Myoelectric signals were detected from the tibialis anterior muscle of 5 subjects with a quadrifilar needle electrode while the subjects generated isometric forces that increased linearly with time (10% of maximal voluntary contraction/s) up to maximal voluntary level. Motor unit firing rates were studied as a function of force throughout the full range of muscle force output. The relationship between force and firing rate was found to contain three distinct regions. At recruitment and near maximal force levels, firing rates increased more rapidly with force than in the intermediate region. Furthermore, in the regions with rapid increases, the rate of change of firing rate was correlated to the recruitment threshold, with higher recruitment threshold motor units displaying greater rates of change. In the intermediate region, all motor units had similar rates of change of firing rate. A weak positive correlation was found between initial firing rate and recruitment threshold. Firing rates of motor units at any instant were found to be ordered according to the recruitment order: at any given time in the contraction motor units with lower recruitment thresholds had higher firing rates than units with higher recruitment thresholds. Firing rates of all motor units were observed to converge to the same value at maximal forces. Mechanisms underlying motor unit recruitment and firing rate modulation are discussed in the context of a conceptual model. © 1996 John Wiley & Sons, Inc.

Key words: motor unit • rank-ordered • discharge • firing rate • recruitment threshold • common drive • motor control

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RANK-ORDERED REGULATION OF MOTOR UNITS

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It is well known that the central nervous system controls two parameters of motor unit activation in producing a desired force output in a muscle: the recruitment of new motor units and the modulation of the average firing rate of the motor units that are already activated. Numerous researchers have investigated these properties of motor unit control and the interaction between them. These investigations have resulted in contradictory reports in the literature regarding various issues related to the activation of motor units. Most notably, conflicting generalizations have been advanced about the behavior of single motor units throughout the complete range of muscle force. Views ranging from constant firing rates independent of force,[2] to firing rates that plateau at submaximal force levels,[1,24] to firing rates that vary monotonically with force[5,22,27] have been expressed. Opinions regarding the firing behavior of motor units with different recruitment thresholds have also diverged. Based on a belief that motor units would be activated at their tetanic fusion frequency in order to optimize efficiency, some researchers have maintained that low-threshold motor units have lower firing rates compared to high-threshold motor units[4,18,29]; whereas other researchers have reported that lower-threshold motor units fire at higher rates than the high-threshold ones.[8,10,17,26,27]

This investigation was undertaken in order to explore the recruitment and firing rate modulation strategies that are used in force generation by the muscle. The recruitment and firing rate properties of the muscle were studied in the whole force range

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of the muscle. Our ability to observe consistently and accurately the individual firing patterns of multiple motor units in contractions where the force output reached the maximal voluntary contraction level provides the opportunity to explore the system in its complete dynamic range.

Preliminary accounts of this work have been presented to the Society for Neuroscience[9] and the International Society of Electrophysiology and Kinesiology.[12] Some findings of this study have been included in a previous review article.[8]

METHODS

Experimental Procedures. Five healthy subjects with no known neurological disorders and with ages ranging from 22 to 38 years (mean ± SD = 29.2 ± 3.0) volunteered for the study. Each subject read and signed an informed consent form approved by the local Institutional Review Board prior to participating in the experiment. The tibialis anterior (TA) muscle was chosen for this study.

Subjects were comfortably seated in a modified dental chair with a specially designed restraining apparatus that attaches to the leg of the subject. This device fixed the ankle at a right angle and contained a stiff (3 μm/N) transducer to monitor the force isometrically generated by the plantar flexion and dorsiflexion of the foot. All 5 subjects had extensive practice with the experimental setup and attempted to activate only the TA muscle in dorsiflexing the foot.

The maximal voluntary contraction (MVC) level for the subject was determined by choosing the greatest of three attempts at generating the maximal voluntary effort. Each of these attempts lasted 3 s and were 2 min apart in time. Then, a 25-gauge quadrifilar electrode was inserted into the belly of the TA muscle. The needle position was adjusted to allow for the stable recording of at least two motor units. The subject was asked to track a force pattern being displayed on a computer screen. The patterns that were generated had a ramp part that increased with a slope of 10% MVC/s, and a plateau of value that was either 20, 50, 80, or 100% MVC. The actual force output of the subject was also displayed real-time on the screen to provide feedback. Details of experiments involving the TA muscle have been described previously.[3] Table 1 details the number of subjects tested, the number of contractions performed, and the number of motor units identified at each force level.

