

Motor Unit Control Properties in Constant-Force Isometric Contractions

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SUMMARY AND CONCLUSIONS

1. The purpose of this study was 1) to characterize the decrease observed in mean firing rates of motor units in the first 8–15 s of isometric constant-force contractions and 2) to investigate possible mechanisms that could account for the ability to maintain force output in the presence of decreasing motor unit firing rates.

2. The decrease in mean firing rates was characterized by investigating myoelectric signals detected with a specialized quadrifilar needle electrode from the first dorsal interosseus (FDI) and the tibialis anterior (TA) muscles of 19 healthy subjects during a total of 85 constant-force isometric contractions at 30, 50, or 80% of maximal effort. The firing times of motor units were obtained from the myoelectric signals with the use of computer algorithms to decompose the signal into the constituent motor unit action potentials. Time-varying mean firing rates and recruitment thresholds were also calculated.

3. Motor units detected from the TA muscle were found to have a continual decrease in their mean firing rates in 36 of 44 trials performed during isometric ankle dorsiflexion at force values ranging from 30 to 80% of maximal effort and a duration of 8–15 s. Likewise, motor units detected in the FDI muscle displayed a decrease in firing rate in 32 of 41 trials performed during constant-force isometric index finger abduction for contractions ranging from 30 to 80% of maximal effort. In 14 contractions (16% of total), firing rates were essentially constant, whereas in 3 contractions (4%), firing rates appeared to increase.

4. Motor units with the higher recruitment thresholds and lower firing rates tended to display the greater decreases in firing rate over the constant-force interval, whereas motor units with lower recruitment thresholds and higher firing rates had lesser rates of decrease. Furthermore, increasing contraction levels tended to intensify the decrease in the motor unit firing rates.

5. Three possible mechanisms were considered as factors responsible for the maintaining of force output while motor units decreased their firing rates: motor unit recruitment, agonist/antagonist interaction, and twitch potentiation. Of these, motor unit recruitment was discarded first because none was observed during the 8–15 s duration of any of the 85 contractions. Furthermore, contractions outside the physiological range of motor unit recruitment (at 80% of maximal effort) revealed the same decreasing trend in firing rates, ruling out recruitment as the means of sustaining force output.

6. The role of agonist or antagonist muscle interaction was investigated with the use of the muscles controlling the wrist joint. Myoelectric signals were recorded with quadrifilar needle electrodes from the wrist extensor muscles while myoelectric activity in the wrist flexor muscles was concurrently monitored with surface electrodes during constant-force isometric wrist extension at 50% of maximal effort. Firing rates of the motor units in the wrist extensor muscles simultaneously decreased while the flexor muscles were determined to be inactive.

7. All the findings of this study regarding the behavior of the firing rates could be well explained by the reported characteristics

of twitch potentiation that have been previously documented in animals and humans.

8. The results of this study, combined with the results of other investigators, provide the following scenario to explain how a constant-force isometric contraction is sustained. As the contraction progresses, the twitch force of the muscle fibers undergoes a potentiation followed by a decrease. Simultaneously, the “late adaptation” property of the motoneuron decreases the firing rate of the motor unit. Findings of this study suggest that voluntary reduction in firing rates also cannot be ruled out as a means to augment the adaptation in motoneurons. As the duration of the contraction increases and the twitch force decreases, the force output of the muscle would be reduced below the intended force level and a voluntary increase in the excitation to the motoneuron pool would be required to sustain the intended force. This excitation would manifest itself in an increase in the firing rates of the active motor units and a recruitment of new motor units.

INTRODUCTION

Many researchers have studied the firing behavior of human motor units during sustained constant-force contractions at various submaximal and maximal force levels. In early 1970s, two research groups reported progressive decreases in the firing rates throughout constant-force contractions (De Luca and Forrest 1973; Person and Kudina 1972). These results were later verified by De Luca et al. (1982b) and Gatev et al. (1986), who reported an increase in the interfiring interval during sustained contractions. Decreasing firing rates were also reported during sustained maximal contractions (Bigland-Ritchie et al. 1983, 1986b; Grimby et al. 1981; Kukulka et al. 1984; Marsden et al. 1971). Person and Kudina (1972), in contradiction to De Luca and Forrest (1973), De Luca et al. (1982b), and Gatev et al. (1986), reported that additional motor units were recruited as the contraction progressed. Shimizu (1990) reported decreasing firing rates during the initial stages of isotonic contractions. Shimizu also reported a second phase of motor unit activity in which the firing rates of active motor units increased and other motor units were recruited. Increasing firing rates have been reported from the onset of the contraction by several researchers. Maton (1981) reported motor unit recruitment and progressive increases in firing rates for high-threshold motor units, >30% of the maximal voluntary contraction (MVC) level, consistent with the later findings of Bigland-Ritchie et al. (1986a) and Maton and Gamet (1989). However, Maton (1981) also noted that low-threshold units could increase, decrease, or maintain their firing rates inconsistently during isotonic contractions. This observation was supported by Kato et al. (1981). Similar motor unit firing behavior was later ob-

served by Nordstrom and Miles (1990) during contractions in which the firing rate of a single motor unit was kept constant. Nordstrom and Miles noted that the firing rates of the other active motor units fluctuated inconsistently with increasing, decreasing, and stable trends.

Several theories have been advanced for the mechanism responsible for maintaining constant force output in the presence of varying trends in firing rates, and the factors causing the average firing rates to be altered throughout the constant-force contraction remain ambiguous. Person and Kudina (1972) and De Luca (1979) have hypothesized that the force output may be maintained by compensating mechanisms such as the recruitment of additional motor units, the effects of agonist/antagonist muscle interaction, or time-varying changes in the twitch forces of the individual motor units. The late adaptation phenomenon (Kernell 1965), whereby a steady decline in firing rate is observed when the motoneurons are activated by constant intracellular current injection; feedback from the periphery (Bigland-Ritchie et al. 1983); and voluntary modulation of the central drive during constant-force contractions have been suggested as likely causes of decreasing firing rates. However, the existence and relevance of one or more of these mechanisms during sustained constant-force isometric contractions have not been demonstrated unequivocally.

In the present study, our first goal was to investigate and characterize the firing behavior of motor units during the first 8 to 15 s of constant-force isometric contractions. Specifically, we aimed to determine the direction and amount of the trends in firing rates, as well as the effects, if any, of the recruitment threshold of the motor unit and the force level of the contraction on these trends. Our second goal was to investigate possible mechanisms that may participate in the production and sustaining of muscle force even when the average firing rates are modified throughout the contraction.

METHODS

Characterization of the decrease in firing rates during constant-force contractions

SUBJECTS. In this study we investigated data collected from 19 motivated subjects, aged 20–44 yr (27.2 ± 6.1 yr, mean \pm SD) and with no previous history of neurological disorders. Local institutional review board approval was obtained and all subjects gave informed consent. The subjects were well trained in the experimental protocol. Force and myoelectric data were collected from either the first dorsal interosseus (FDI) or tibialis anterior (TA) muscles as described below.

ISOMETRIC FORCE RECORDINGS. The measurement of the torque generated during index finger abduction and ankle dorsiflexion was accomplished with the use of the same techniques as described by Broman et al. (1985). An estimate of the MVC produced by the subject was performed in the following manner. The subject attempted to abduct the index finger or dorsiflex the ankle maximally against the restraining device while the torque produced during the effort was measured. The measured torque was compared over three consecutive trials to verify that the three values were within 10% of each other. The largest value of the three trials was used as the MVC for the subject. During the experiments, all subjects were asked to follow a trapezoidal trajectory, with a plateau at either 30, 50, or 80% of MVC and increasing

and decreasing slopes of +10 and –10% MVC per second, respectively. The plateau duration varied from 8 to 15 s depending on the force level, with the plateaus at lower force levels lasting longer than those at higher levels. The desired force trajectory was displayed on a computer screen along with the output of the force transducer, providing real-time visual feedback for the subjects.

MYOELECTRIC SIGNAL RECORDINGS. Once the subject had shown proficiency in tracking the target trajectory, a quadrifilar needle electrode, described in detail by Mambrito and De Luca (1983), was inserted into the belly of the appropriate muscle. The electrode detects three channels of myoelectric activity. It was positioned to detect from three to five independent, continually firing motor units as the force level gradually increased. When a suitable needle position was found, the subject was asked to contract and follow the target trajectory. Myoelectric signals detected from the quadrifilar needle electrode during the contraction were amplified, band-pass filtered from 1 to 10 kHz, and recorded on tape. The myoelectric signals were then time compressed, digitized at 50 kHz, and decomposed into the constituent motor unit action potential trains with the use of the precision decomposition algorithm (De Luca 1993; LeFever and De Luca 1982; LeFever et al. 1982; Mambrito and De Luca 1984). Precision decomposition develops unique motor unit action potential templates from three concurrently acquired needle electrode channels. The decomposition is then accomplished by the use of template matching, template updating, firing statistics, and superposition resolutions to identify the individual motor unit firings. Previous reports have shown that when this technique is used, the firing times can be obtained with an accuracy reaching 100% (De Luca 1993; Mambrito and De Luca 1983).

