  $dT/dt_{max}$ . It exhibited a *phasic-tonic* firing pattern except at the highest torque level, where its pattern became essentially tonic, i.e., the mean phasic firing rate was not statistically different from the mean tonic firing rate. Since MUs were characterized by their patterns at moderate force levels, MU 2 was classified as a phasic-tonic MU.

Both MUs in Fig. 9 increased their tonic firing frequencies during the hold period with greater static torque. When mean tonic firing frequency over the specified interval was plotted against the corresponding static torque

TABLE 1. Rate-torque slopes for MUs with different firing patterns

Unit	Characteristics		No. of Torques Studied	Linear Static Rate-Torque Range				
	Firing Pattern	Type		N	r	Slope	% MBC	Threshold
38CH1 ○	T	E	5	4	1.00	0.8	6-21	-1.5
53PAS4 ○	T	E	5	4	0.96	4.3	17-32	2.8
79PAS1 ▼	D	E	4	3	0.99	3.0	18-34	3.1
37CH1 △	P-T	E	3	3	0.98	2.5	21-32	4.9
56PAS1 ◇	D	F	3	3	1.00	7.0	18-24	5.1
82PAS4 *	D	F	3	3	0.93	3.4	27-35	6.1
53PAS1 ■	P-T	E	4	3	0.99	2.4	20-30	6.5
20CH1 ●	D	F	4	3	0.97	1.6	35-53	9.1
20CH2 ▲	D	F	4	3	0.90	5.4	31-37	9.7
20CH3	P-T	F	4	2		1.0	31-45	
53PAS3	P-T	E	4	2		3.0	17-22	
79PAS2	T	F	3	2		1.2	15-26	
82PAS1	D	F	2	2		1.0	41-52	
82PAS2	D	F	2	2		3.7	51-66	
82PAS3	D	F	2	2		2.0	34-47	

D, decremting; T, tonic; P-T, phasic-tonic; E, extensor; F, flexor. Information about the linear range of mean firing rate vs. static torque during the hold period indicates the number of torque levels included in the linear range (N), the correlation coefficient (r), (which was invariably >0.90 because it was calculated for only 3-4 points), the rate-torque slope (imp/s per  $10^5$  dyn · cm), the torque range in %MBC, and the extrapolated torque threshold ( $\times 10^5$  dyn · cm). Symbols by the first 9 units are those used in Fig. 10.

level, both units showed a linear relation at low to moderate torque levels. The firing rate of MU 1 became stabilized at a torque level of 32% MBC ( $11 \times 10^5$  dyn · cm); the mean rate-torque slope determined from the first four torque levels (cf. Table 1) was 4.3 imp/s per  $10^5$  dyn · cm. MU 2 had a mean rate-torque slope of 2.4 imp/s per  $10^5$  dyn · cm; this slope represented a range that included all torque levels studied, except the lowest, which involved negligible tonic discharge. An approximately linear increase in tonic firing frequency with static torque up to moderate torque levels indicates the importance of MU rate coding of static torque at low to moderate torque levels.

Figure 10 illustrates the rate-torque relation of nine MUs for which a linear slope was established over at least three different torque levels. The linear ranges occurred at torque levels < 53% MBC. The mean rate-torque slope of these nine MUs was  $3.4 \pm 1.9$  imp/s per  $10^5$  dyn · cm (mean  $\pm$  SD). There was no statistical difference ( $P < 0.50$ ) in the rate-torque slopes for MUs of flexor and extensor muscles:  $4.1 \pm 2.8$  ( $n = 4$ ) and  $2.6 \pm 1.3$  imp/s ( $n = 5$ ) per  $10^5$  dyn · cm, respectively.