Table 1. Numbers of subjects tested, contractions performed, and motor units identified at each force level.

Level (% MVC)	Subjects	Trials	Motor Units
100	2	5	8
80	4	18	47
50	3	8	28
20	4	12	41

Acquisition of Motor Unit Action Potential Train. The myoelectric signal was acquired and decomposed into its constituent motor unit action potential trains (MUAPTs) with a technique reported by LeFever et al.[19,20] and Mambrito and De Luca,[21] and more completely described in a recent report by DeLuca.[7] The technique is now referred to as Precision Decomposition. Three channels of myoelectric signal were detected using a specialized quadrifilar needle electrode. These signals were amplified, band-pass filtered from 1 kHz to 10 kHz, and along with the muscle force measured from the transducer, were stored on frequency modulation (FM) magnetic tape. The myoelectric signals were time-compressed, digitized at 50 kHz, and decomposed into individual MUAPTs. The Precision Decomposition algorithms use template matching, template updating, and motor unit firing statistics to identify individual motor unit firing times. Earlier studies have shown that with proper use, this technique can provide 100% accuracy.[21] All the MUAPTs analyzed in this study were decomposed and all the interfiring intervals were confirmed by the operator to be correct by accounting for all the action potentials identified and inspecting all the motor unit action potential trains to verify that no unexpectedly long or short firing interval was present. Figure 1 shows typical information derived using the Precision Decomposition technique.

Signal Analysis Procedures. The parameters that were investigated in this study were estimated in the following manner. The *recruitment threshold* of a motor unit was defined as the average of the force recorded in a window of 15 samples (corresponding to 7.32 ms) placed around the first firing of the motor unit. The *initial firing rate* was calculated by inverting the average of the first three interfiring intervals corresponding to the first four firings of the unit. The continuous *mean firing rate* signal for a motor unit was calculated by passing a 400-ms Hanning window over an impulse train corresponding to the firing times of that motor unit. The mean firing rate signals plotted as a function of time in Figures 4 and 5 were obtained in this manner. In investigating how motor units modified their firing rates in response to intended force levels, we have used the force output

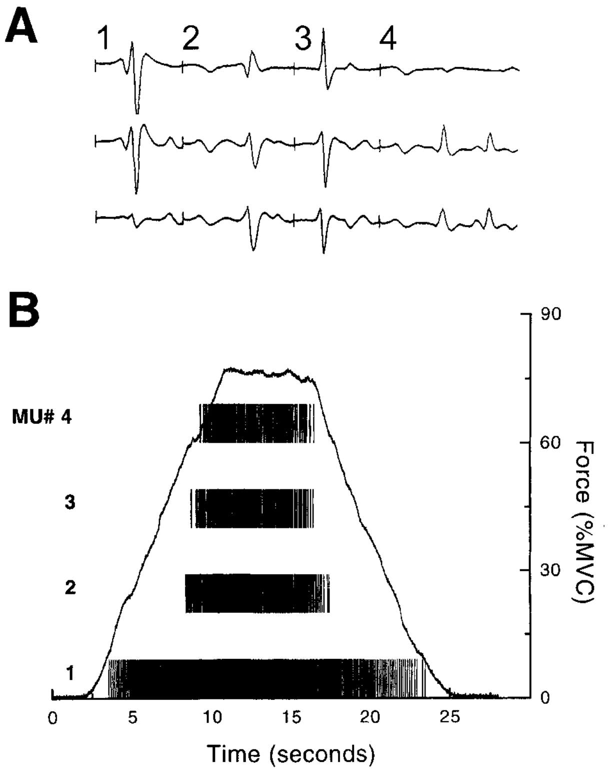

FIGURE 1. Typical information provided by the Precision Decomposition technique. **(A)** The distinct action potentials of four motor units recorded during a 80% MVC of the tibialis anterior muscle. The activity of each motor unit is represented in three channels, displayed below one another, for improved identification. **(B)** Bar plot representing the firing times of each motor unit throughout the contraction. The dark solid line represents the corresponding force output of the muscle as a percentage of the subject's MVC level.