Investigation of agonist/antagonist muscle interaction during constant-force contractions

SUBJECTS. Four subjects aged 21–35 yr (26.2 ± 6.2 yr, mean \pm SD) participated in the set of experiments to investigate the role of agonist/antagonist interaction in maintaining constant-force contractions. However, the agonists and/or antagonists of both the FDI and TA muscles proved difficult to investigate because of either their anatomic location or the design of the constraining apparatus. Consequently, the muscles controlling wrist flexion and extension were chosen for their proximity to the skin surface and the availability of a device that allowed easy access to both the wrist extensor and flexor muscles during wrist extension.

The subjects were seated at a lab bench and the right hand and forearm were placed in a constraining device. The device consisted of a cast that rigidly held the forearm, and a hand mold affixed to two high-stiffness (2.20 N/mm) force transducers set on perpendicular linear bearings. The linear bearings made it possible to measure two rotational degrees of freedom that isolated the wrist extension-flexion forces from the ulnar-radial flexion forces. The subjects were asked to isometrically extend the wrist following the 50%-MVC trapezoidal trajectory used in the FDI and TA studies, while minimizing the ulnar-radial flexion forces. During these contractions, needle myoelectric signals were recorded from the extensor carpi radialis longus (ECRL) and extensor carpi ulnaris (ECU) muscles. Additionally, surface myoelectric signals were detected from the flexor carpi radialis (FCR), flexor carpi ulnaris (FCU) and flexor digitorum superficialis (FDS) muscles. The surface signals were detected with active electrodes having detection surfaces consisting of two parallel silver bars 1.0 cm long, 1 mm in width, and spaced 1.0 cm apart. The surface myoelectric signals were amplified and band-pass filtered from 20 to 400 Hz.

Data analysis

DETERMINATION OF THE CONSTANT-FORCE INTERVAL. To ensure that the motor unit control strategy observed in each trial

was consistent with the production of constant-force output, only contractions that had a constant-force region were analyzed. The region selected for analysis consisted of the largest interval where the subject had achieved the plateau portion of the trajectory and the force output was determined to be stable. The force output was accepted as stable when the magnitude of any deviations in the force trace and the SD about the mean of the force trace were within set tolerance limits. For isometric dorsiflexion of the ankle, the tolerance limits were set as a maximum allowable deviation from the mean force trace value of $\pm 2.0\%$ of MVC and an SD about the mean $\leq 1.0\%$ of MVC. In general, subjects were unable to produce force traces during isometric index finger abduction that were as stable as force traces produced during isometric ankle dorsiflexion. It is likely that the smaller number of motor units in the FDI muscle and the higher levels of contractions performed in this study were the dominant factors for this relative instability. Consequently, for isometric index finger abduction, the tolerance limits were increased to a maximum deviation from the mean of $\pm 3.0\%$ of MVC and an SD about the mean ≤ 1.25 . A typical example of a force trajectory is shown in Fig. 1. The constant-force interval in Fig. 1, shown by the shaded area, illustrates low-frequency fluctuations that occur naturally and within the bounds of the tolerance limits. These fluctuations were previously described by Milner-Brown et al. (1973) and later attributed to common fluctuations in the firing rates of the active motor unit population (De Luca et al. 1982b).

MOTOR UNIT PARAMETERS. For each contraction where a constant-force region was present, motor unit firing characteristics were analyzed by calculating the recruitment threshold and time-varying firing rate for each motor unit. The recruitment threshold, defined as a percentage of MVC, was calculated for each motor unit in the following manner. A 7-ms unit-area rectangular window

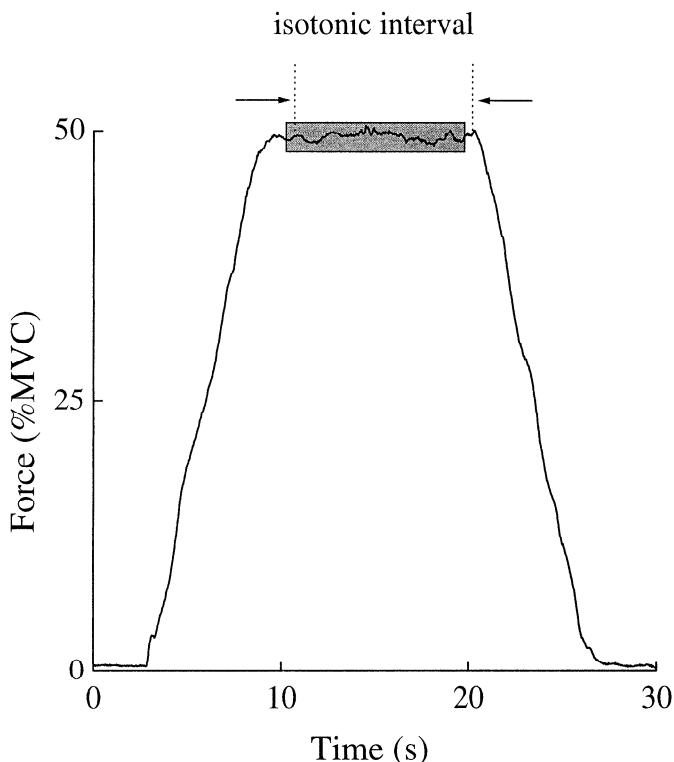


FIG. 1. Typical isometric force trace produced by a healthy subject performing dorsiflexion of the right ankle at 50% of the maximal voluntary contraction (MVC) level. Gray box: $\pm 2\%$ -MVC tolerance limits over the interval determined to be constant-force according to the criteria used in this study. Myoelectric signals were analyzed in this interval.

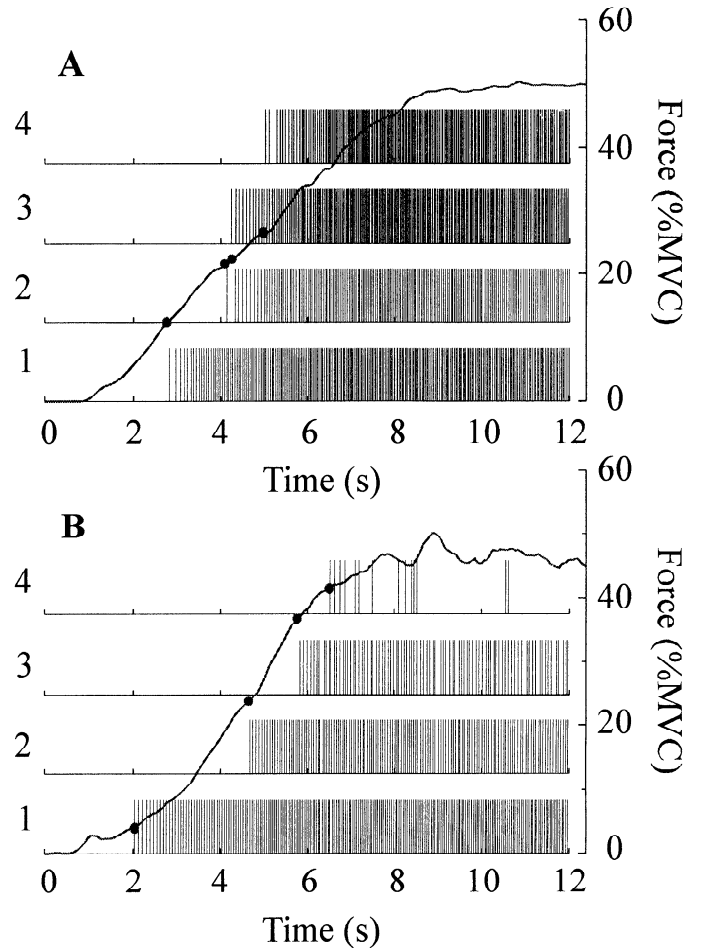


FIG. 2. Force recorded during 2 isometric abductions of the index finger and the associated firing times of the detected motor units as identified by the precision decomposition technique. Dark solid line with the axis on the right: force trace. Vertical lines with the motor unit number on the left: firing times of detected motor units. The recruitment threshold of each motor unit is indicated by a dot on the force trajectory. In A, all 4 motor units are recruited within the 1st 85% of the plateau level and all 4 motor units display continual firing patterns. In the contraction in B, motor unit 4 has a recruitment threshold above 85% of the plateau and its firing pattern shows unstable periods of activation and deactivation.

was centered on the force signal at the time index corresponding to the first discharge of the motor unit. The time-varying mean firing rate, defined as the number of pulses per second (pps) a motor unit discharged, was calculated by passing a 1,600-ms unit-area symmetric Hanning window over an impulse train corresponding to the firings of the motor unit (De Luca et al. 1982a). The Hanning window length used in this study was chosen to be significantly larger than the 400-ms window used in our previous studies so that the slowly varying trends in the firing rate could be specifically studied. The average firing rate was defined as the average of the mean firing rate over the whole duration of the constant-force region.