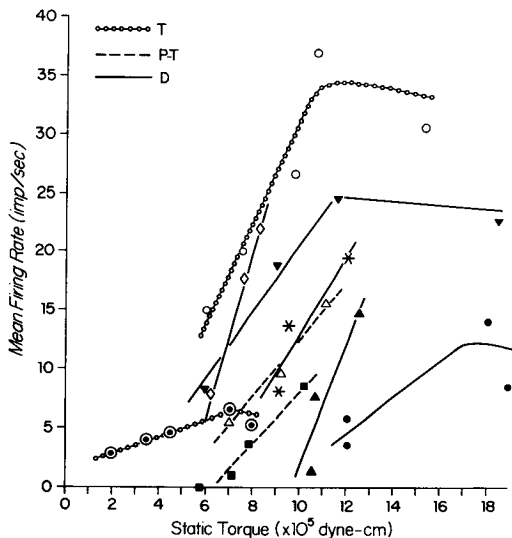


FIG. 10. Mean firing rate during the hold period versus mean static torque level for 9 MUs studied as a function of torque. The best linear fit of the rate-torque slope over at least 3 points is illustrated. The firing rate threshold given in Table 1 was the axis intercept of the extrapolated linear slope. MU firing pattern is indicated as tonic (T), phasic-tonic (P-T), or decrementing (D).

Grouped by their firing patterns, the average slopes were  $4.1 \pm 2.1$  ( $n = 5$ ) for decrementing MUs,  $2.5 \pm 0.1$  ( $n = 2$ ) for phasic-tonic MUs, and  $2.6 \pm 1.4$  ( $n = 2$ ) imp/s per  $10^5$  dyn · cm for tonic MUs; these differences were also statistically insignificant.

Table 1 indicates the characteristics of 15 MUs that were studied as a function of torque, their firing patterns, and the slopes of the rate-torque relation in the linear range. For the nine MUs illustrated in Fig. 10, at least three torque levels were used to calculate the rate-torque slope, and the correlation coefficient of linear regression ( $r$ ) is given. Slopes were calculated as impulses per second per  $10^5$  dyn · cm. Also given for these nine MUs is the firing-rate threshold extrapolated from the linear slope. Tonic MUs had the lowest extrapolated thresholds.

## DISCUSSION

### *MU firing patterns*

The forelimb MUs of this study were characterized by their parent muscles and their firing patterns during isometric ramp-and-hold torque trajectories. It would be of interest to know whether the firing patterns correlate with particular physiological MU types (9, 23). For technical reasons we could not identify such physiological properties as their twitch tension, contraction time (14, 17, 26, 36), or axonal conduction velocity (3, 4, 24). The torque signal was not sufficiently sensitive to extract twitch tensions of individual MUs with MUTAs of torque. With the hand held between styrofoam pads, the twitch tension of individual MUs was apparently dampened by the elastic properties of muscles and surrounding connective tissue, as well as the padding holding the hand. Other properties previously studied in humans, such as the relative amplitude of MU action potentials contributing to the EMG (38, 44) or recorded at the MU microelectrode (45) might have been used in this study for comparisons within the same muscles; however, since the multiunit EMG recording was intramuscular rather than transcutaneous, the proximity of the wire electrodes to fibers of the MUs would arbitrarily influence the amplitude of the MU signature.

A systematic study of the recruitment threshold of each MU was not undertaken.

Under our experimental conditions, the closest approximation to a recruitment threshold may be the lowest static torque level associated with discharge during the hold period. The extrapolated thresholds from rate-torque plots (Fig. 10) may be used to estimate relative recruitment order; these extrapolated thresholds were lower for two tonic cells than for five decrementing cells, which were in the same range as those for two phasic-tonic cells (Table 1). Of the 15 MUs studied as a function of torque, most MUs recruited at higher torque levels were decrementing MUs (Fig. 10). Relative onset time of MU firing during the ramp-and-hold torque response may also be related to relative recruitment order, but other factors would significantly influence onset time, including the ramp speed (7), differences in activation times of different synergist muscles, and the presence of a phasic component in the discharge pattern.