of the muscle as an indicator of the intended or targeted task. Hence motor unit firing rates were studied as a function of muscle force by simultaneously computing averages of 1-s windows spaced 1 s apart from both the mean firing rate signals (calculated with the procedure described above) and the force recording. Firing rate average values were plotted against force averages in the same time window. This was the procedure used in creating the plots in Figures 2 and 3. In a given contraction averaging windows were placed according to the same time reference so that the comparison of the firing rate of one unit to that of another in the same contraction was possible at any given instant or force value. The lengths of the averaging windows in the above definitions were selected as a compromise (between representing instantaneous changes at the risk of noisy estimates and reliable estimates that averaged out events with shorter duration) dictated by our experience.

RESULTS

Firing Rate as a Function of Force. Firing rates of motor units were investigated as a function of muscle force output by plotting out mean firing rate/force pairs that were calculated as described above. Even though the actual force trajectories were trapezoidal, for this aspect of the study we considered only the ramp portion of the contractions where the force linearly increased with time because we did not wish to include factors such as fatigue or twitch potentiation to overshadow our investigation. All the contractions summarized in Table 1 were investigated by superimposing (a) the firing rate/force curves for all motor units detected in a contraction; (b) the curves for all the motor units in all the contractions of the same level performed by a subject on a given day; and (c) the curves for all the motor units in all the contractions of the same level performed by all the subjects, in order to reveal any trends in the firing rates of motor units as a function of force.

Of utmost interest were 100% MVCs, whereby the firing rate behavior of motor units could be observed throughout the complete range of possible force values. Parts A and B of Figure 2 represent the data obtained in two different contractions performed by the same subject; part C presents the data recorded in all of the 100% MVCs performed by the same subject; and part D presents the data collected in all the 100% MVCs performed by 2 subjects in whose data multiple motor units were reliably identified. Each curve represents the force-dependence of the firing rate of a single motor unit. In these trials, even though the subject was attempting to reach 100% MVC, the actual force output fell short of the maximal force level exerted prior to the test. This could be explained by the fact that in determining the MVC value the subject was asked to exert their maximal force without any restrictions on the speed with which to attain that level, whereas in the experiments where the subjects were asked to reach 100% MVC by tracing a specified force trajectory, the contraction rate was specified to be 10% MVC/s. Hence, the two paradigms were essentially different and the fatigue process probably had a more dominant effect in the latter.

The curves displayed in Figure 2 are representative of the other curves not presented here in that the firing rates increased monotonically with increasing force in the region studied. The calculated curves exhibit a relationship, between the firing rate of a motor unit and the force output of the muscle, that can be characterized in three regions. In the first region, beginning with the recruitment of the motor unit, firing rates increased rapidly with increasing