DETERMINING THE STABILITY OF A MOTOR UNIT. In accordance with our previous observations, we noted that motor units operating at force levels that are too close to their recruitment thresholds displayed unstable firings. Figure 2 provides two examples of firing patterns from concurrently active motor units identified with the precision decomposition technique. In Fig. 2A, all motor units were recruited below 85% of the plateau level. The firing patterns of these motor units displayed a continual activation and consistent interfiring intervals. Figure 2B shows another exam-

ple of the firing patterns for four concurrently active motor units. *Motor units 1, 2, and 3* were recruited below 85% of the plateau level and demonstrate well-behaved firing patterns, similar to the example provided in Fig. 2A. *Motor unit 4*, which had a recruitment threshold of 42% of MVC (88% of the 48%-MVC level achieved by the subject), however, displayed an unstable firing pattern. In general, it was established that the motor units recruited above 85% of the target levels displayed unstable firing patterns. These motor units often had repeated periods of activation and inactivation, in contrast to the remaining motor unit population, which discharged continuously throughout the contraction. It appears that the level of excitation was not consistently maintained above the relatively high recruitment thresholds of motor units that were recruited above 85% of the target levels. Therefore these motor units were never fully activated. Consequently, although the recruitment timing and recruitment threshold of every motor unit was carefully monitored to identify motor unit activation patterns, the firing rates of motor units with recruitment thresholds $>85\%$ of the plateau level were considered unstable and were not used for further firing rate evaluation.

RESULTS

Motor unit recruitment and firing rate modulation during constant-force contractions

Motor unit recruitment occurred continuously throughout the increasing ramp of the trapezoid trajectory from near 0% of MVC to $\sim 50\%$ of MVC for the FDI muscle and 70% of MVC for the TA muscle. However, motor unit recruitment was not observed during the 8- to 15-s duration of the constant-force region for either the TA or FDI muscles at any of the force levels investigated. In several trials where the subject failed to maintain a constant-force contraction, and instead increased the force during the intended plateau, motor unit recruitment was observed. An example is presented in Fig. 3. Also, on occasion, we have seen examples of motor

unit recruitment occurring at a later time such as 30 s into a contraction. However, this study was limited to investigating the behavior of constant-force isometric contractions that lasted up to 15 s.

To quantify the decrease in mean firing rates of motor units, linear least-squares regression was used. The control strategy employed in each contraction was classified into one of three possible categories: decreasing firing rates, increasing firing rates, and quasiconstant firing rates. Categories were assigned on the basis of the regression slopes used to estimate the firing rates of the motor units detected during the trial. Firing rates with regression slopes less than -0.1 pps² were considered decreasing; those with regression slopes >0.1 pps² were considered increasing; and those with regression slopes between -0.1 and 0.1 pps² were considered quasiconstant. In trials where more than one trend was observed in the motor unit population, the dominant trend was reported.

The tendency of mean firing rates to decrease during the constant-force region significantly dominated the results from both muscles at all contraction levels. In six of the seven contractions of the TA muscle at 80% of MVC, motor units showed a substantial and continuous decrease in their mean firing rates over the plateau region, as exemplified in Fig. 4A. In 8 of 11 trials performed at 50% of MVC, motor units displayed a continual decrease throughout the contraction. An example is provided in Fig. 4B. Likewise, motor units in 22 of 26 trials performed at 30% of MVC showed a decrease in firing rates, as exemplified in Fig. 4C.

Motor units recorded from the FDI muscle during isometric index finger abduction showed trends in firing rate behavior similar to those displayed by motor units in the TA muscle. At 80% of MVC, motor units in all five trials with constant-force intervals showed a progressive decrease in their firing rates throughout the contraction, as exemplified

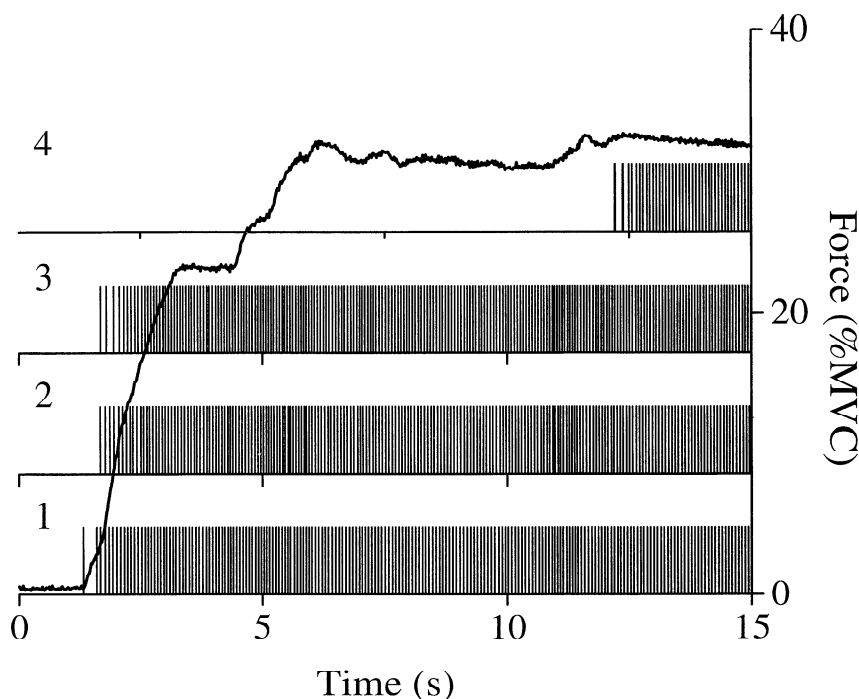


FIG. 3. Motor unit firings from an isometric contraction in the tibialis anterior (TA) muscle, where the subject was not able to maintain a constant force level. The force trace had a slight increase in the 11- to 12-s range, resulting in the recruitment of *motor unit 4*. Dark solid line with the axis on the right: force trace. Vertical lines with the motor unit number on the left: firing times of detected motor units.

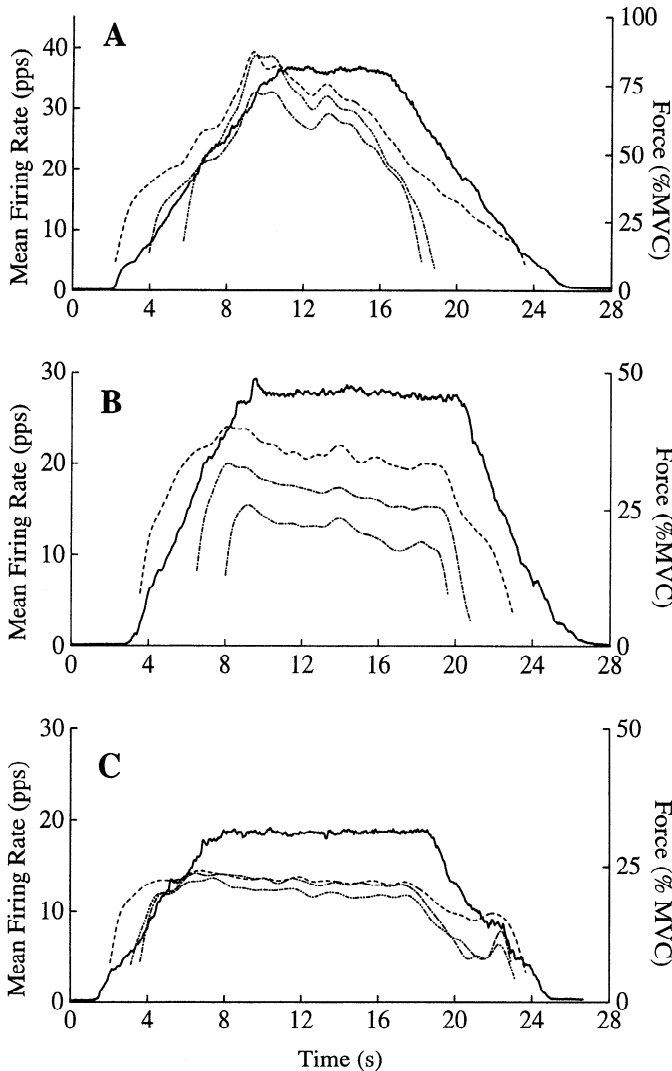


FIG. 4. Firing rate plots for MUs detected in the TA muscle during isometric dorsiflexion of the ankle at (A) 80%, (B) 50%, and (C) 30% of the MVC level. Dark solid line with the axis on the right: force trace. Dot-dash lines with the axis on the left: mean firing rates of detected motor units. The firing rates of the motor units show a rapid and progressive decrease throughout the constant-force interval in A. The same behavior, even though becoming progressively less pronounced, is evident in B and C. pps, pulses per second.

in Fig. 5A. Similarly, motor units in all 12 contractions performed at 50% of MVC showed a pronounced decrease in firing rates, represented in Fig. 5B. At 30% of MVC, motor units in 15 of 24 trials were found to have a continual decrease in the mean firing rate, exemplified in Fig. 5C. These results amounted to 80% of all contractions where a constant-force region was successfully maintained displaying decreasing firing rates.