Information obtained from human subjects (17, 23–25, 27, 38) suggests that our *tonic* MUs may correspond to “slow-twitch” MUs and that the *decrementing* MUs may correspond to “fast-twitch” MUs. The firing frequency of tonic units was usually low (<10 imp/s), but sometimes as high as 30 imp/s. In their ability to fire regularly over a range from low to high frequencies, tonic MUs resemble the continuously firing long-interval MUs in humans (29) that have been correlated with type 1 fibers and with low conduction velocities. In contrast, decrementing MUs attained regular interspike intervals only at higher firing frequencies (15–25 imp/s), comparable to the patterns of intermittently firing short-interval MUs in humans (29) that have been correlated with MUs of fast conduction velocities. Second, tonic MUs sometimes attained their maximum (or stabilized) firing rates at lower torque levels than decrementing MUs (cf. Refs. 30, 38). Third, onset times of tonic MUs were slightly earlier than those of decrementing units, consistent with tonic MUs having a lower recruitment threshold in humans (17, 38) and in monkeys (14). Fourth, the extrapolated thresholds of two tonic MUs were the lowest of nine MUs of different firing patterns (Table 1). Finally, decrement in firing rate may reflect accommodation, which has been associated with fast-twitch MUs in cats (10).

Our *phasic-tonic* MUs are more difficult to identify reliably with a physiological type of MU. Their recruitment thresholds ranged

from low to high. Their phasic discharge obviously contributed to change of force. Whether fast- or slow-twitch MUs preferentially contribute to the dynamic change of force remains to be shown (1, 11, 30). Our *phasic* MUs were usually recruited at high torque levels and probably correspond to fast MUs.

The firing patterns of MUs may be compared with those of CM cells, which directly facilitate the MUs (20–22). Under similar behavioral conditions, motor cortex CM cells also showed four types of firing patterns (12): phasic-tonic (59%), tonic (28%), phasic-ramp (8%), and ramp (5%). The phasic component of firing of the CM neurons could well contribute to a phasic component of MU firing. None of the CM cells exhibited a decrementing firing rate during the hold period; in fact, the ramp and phasic-ramp neurons exhibited the reverse pattern: a gradual increase in firing rate during the hold. The observed decline in MU firing rate during the hold period may be due to a mechanism at the motoneuron level, e.g., accommodation (10). Adaptation of motoneuron firing, observed in response to steady current injection (1, 33), could also cause some initial decrease of firing rate, and could contribute to the transition from the phasic to the tonic component of discharge. The ramp firing pattern of CM cells would provide increasing synaptic input, acting to compensate for such accommodation.

In these studies, net torque levels were maintained during the hold period even though a significant percentage of the MUs decremented in firing rate. Similar results have been reported for human motor units, and may reflect hysteresis in the relation between muscle tension and firing rates during increasing versus decreasing firing rates (13, 16, 41, 43). Some of the hysteresis may be due to the time delay between muscle fiber activation and force development, as well as to force-velocity effects (2), or length-tension effects that occur at the sarcomere level during isometric activity. At the end of the ramp phase, passive tension would increase if lengthening of sarcomeres occurs. In addition, greater firing rate at the onset of the ramp-and-hold response may be necessary to overcome any remaining coactivation of antagonist muscles (cf. Fig. 1).

ONSET OF MU FIRING AFTER BEGINNING OF RAMP. The onset of MU firing relative to at-

tainment of zero torque varied from  $-280$  to  $+240$  ms (Fig. 7), with a mean onset time for all MUs of  $-10 \pm 370$  ms. The twitch tension begins to rise a few milliseconds after the MU action potential (27) and reaches a maximum between 30 and 100 ms later, depending on the unit's contraction time. Although the difference between the mean onset times of decrementing MUs ( $0 \pm 102$  ms) and tonic MUs ( $-55 \pm 66$  ms) was not statistically significant, the tonic MUs tended to be recruited sooner, and perhaps at lower torque levels, than decrementing units.