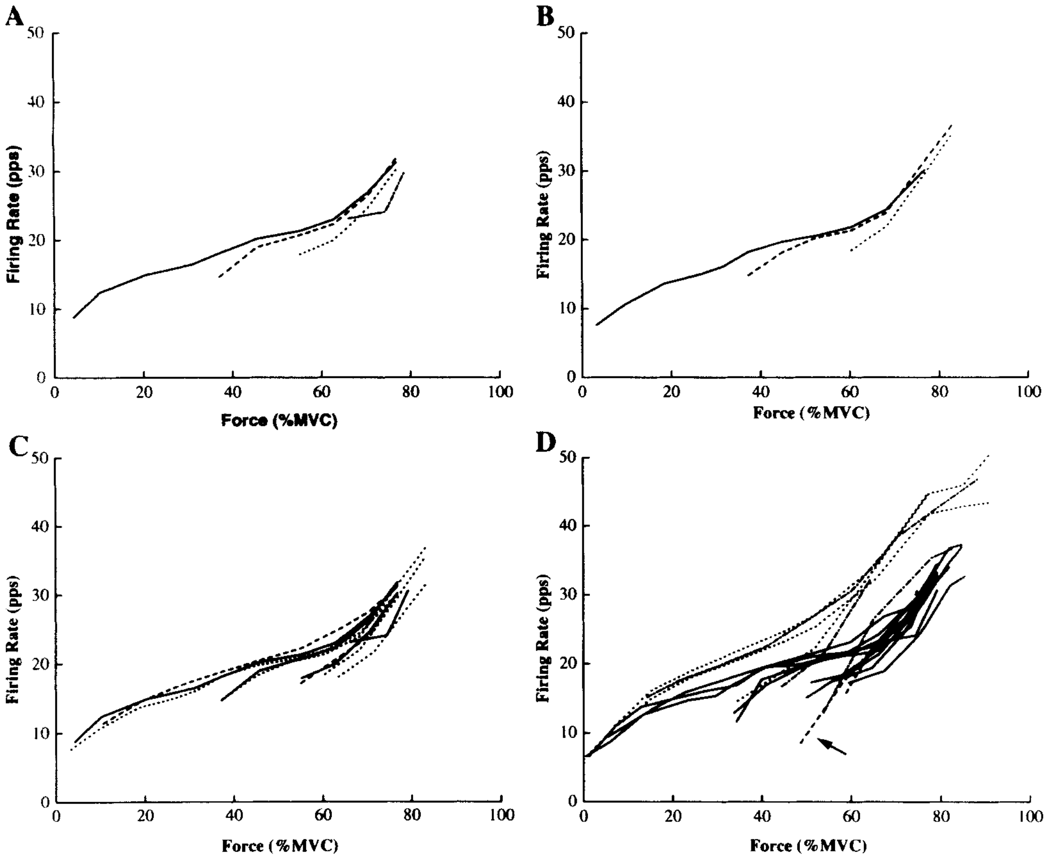

FIGURE 2. Firing rates of motor units as a function of muscle force during isometric contractions. Each curve represents the behavior of the firing rate of a given motor unit in a given contraction as muscle force is increased. Firing rates and force averages were computed over 1-s windows at 1-s intervals while muscle force was linearly increased with time up to 100% of the subject's maximal voluntary contraction (MVC) at a rate of 10% MVC/s. The resultant curves were smoothed to emphasize the main trends. **(A)** Four motor units detected in an isometric contraction of the tibialis anterior muscle. **(B)** Three motor units detected in another contraction of the same muscle in the same subject as in **(A)**. **(C)** All the motor units detected in four separate contractions performed by the same subject. Curves with the same line type represent motor units detected in the same contraction. **(D)** All the motor units detected in a total of nine contractions performed by 3 different subjects. Curves with the same line type represent data obtained from the same subject (but not necessarily the same contraction). (From De Luca and Erim,[8] © 1994, *Trends in Neurosciences.*)

force. This region was observed to last for 10–20% MVC. In the second linear region, the firing rates increased less sharply with increasing force. The third region, which extended from approximately 70% MVC to maximal force in all cases, displayed a greater slope than the previous region.

A word of clarification may be in order here. It might appear incorrect to investigate motor unit firing rates as a function of force. Since it is the firing rates that initiate the force output, one may consider studying the firing rate as the independent variable and force as the dependent variable. However, it is important to note here that the observed force is the combined outcome of the firing activity of all the motor units active in the contraction. Hence, it is not a cause–effect relationship that we wish to establish between the firing rate of a single motor unit and the overall force output of the muscle, but rather a relationship that shows how a given motor unit modulates its firing rate in order to generate a desired or targeted force level. Thus, we are using the force as an indicator of the intent or the target of the central nervous system as opposed to the immediate outcome of the activation of a motor unit.

Dependence of Firing Rate on Recruitment Threshold. In order to study the dependence of the force/firing rate profile of a motor unit on its recruitment threshold, it was desirable to group force/firing rate profiles according to recruitment thresholds. There was only 1 subject from whom we were able to record a considerable number of motor units with varying recruitment thresholds, making such grouping possible. Figure 3 presents the data that were collected from this subject in four separate 100% MVCs. Motor units were divided into three groups: low