Among the rest of the trials, quasiconstant firing rates were observed in a total of 14 trials (3 trials at 50% of MVC in the TA muscle, 2 trials at 30% of MVC in the TA muscle, and 9 trials at 30% of MVC in the FDI muscle), representing 16% of the total number of trials. An example is provided in Fig. 6. Increasing firing rates were only observed in the TA muscle in three trials (1 trial at 80% of MVC and 2 trials at 30% of MVC), amounting to 4% of the total. These results are summarized in Table 1.

The firing rate trends described above express the dominant firing behavior of the group of motor units detected during a given contraction. It should be noted that among motor units active in a contraction, increasing and decreasing firing rates never coexisted. Instead, trials existed where some motor units would remain quasiconstant while other motor units either decreased or increased their firing rates.

Effects of recruitment threshold and average firing rate on the decrease in mean firing rates

The slopes from the linear regressions that were found to be reliable ($r > 0.7$), exemplified in Fig. 7A, were independently plotted against both the recruitment thresholds and the average firing rate of the motor units for each contraction. Examples are provided in Fig. 7, B and C. In this context, the average firing rate is defined as the mean discharge rate

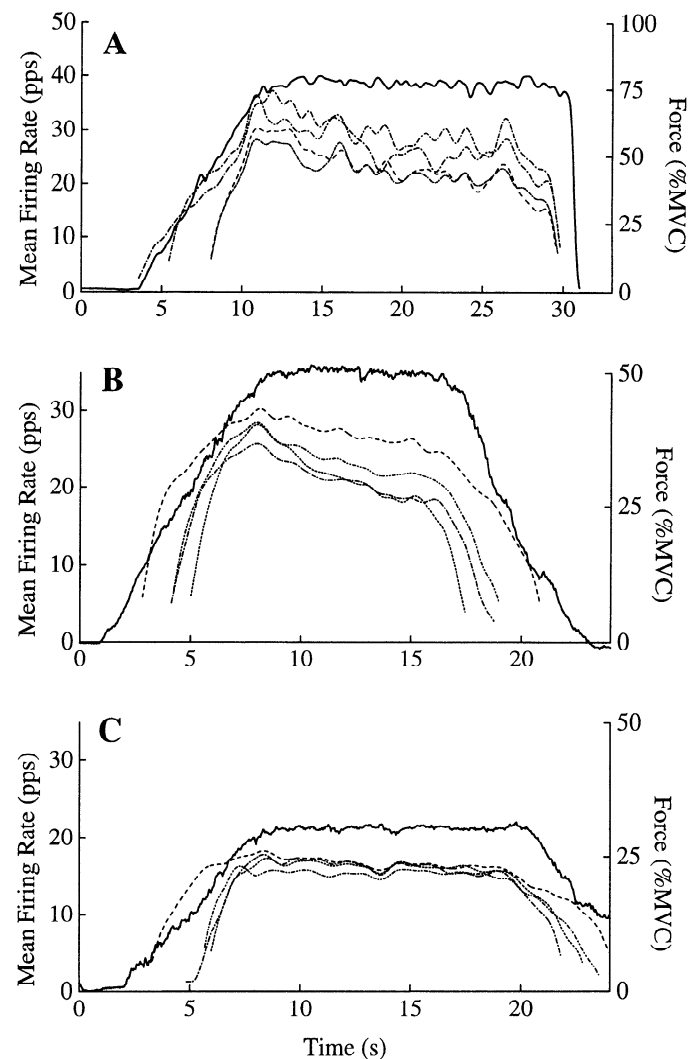


FIG. 5. Firing rate plots for MUs detected in the 1st dorsal interosseus (FDI) muscle during isometric abduction of the index finger at (A) 80%, (B) 50%, and (C) 30% of the MVC level. Dark solid line with the axis on the right: force trace. Dot-dash lines with the axis on the left: mean firing rates of detected motor units. The firing rates of the motor units show a progressive decrease throughout the constant-force interval in all contractions.

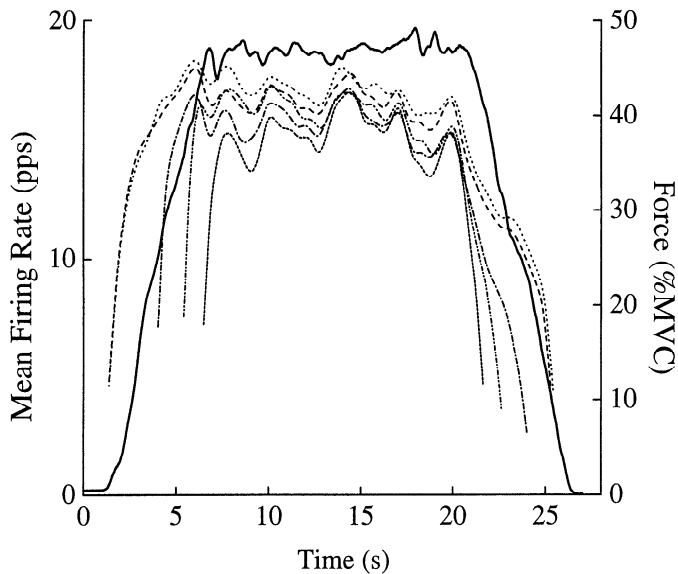


FIG. 6. Example of quasiconstant mean firing rates. The mean firing rates of the motor units, shown in broken lines with the axis on the left, were detected in the FDI during isometric abduction of the index finger at 50% of the MVC level. Dark solid line with the axis on the right: force trace. The firing rates show neither an increasing nor a decreasing trend and were consequently labeled as quasiconstant. This firing rate behavior occurred only at 30 and 50% of MVC and was atypical.

over the entire constant-force interval. Figure 7B shows a negative correlation between firing rate slope and recruitment threshold for motor units within a single contraction, whereas Fig. 7C shows a positive correlation between firing rate slope and average firing rate. This observation is reflective of the negative correlation between the recruitment threshold and firing rate of a motor unit (De Luca and Erim 1994). Similar effects of recruitment threshold and thus average firing rate on the decrease in mean firing rates were observed in the majority of contractions at 80 and 50% of MVC, whereas the relationship was not pronounced at 30% of MVC in either muscle. Table 2 summarizes the percentage of contractions in which firing rates decreased systematically with respect to the recruitment threshold and firing rate of the motor unit.

Effect of force level on the decrease in mean firing rates

It was observed that the rate of decrease in the time-varying mean firing rate during the constant-force region was greater at the higher contraction levels. This phenomenon was investigated by performing a common linear regression (Zar 1984) between firing rate slope and both recruitment threshold and average firing rate for each force level. Common regression pools together data from all the contractions at a single force level and compares the pooled data results with the results of the individual data sets. If the data are such that the pooled data and the individual data are derived from a homogenous population, then an estimate of the common regression can be calculated from the pooled data. The common regression allowed us to represent each force level with a linear regression line similar to those shown in Fig. 7, B and C. Figure 8 shows the values of the slopes calculated from the common regressions mentioned

above. These data confirm that for the TA muscle, the rate of decrease in the time-varying mean firing rate is related to the force level, where the magnitude of the common regression slopes (both as a function of recruitment threshold and average firing rate) are greatest at 80% of MVC and smallest at 30% of MVC. In the FDI muscle, it was observed that the relationship between 50% of MVC and 30% of MVC was similar to that in the TA muscle, where 50% of MVC contractions were found to have a greater rate of decrease in the mean firing rate. However, it was observed that 80% of MVC had the slowest rate of decrease for mean firing rate slope versus recruitment threshold, and the second slowest rate for mean firing rate slope versus average firing rate. The significance of this behavior is examined in the DISCUSSION.

Effects of agonist/antagonist muscle activity on motor unit firing rates

The ECRL and ECU muscles are the two major muscles that extend the wrist. Because, however, it may be possible to gain added force contributions from the extensor digitorum communis (EDC) muscle, activity in the EDC muscle was initially monitored. As expected, motor unit activity in the EDC muscle could only be observed when the fingers were extended. Consequently, myoelectric activity from the EDC muscle was not monitored in the remaining trials. Instead, the subject slightly flexed the fingers to avoid generating activity in the EDC muscle.

In the majority of trials of isometric wrist extension, the subjects were unable to isometrically extend the wrist without causing significant isometric ulnar or radial flexion forces. The concurrent ulnar and/or radial flexion resulted in unstable motor unit firing patterns with both increasing and decreasing trends in the two muscles. In the trials where the subjects were able to extend the wrist with minimal ulnar or radial flexion forces, however, the control strategy employed in Fig. 9 was observed. Figure 9, A and B, show concurrent motor unit firing rates in the ECRL and ECU muscles, respectively, with the force outputs measured in two directions superimposed as solid lines on each plot. The force trajectory that reached 50% of MVC corresponds to wrist extension, and the trajectory that was maintained at

TABLE 1. Summary of motor unit firing patterns during sustained constant-force isometric contractions

	Decreasing	Increasing	Quasiconstant
TA, 80% MVC	6	1	0
TA, 50% MVC	8	0	3
TA, 30% MVC	22	2	2
FDI, 80% MVC	5	0	0
FDI, 50% MVC	12	0	0
FDI, 30% MVC	15	0	9
Totals	68 (80)	3 (4)	14 (16)

Values in parentheses are percentage of total. TA, tibialis anterior; MVC, maximal voluntary contraction; FDI, 1st dorsal interosseus. Trials were considered decreasing if the regression slopes fit to the time-varying mean firing rate of the individual motor units within the trials were less than -0.1 pulse per second (pps)², increasing if the slopes were >0.1 pps², and quasiconstant if the slopes were between these limits.