One complication in relating recruitment order of MUs to their onset times is the variability observed in the ramp slopes at different moderate torque levels, and across recording sessions. Comparisons between onset times of MUs recorded from different monkeys and different muscles involve further difficulties. Synergist muscles became active at approximately the same time,  $\sim 100$ – $150$  ms before zero torque. However, MUs of one muscle may develop force earlier (and therefore not have lower absolute force threshold) than MUs in another muscle. The effect of ramp speed on recruitment threshold of MUs has been amply documented (7, 17, 45). During ballistic responses, Desmedt and Godaux (17) found that 11% of recordings showed an altered relative recruitment order of MUs of different "size" for ballistic responses to particular torque levels (cf. Ref. 28), although fast-twitch MUs were never recruited without slow-twitch MUs for ballistic responses to particular torque levels.

Although we could not establish that MUs with different patterns were identical to classes described previously for humans, a difference in onset times of MUs sampled supports the assumption that MUs of different recruitment thresholds were studied. Different MUs active at moderate torque levels were probably sampled in proportion to their incidence. The weighted sum of the firing patterns of seven MUs sampled from FCR closely resembled the response average of EMG activity recorded from FCR (cf. Fig. 10 in the accompanying paper).

**MU FIRING FREQUENCY VERSUS TORQUE.** For a given MU, the firing rate increased with torque at low to moderate torque levels; at higher levels, firing rates became stabilized (Fig. 10). At moderate levels, the firing rate of

many MUs closely followed the torque trajectory, consistent with Person and Kudina's (41) hypothesis that firing-rate changes may be responsible for smooth gradation of force, whereas MU recruitment may be responsible for large "step-by-step" increases in force, as occurs in going from one torque level to another.

The rate-torque slopes of the MUs in this study were in the same range as the rate-force relation found previously for other muscles of humans and monkeys. The mean rate-force slope of the first nine MUs in Table 1 was 1 imp/s per 15.7 g (range: 1 imp/s per 5–34 g; cf. METHODS for conversion factors). The relation between firing frequency and force for MUs of the human first dorsal interosseus (FDI) had slopes of 1 imp/s per 10–100 g, depending on the load level (15). These human FDI MUs also showed some stabilization of firing frequency at high loads; at low loads the slope of the relation was about 1 imp/s per 10 g. Milner-Brown et al. (37) estimated the slope of firing frequency versus force for MUs in the human FDI to be 1 imp/s per 70 g (also cf. Ref. 34). Clark et al. (14) related MU firing frequency to force in monkey temporalis muscle. In their study, the slopes were based on the linear regression lines drawn through plots of mean firing frequency versus mean force obtained from monkeys that held static force at different force levels. The majority of temporalis MUs had slopes of 1 imp/s per 50–100 g, slightly lower than the rate-force slopes found here for forearm MUs. These results suggest that changes in firing rate of MUs contribute significantly to changes in static force in the muscles. Since lower threshold units soon reach a plateau of firing, increases of force at higher levels are significantly dependent on recruitment of additional high-threshold MUs (36, 37).

In contrast to our MUs, CM cells showed less evidence for recruitment into activity at higher static torque levels (12). Most CM cells were active at the lowest levels, and contributed to increased torque with increased firing rates. The increased firing rate of CM cells probably contributes to a concomitant increase in the firing rate of active MUs, as well as to recruiting additional MUs. The rate-torque slopes of MUs were comparable to those of CM cells obtained previously during similar isometric responses (12). The rate-torque slopes of extensor CM cells (4.8 imp/s

per  $10^5$  dyn · cm) were significantly greater than the slopes of flexor CM cells (2.5 imp/s per  $10^5$  dyn · cm), but we found no significant difference in the rate-torque slopes for extensor (2.6 imp/s per  $10^5$  dyn · cm,  $n = 5$ ) and flexor (4.1 imp/s per  $10^5$  dyn · cm,  $n = 4$ ) MUs. These results are consistent with a difference in the cortical control of extensor and flexor muscles. If the difference in the rate-torque slopes of extensor and flexor CM cells had been due to a mechanical advantage for flexor versus extensor muscles (12), the same difference would be expected for MUs. The absence of this difference would suggest that the cortex contrib-

utes more excitation to extensors than to flexors.

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