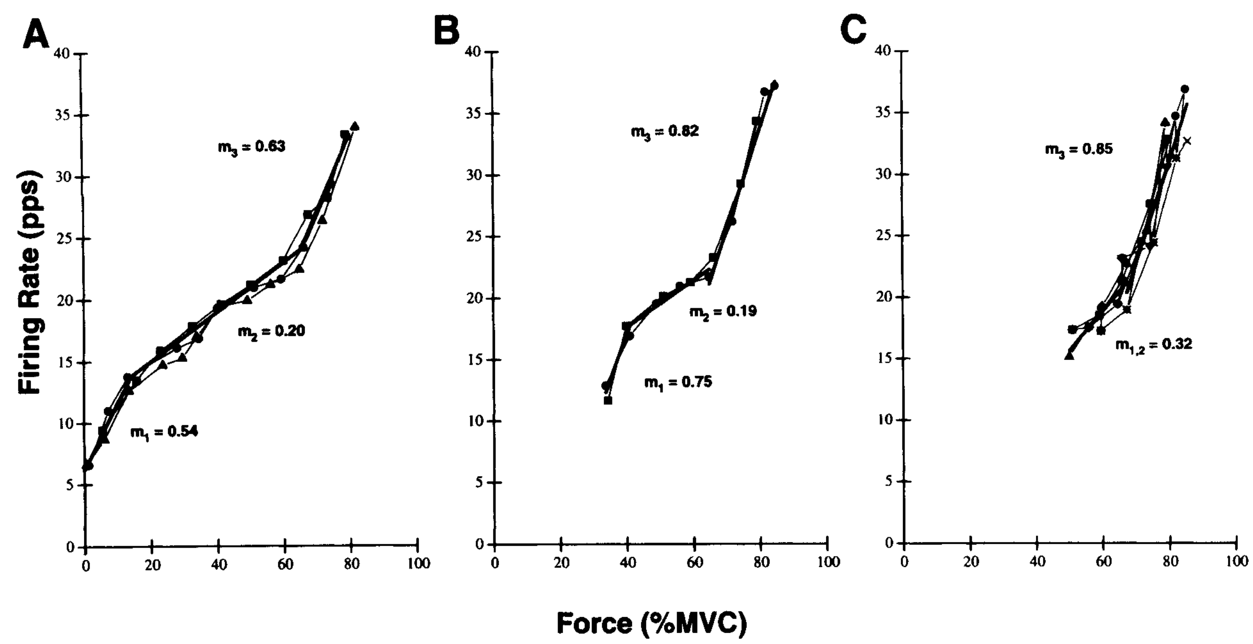

FIGURE 3. The firing rate curves for **(A)** low, **(B)** medium-, and **(C)** high-threshold motor units as a function of muscle force. A line was fitted for each of the three linear regions discussed in the text using the least-square technique. These lines and the slopes describing them are displayed on each graph. Notice that in general, higher-threshold motor units have higher slopes than lower-threshold motor units. This can be interpreted as a higher sensitivity to excitation, whereby higher-threshold motor units increase their firing rates more in response to an increase in the desired force output.

(0–20% MVC), medium (20–50% MVC), and high (greater than 50% MVC) recruitment threshold. The data from each group were analyzed in the three linear regions discussed previously. For each group, a line was fitted to the combined data in each of these regions, using the least-square method. The borders of the regions were selected to reflect the natural breakpoints observed in the plots. These lines and their slopes are displayed on each graph in Figure 3. Even though the small number of motor units identified in each group limits the analysis, it is seen that the medium-threshold motor units have a higher slope (0.75) than the low-threshold ones (0.54). In the second region, the low- and medium-threshold units had comparable (0.19 and 0.20) slopes, while the slope of the medium-threshold units (0.82) was greater than that of the low-threshold units (0.63) in the last region. The high-threshold units did not have clearly separated first and second regions, but had a higher slope than both low and medium-threshold motor units in the third region (0.85).

Another observation related to the dependence of the firing rate on recruitment threshold was that at submaximal force levels, the firing rates of motor units displayed a hierarchy that was dictated by the recruitment rank of the units. At any given point in the contraction, the earlier-recruited motor units with lower thresholds fired at higher rates than later-recruited motor units with higher thresholds. This recruitment-ordered behavior of firing rates, which is evident in Figure 2 for the ramp portion of the contraction, prevailed throughout the contraction, including the ramp-up, plateau, and the ramp-down sections. When the firing rates of motor units are plotted as a continuous function of time, the recruitment-ordered hierarchy among the firing rates results in the nesting of firing rate curves under one another. The appearance of these nested curves brings to mind the term "onion skin" for describing this phenomenon. Figure 4 represents an example of the onion skin phenomenon.