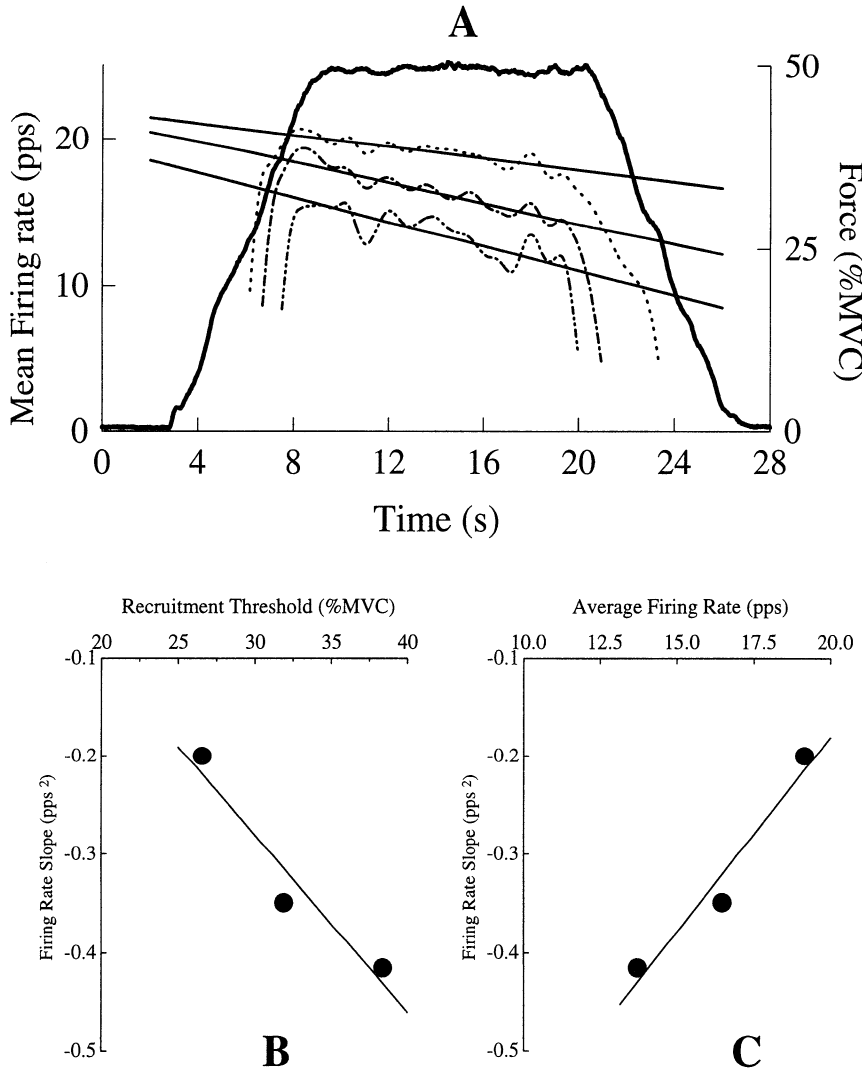


FIG. 7. Quantification of the decrease in firing rates during constant-force contractions. A: regression lines fit to mean firing rates of 3 motor units detected in the FDI during isometric abduction of the index finger at 50% of the MVC level. Broken lines with the axis on the left: mean firing rates. Light solid lines: linear least-squares regression lines that were fit to the firing rates over the constant-force interval. Dark solid line: force trace produced by the subject. B: slope of the mean firing rate regression plotted against the recruitment threshold of the motor units. C: slope of the linear regression plotted against the average firing rate (defined as the mean rate over the entire constant-force interval). The negative correlation between regression slope and recruitment threshold and the positive correlation between regression slope and average firing rate are indicative of the negative correlation between recruitment threshold and average firing rate.

approximately -10% of MVC corresponds to the ulnar-radial flexion (positive forces represent wrist extension and ulnar flexion, and negative forces represent wrist flexion and radial flexion). As shown in Fig. 9A, while the wrist extension force is maintained at a constant level of 50% of MVC and the ulnar-radial flexion force is stable, the firing rates

TABLE 2. Contractions in which the motor units displayed systematic decreases in firing rate during the constant-force interval

	<i>n</i>	%
TA, 80% MVC	4 of 6	67
TA, 50% MVC	8 of 8	100
TA, 30% MVC	9 of 22	41
FDI, 80% MVC	4 of 5	80
FDI, 50% MVC	11 of 12	92
FDI, 30% MVC	7 of 15	47

Number (*n*) and percentage of contractions in which the firing rate decrease was directly related to the magnitude of the firing rate and inversely related to the recruitment threshold of the motor units. For abbreviations, see Table 1.

of motor units (---) in both ECRL and ECU muscles show a progressive decrease throughout the contraction.

To investigate the magnitude and origin of activity detected in the flexor muscles during the wrist extension, the FCR, FCU, and FDS muscles were simultaneously monitored with surface electrodes. The root-mean-square (RMS) value and power spectral density functions were then calculated for these signals. Figure 9C shows the RMS myoelectric activity of the FCR, FCU, and FDS muscles during the 50% wrist extension shown in Fig. 9, A and B (solid lines), and a 5%-MVC wrist flexion (---) performed later in the same experiment. The 5% wrist flexion values are shown for comparison of the intensity of the muscle activity. In Fig. 9C, the level of activity in the FCR muscle during the 50%-MVC wrist extension contraction (represented in Fig. 9, A and B) and the level of activity recorded during a 5%-MVC wrist flexion are nearly identical. Similar levels of RMS activity between the 50% wrist extension contraction and the 5% wrist flexion were also seen in the FCU muscle. The RMS activity recorded in the FDS muscle during the 5%-MVC wrist flexion, however, was found to be far greater than that of the 50%-MVC wrist extension. This difference

■ Common regression slopes for recruitment threshold (pps² / % MVC)
 ■ Common regression slopes for average firing rate (Hz)

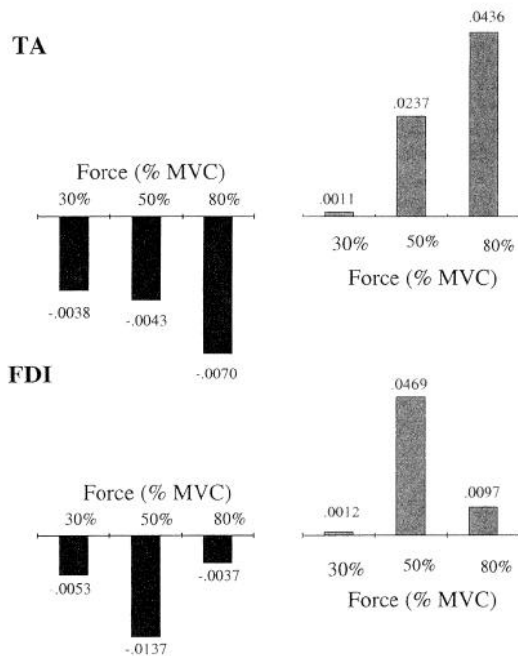


FIG. 8. Common regression slopes calculated for the TA and FDI muscles at the 3 different force levels. *Top*: common slopes for firing rate slope vs. recruitment threshold (*left*) and average firing rate (*right*) for the trials performed in the TA muscle at 30, 50, and 80% of MVC. *Bottom*: same relationships for the FDI muscle.

in RMS values was attributed to the subject's conscious effort not to extend the fingers. Consequently, overflexing of the fingers may have occurred during wrist flexion. The level of RMS activity indicated that the flexor muscles were active at a maximum of 5% of their capability during the 50%-MVC wrist extension. More importantly, there was no accompanying decrease in antagonist activity that could account for the decreasing firing rates in the agonist muscles. The power spectral density functions for the surface signals detected during both contractions are shown in Fig. 9D. The spectrum analysis performed on the surface myoelectric signals indicated that the signal power was shifted to higher frequencies during the 5%-MVC flexion compared with the 50%-MVC extension. This shift in frequencies indicates that the origin of the two signals may not be identical (De Luca 1984). This point is examined further in the DISCUSSION.

DISCUSSION

Characteristics of the firing rate decrease during constant-force isometric contractions

The firing rates of motor units were found to decrease during the first 8–15 s in 80% of the contractions at all force levels in both the TA and FDI muscles. The rate of decrease in firing rate was found to have a systematic trend related to the recruitment threshold and average firing rate of the motor unit. Specifically, motor units with lower recruitment thresholds and greater average firing rates decreased their firing rates more slowly than motor units with higher recruitment thresholds and lower average firing rates. In general,

the decrease in firing rate was directly proportional to the force level obtained; the greater the force, the greater the decrease. FDI motor units at 80% of MVC were the only exception. Although seemingly inconsistent, this result will be shown to be consistent with the explanation provided for the rest of the observations of this study.

Sixteen and one half percent (16%) of the contractions revealed quasiconstant firing rates, whereas 4% displayed increasing trends in firing rates. To explain this observation, we refer to the stringent criteria used to characterize the firing rate as decreasing. The first requirement concerned the slope of the firing rate. In a contraction where the firing rate had large oscillations, and the decrease was shallow (such as that shown in Fig. 6), it was difficult to obtain a meaningful estimate of the slope that could be dominated by transient changes in drive. Second, although every attempt was made to stabilize the biomechanics of the hand and foot with respect to the force gauges, it is conceivable that in some trials the subject may have in fact increased the force output in a direction not sensed by the force transducer, or agonist/antagonist activity from other muscles may have been involved. Third, 11 of the 14 quasistable contractions occurred at 30% of MVC, the lowest force level tested. It is conceivable that at low levels, motor units were only weakly influenced by the factors that cause the firing rates to decrease.

How is the force output maintained constant while the firing rates of active motor units decrease?

The muscle's ability to sustain constant force output while motor units decrease their firing rates has been attributed to three possible mechanisms: 1) recruitment of additional motor units during the course of the contraction; 2) increases in agonists and/or decreases in antagonist activity that compensate for reduced force contribution from the investigated muscle; and 3) changes in the mechanical properties of the motor units (twitch potentiation) that allow the net force to remain constant while the firing rates decrease. We consider each of these possibilities below.

MOTOR UNIT RECRUITMENT. Reports of both the presence and lack of motor unit recruitment in constant-force contractions can be found in the literature, possibly as a consequence of different experimental paradigms employed. In this study, motor unit recruitment was not observed during the 8- to 15-s contractions that were defined to be constant-force by the criteria described in the METHODS section. Occasionally, a motor unit was seen to be recruited within this time frame, but in each case the subject inadvertently caused minor increases in the force level. The example in Fig. 3 emphasizes the importance of carefully monitoring the force produced by the muscle.

Maton (1981) and Maton and Gamet (1989) reported motor unit recruitment during the onset of apparent constant-force contractions. They did not describe, however, the characteristics of the force generated by the muscle. Consequently, it remains unclear whether the motor unit recruitment these researchers observed was required to maintain force constant or was the result of significant deviations in the force output. Person and Kudina (1972) similarly reported observing motor unit recruitment during constant-

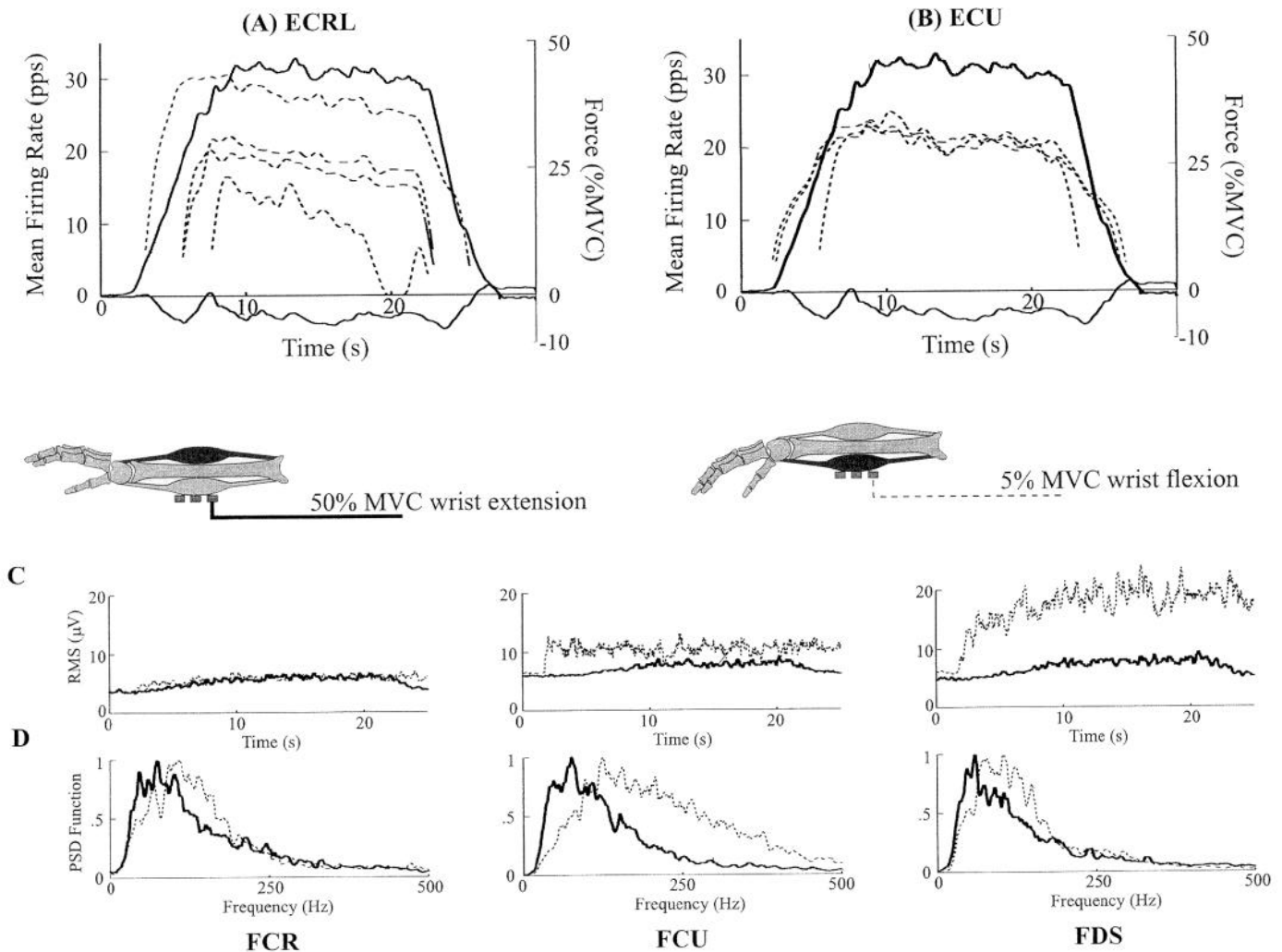


FIG. 9. Myoelectric activity in the wrist extensor and flexor muscles during isometric wrist extension. *A*: mean firing rates of motor units detected in the extensor carpi radialis longus (ECRL) muscle during isometric extension of the wrist at 50% of the MVC level along with the wrist extension (dark solid line reaching 50% of MVC) and ulnar-radial flexion (light solid lines) forces. *B*: mean firing rates of motor units in the extensor carpi ulnaris (ECU) muscle in the same contraction as in *A* along with the same forces. (Note that firing rates in both muscles are decreasing, ruling out agonist compensation.) *C*: root-mean-square (RMS) values of the myoelectric activity in the 3 flexor muscles [flexor carpi radialis (FCR), flexor carpi ulnaris (FCU), and flexor digitorum superficialis (FDS)] in the 50%-MVC wrist extension shown in *A* and *B* (solid line), and in a separate 5%-MVC wrist flexion performed during the same experiment (- - -). *D*: power spectra of the signals detected at the 50%-MVC wrist extension (solid line) and the 5%-MVC wrist flexion (- - -). Note that there is no accompanying activity in the flexor muscles that could compensate for the decreasing firing rates in the 2 extensors.

force contractions. The duration of the contractions these researchers investigated, however, varied from 2.5 to 13.5 min, far greater than the length of the contractions studied here. The recruitment observed by Person and Kudina was reported to occur near the end of these contractions. Such behavior, specifically if accompanied by firing rate increases in already active motor units, would be consistent with the time-dependent twitch potentiation and CNS modulation proposed below to account for the maintaining of constant force.

In all the contractions we studied, we never observed recruitment of motor units while previously active motor units decreased their firing rates. In the few contractions where recruitment was observed during the constant-force region, it was accompanied, and in most cases preceded, by an increase in the firing rates of the already active motor

units. In the test reported in Fig. 10, the subject was asked to increase the force after a constant-force region. The firing rates of the first three motor units, which were active from the beginning of the initial force plateau and thus had gone through considerable firing rate decrease, increased readily as the force output was increased. As the force was further increased, a new motor unit was recruited around the 14-s mark. This example shows that the motor units in a muscle producing constant force maintain the ability to increase their firing rates subsequent to a sustained decrease, and that recruitment occurs to supplement, not to replace, such an increase.

However, the strongest evidence for the maintainability of force in the presence of decreasing firing rates without the recruitment of additional motor units is provided by contractions performed at force levels beyond the recruitment

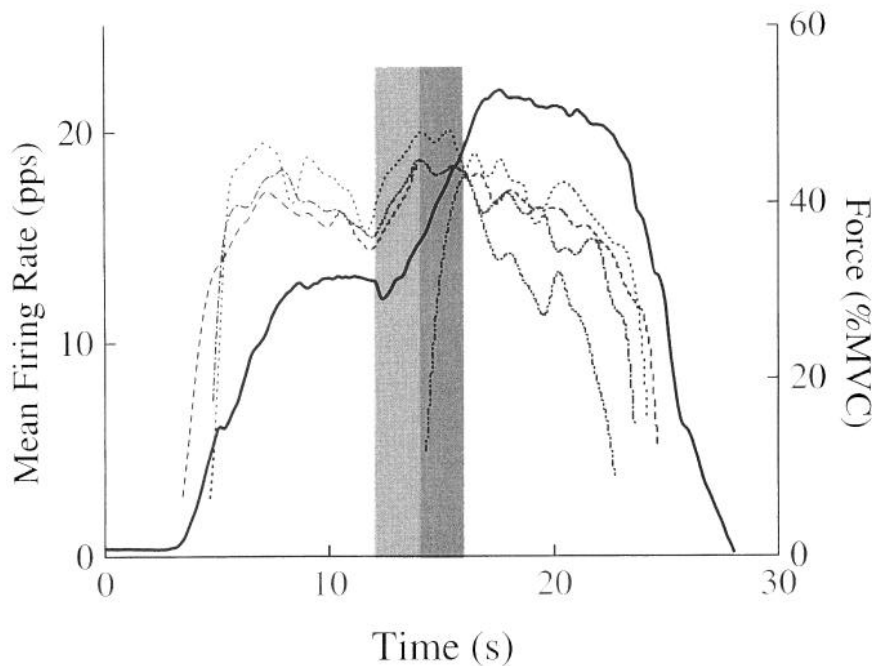


FIG. 10. Contraction where the force level was maintained constant at an initial level and then increased. Heavy solid line: force trajectory produced by the subject during isometric dorsiflexion of the ankle. The force level is raised to 30% of MVC, held constant, and then raised to 50% of MVC, where the subject slowly begins to relax. The mean firing rates of 3 motor units are seen to decrease during the constant-force interval at 30% of MVC, and to increase as the force level is increased (light gray shaded area). As the force continues to increase, an additional motor unit is recruited (dark gray shaded area).

range of the specific muscle. Several researchers have shown that motor unit recruitment is completed by ~50% of MVC in small muscles (Kukulka and Clamann 1981 for the adductor pollicis; De Luca et al. 1982a,b and Milner-Brown et al. 1973 for the FDI), and 70–80% of MVC in large muscles (Kukulka and Clamann 1981 for the biceps muscle; De Luca et al. 1982a,b for the deltoid; Erim et al. 1996 for the TA muscle). The fact that firing rates decreased in constant-force contractions at 80% of MVC in the TA and 50% of MVC and especially 80% of MVC (30% of MVC beyond the recruitment of all motor units) in the FDI demonstrates that a constant-force isometric contraction can be sustained with decreasing firing rates and no recruitment of additional motor units.

AGONIST/ANTAGONIST MUSCLE INTERACTION. Another possible mechanism that could account for the net force output remaining constant while the firing rates decrease is the interaction between agonist/antagonist muscles. An agonist muscle could increase its activity while firing rates in the muscle being investigated decrease, thus resulting in the net force or torque at the monitored joint remaining constant. Likewise, an antagonist muscle could cause the net force to remain constant while the investigated muscle undergoes firing rate decreases, by reducing its activity. To investigate these possible interactions, we studied the behavior of muscles around the wrist joint. ECRL and ECU (agonists in wrist extension) both displayed decreasing firing rates (while the other extensor, ECU, was inactive), ruling out the possibility of compensation by agonists.

The possibility that the torque at the wrist joint could be maintained by decreasing antagonist muscle activity was ruled out by the low and constant level of activity observed in the flexors. Furthermore, power spectrum analysis performed on the surface myoelectric signals detected from the flexors indicated that the frequency bandwidth of the myoelectric signals detected over the flexors during the 5%-

MVC wrist flexion was greater than the bandwidth for the signals detected over the same muscles during the 50%-MVC wrist extension. A shift toward lower frequencies in the power spectrum is expected from spatial filtering effects if the signals detected on the flexor muscles actually originated from more distant muscles (De Luca and Merletti 1988). Consequently, it is highly likely that the signals detected over the flexor muscles were cross talk signals originating in the extensor muscles and that the flexors (antagonists) were not active.

TWITCH POTENTIATION. Twitch force potentiation in human muscles has been studied in detail and with consistent results (Botelho and Cander 1953; MacIntosh et al. 1994; Takamori et al. 1971; Vandervoort et al. 1983, among others). These reports agree that during repeated activation of a muscle, the force output will increase over a limited time. The findings of Vandervoort et al. (1983) are of particular interest to the present study. They have shown that potentiation of the twitch force, elicited from supramaximal stimulation in the TA muscle, begins at the onset of a voluntary contraction and produces rapid gains in force output. They also found that the degree and duration of potentiation varied between the TA muscle and the plantar flexor muscles. These findings are consistent with the findings of this study, as are the observations of Burke (1981), who found that fast-twitch motor units displayed greater potentiation than slow-twitch motor units.

Given that twitch forces potentiate, in the present experiments, if the firing rate of the motor units were maintained constant once the target level was achieved, the force output would overshoot the target level. This effect has been described by Kernell and Monster (1982b), who, with constant current injection in the motoneuron, observed a short-duration increase in the net force produced by a single motor unit. This effect can also be verified *in situ* muscles by electrically stimulating the muscle at one of its motor points at a fixed frequency and

intensity. The force generated by the muscle will increase as time progresses until the muscle fibers diminish their capacity to generate force (personal observation).

Although twitch potentiation of single motor units has been reliably measured in animals (Bagust et al. 1974; Burke et al. 1976), it is difficult to measure the potentiation of a specific motor unit twitch force in human muscles during voluntary contractions. The technical complications of these measurements have been discussed in detail by Nordstrom et al. (1989) and more recently by Lim et al. (1995). The present set of experiments were performed at relatively high force levels. Consequently, the number of active motor units and the magnitude of the firing rates achieved by these motor units made estimation of single-motor-unit twitch forces by spike-triggered averaging techniques unreliable for this study.

The suggestion that twitch potentiation and the decrease in the firing rates combine to maintain the net force produced by a muscle constant is consistent with the present findings. Consider the following two points. We found that, at 30% of MVC and 50% of MVC, the magnitudes of the common regression slopes of the firing rate decrease versus recruitment threshold relationship were greater for the FDI than the TA muscle. This behavior complements the mechanical aspects of the motor units in these two muscles. The FDI muscle has been shown to have a greater percentage of type II muscle fibers than the TA muscle (Johnson et al. 1973). Consequently, although the firing rates of motor units in the FDI muscle decreased at a faster rate, the twitch potentiation in this muscle would also be greater, potentially resulting in a constant force output. The effects of force on twitch potentiation can explain how the force output could remain constant at different force levels when the decrease in the firing rates varied between force levels. At higher force levels, the motor units would fire at greater rates and, therefore, potentiate more rapidly. As a result, while the motor units would decrease their firing rates more quickly at the higher level, their twitches would also potentiate more. These two complementing effects could combine to maintain the force constant. In this fashion, the rate-dependent potentiation could explain the behavior of the TA muscle and the FDI muscle at 30 and 50% of MVC.

In considering 80%-MVC contractions in the FDI muscle, it is important to note that the previous work of Vandervoort et al. (1983) in the plantar and dorsiflexor muscles of humans, and of MacIntosh et al. (1994) in the gastrocnemius muscle of the rat, showed that the mechanical changes in the twitch force did not continue to potentiate at the same rate as a contraction progressed. Instead, these researchers noted that the rate of increase in the twitch force was more rapid during the initial stage of a contraction. As a contraction progressed, the rate of potentiation began to decrease, and, if a maximal level contraction continued past 10 s, the amplitude of the twitch force began to actually decrease, eventually becoming smaller than the initial twitch force. In the FDI muscle, all the motor units are recruited by 50% of MVC (De Luca et al. 1982a,b; Milner-Brown et al. 1973), compared with the TA muscle, which recruits motor units up to 70% of MVC (Erim et al. 1996). Consequently, during the 80%-MVC contractions (with a ramp of 10% MVC/s) in the FDI, all the motor units in the muscle will have been

active for ≥ 3 s before reaching the plateau. It is in these 3-s periods, after which all the motor units have been recruited, that according to both Vandervoort et al. (1983) and MacIntosh et al. (1994), the greatest increases in twitch force would occur. Furthermore, in these 3 s, the motor units will be firing at higher rates than they would at lower force levels, thereby accentuating the effects of twitch potentiation. Once the target level had been achieved, the twitch forces would continue to potentiate, but at a slower rate. It is also conceivable that, toward the end of the plateau, twitches may begin to decrease. Therefore, on the average, a lesser amount of potentiation would be observed throughout the plateaus at 80% of MVC in the FDI muscle compared with the TA at the same level, as well as with the FDI at lower forces. It is consistent that the decrease in the firing rates of the motor units in the 80% of MVC is less than that in 50% of MVC and 30% of MVC.

The works of MacIntosh et al. (1994) and Vandervoort et al. (1983) provide further insight as to why motor unit recruitment may not be necessary during the first 15 s of a constant-force isometric contraction. Vandervoort et al. (1983) showed that in both the dorsiflexor and the plantarflexor muscles, twitch potentiation subsided subsequent to voluntary contractions that lasted >30 s. MacIntosh et al. (1994) have shown that, when stimulated at 10 Hz, the gastrocnemius muscle of a rat displayed a decrease in the amplitude of the twitch force after 20 s of stimulation. Thus, if a constant-force isometric contraction were sustained for 30 s, the force-generating capability of the muscle could diminish. To compensate for this, an increase in the firing rates of the active motor units would occur, possibly accompanied by motor unit recruitment. Such an example is shown in Fig. 11, where a motor unit is observed to be recruited at the 29-s mark during an isometric constant-force contraction in the FDI. Also shown in this figure is a gradual increase in the firing rates of the motor units beginning at the 22-s mark. Interesting as this result is, it was never observed in any of the contractions of both muscles that lasted <15 s.

What is the cause of the firing rate decrease?

During the past three decades, three mechanisms have been advanced as possible candidates for causing the firing rate to decrease: feedback mechanisms, "late adaptation" property of the motoneuron, and voluntary modulation of the firing rate. We now consider each of these in relation to our study.

FEEDBACK MECHANISMS. It has been suggested by Bigland-Ritchie et al. (1983, 1986b) that feedback mechanisms may participate in decreasing the firing rate. These researchers noted that the decreasing firing rates did not recover after a 3-min rest under ischemic condition. Consequently, the researchers hypothesized that the decrease in firing rate might be caused by peripheral feedback. This speculation was consistent with suggestions that a decrease in firing rate could be caused either by reduced afferent input from muscle spindles (Bongiovanni and Hagbarth 1990) or by an increased inhibitory drive initiated from group III and IV nerve endings that may become sensitive to fatigue-related metabolic events (Kniffki et al. 1981). If these were the domi-

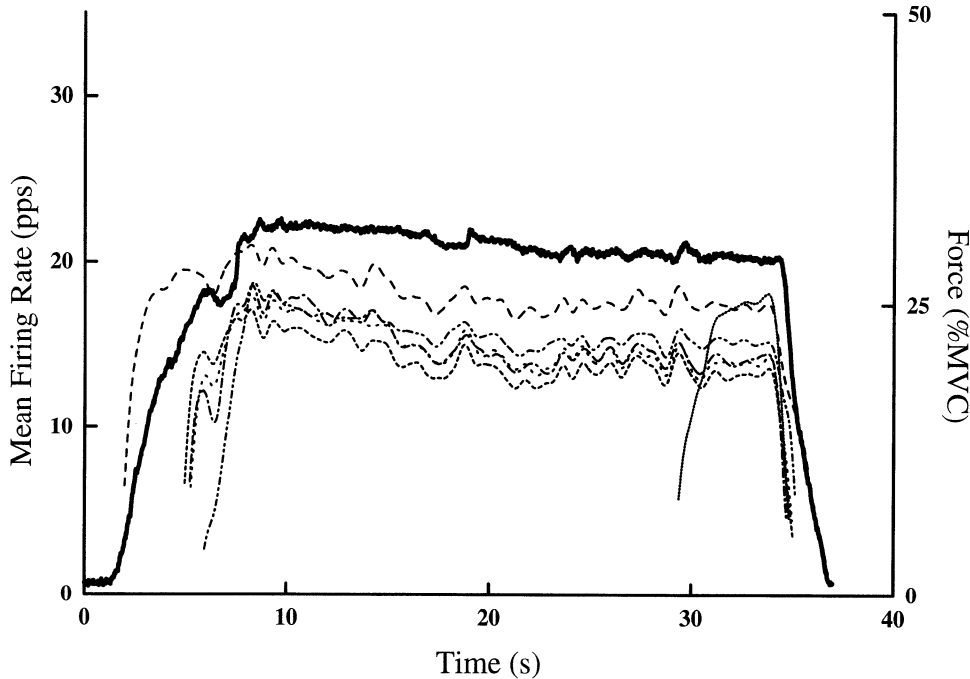


FIG. 11. Constant-force isometric contraction of the FDI that shows an increase in the firing rate of coactive motor units at the 22-s mark and a recruitment of a new motor unit at the 29-s mark. Such increases in firing rates and motor unit recruitment were not observed in constant-force contractions sustained for <15 s.

nant effectors of the firing rate decrease, then higher-force-level contractions (in which the excitation of peripheral receptors and the accumulation of metabolites would be greater) should all demonstrate an increasingly greater decrease in the firing rates. Such behavior is inconsistent with the present experimental results, which show that the firing rates decreased more slowly at 80% of MVC in the FDI muscle than at either 30 or 50% of MVC. Given this discrepancy, and given that these effects have not yet been clearly demonstrated to cause the firing rate to decrease, the feedback mechanism suggestion remains speculative.

LATE ADAPTATION OF THE FIRING RATES. This intrinsic property of the motoneuron was first described by Kernell (1965) and Kernell and Monster (1982a,b), who showed that the firing rate of motoneurons decrease when they are excited with a constant current stimulation. This decrease was also found to be dependent on the fiber type, with motoneurons innervating muscle fibers that the researchers classified as fast fatiguing and fast fatigue resistant having a greater decrease in firing rate than motoneurons innervating slow-fatiguing muscle fibers. Our results also show an indication of this intrinsic behavior in that the rate of decrease in the firing rate was found to be greater in higher-threshold motor units, which are more likely to be composed of fast-fatiguing and fast-fatigue-resistant muscle fibers. Kernell and colleagues also found that the decrease in firing rate was related to the stimulus level, observing that at higher levels of stimulation the decrease was faster. The agreement between the findings of Kernell (1965) and Kernell and Monster (1982a,b) and the results of the present study regarding the effects of recruitment threshold of the motor unit and the level of the contraction on the decrease in firing rates suggest that late adaptation is an important factor in the decreasing of firing rates during constant-force contractions. Figure 11 also provides indirect support for the existence of

late adaptation. The first five motor units detected are recruited during the early stages of the contraction and undergo significant firing rate decreases, especially during the first 22 s. On the other hand, the last motor unit, which becomes recruited around the 29-s mark, has not gone through the effects of late adaptation. This unit fires at a rate comparable with the firing rate displayed by the rest of the motor units in the beginning of the force plateau. If not for the phenomenon of late adaptation causing the firing rates of the previously active motor units (which have been active for ≥ 23 s before the last motor unit is recruited) to gradually decrease, the last unit would be expected to fire at a rate lower than those of the units recruited before it, because of the negative correlation between recruitment threshold and firing rate (De Luca and Erim 1994).

However, the behavior of the firing rates of the FDI muscle at 80% of MVC demonstrates that late adaptation cannot be the only factor causing the firing rates to decrease. If the decrease in firing rate reported in the present study were due exclusively to the intrinsic factors described by Kernell (1965) and Kernell and Monster (1982a,b), it would be expected that the contractions at 80% of MVC in the FDI muscle would have a faster rate of decrease than the 50%- and 30%-MVC contractions, but this was not the case. This inconsistency suggests that at least one other mechanism participates in decreasing the firing rate.

VOLUNTARY MODULATION OF FIRING RATES. In the production of muscle force, there are three major components: the central drive to the motoneuron, the electrical response of the motoneuron to the drive, and the twitch properties or mechanical response of the muscle fiber. At the onset of a constant-force contraction, two of these components undergo complementary changes: late adaptation causes the motoneuron to respond to the same level of drive with a lower firing rate, thus acting toward a decrease of force while

twitch potentiation enhances the mechanical response to each firing of the motorneuron, thus contributing to an increase in force. Even though theoretically possible, it is not likely that, without intervention from the CNS, a fine balance between the time-dependent effects of these two phenomena is maintained throughout the contraction so as to yield a constant force level. It is proposed that the drive to the motoneuron pool is modulated to fine-tune the net effect of the complementary changes in the electrical and mechanical aspects of force production. The direction in which the central drive is altered during the early stages of the contraction escapes scrutiny, because the drive itself is inaccessible and it is not clear which of the changes in the electrical or mechanical properties dominates the other.

The situation during the later portions of the contraction allows for clearer deductions regarding the central drive. In this case, with twitch potentiation declining and ultimately becoming lower in amplitude, the electrical and mechanical properties act in the same direction—to decrease the force output. Thus the central drive must be increased in order to sustain constant force output. Evidence of this behavior is seen in Fig. 11, where the decrease in firing rates levels off around the 21-s mark, probably signaling the decline in twitch potentiation. As the need to maintain constant force output persists, an increase in the firing rates of coactive motor units is observed, most likely indicative of a greater increase in the drive in order to overcome the effects of late adaptation and to compensate for diminished twitch forces. As the drive progressively increases to compensate for the diminutive changes in the electrical and mechanical properties, around the 29-s mark, it reaches the level that corresponds to the recruitment threshold of the last motor unit recruited.

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