Dependence of Initial Firing Rate on Recruitment Threshold. The initial firing rates of motor units also displayed a dependence on the recruitment threshold. As evident from the increase in the starting firing rate values of curves that start at higher recruitment threshold values in Figure 2, there was a positive correlation between the initial firing rate of a motor unit and its recruitment threshold: the earlier-recruited motor units with lower recruitment thresholds start their firing at lower rates than do their later-recruited counterparts with higher thresholds. This dependence is further investigated in Figure 5. In this figure, the initial firing rates of all the motor units that were identified in all the contractions in

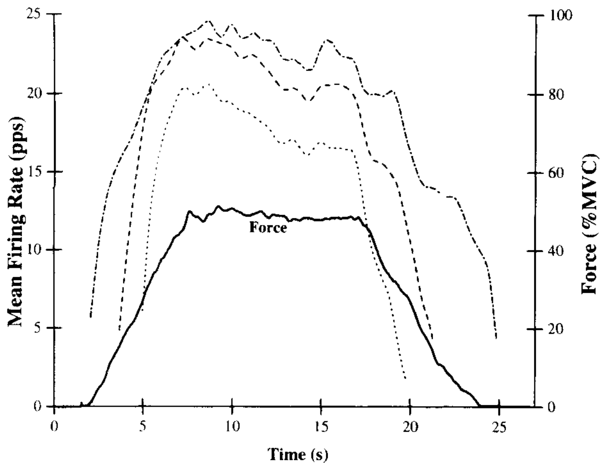

FIGURE 4. The rank-ordered firing rates of motor units during an isometric contraction of the tibialis anterior muscle. Notice that the earlier-recruited motor units maintain higher firing rates than the later-recruited units at all instants during the contraction. The orderly nesting of the firing rate curves has lead to the term "onion skin" for the negative correlation between the recruitment threshold and the firing rate of a motor unit.

this study are displayed. Different symbols are used to differentiate between the four force levels studied, i.e., 20, 50, 80, and 100% MVC. However, regression analysis was performed on the combined data and not separately for each contraction level, as there is no logical reason to expect the force level that will be reached later in the contraction to have an effect on the firing behavior of the motor units at the onset of contraction. Indeed, no such dependence on target force level is observed in Figure 5. The regression line displayed in Figure 5 predicts the relationship between these two variables to be

$$\lambda_O = 0.22\ (F_0 + 35)$$

where λ_O is the initial firing rate in pulses per second (pps) and F_0 is the recruitment threshold expressed as a percentage of the MVC.

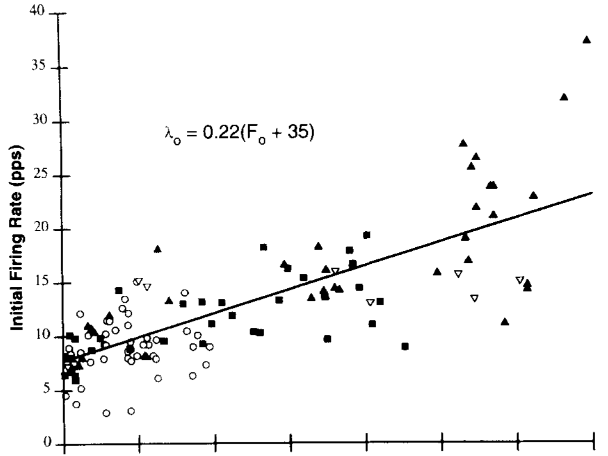

FIGURE 5. Initial firing rates (λ_0) of all the motor units that were identified in all the contractions in this study displayed against their calculated recruitment thresholds (F_0). Different symbols were used to differentiate between force levels targeted in the contractions (circles represent 20% MVC, squares 50% MVC, filled triangles 80% MVC, and open triangles 100% MVC), but regression analysis was performed on the combined data.

Convergence of Firing Rates at Maximal Force Levels. In a given contraction, the firing rates of motor units converged to the same maximal value as the targeted force level reached the maximal voluntary contraction level. This phenomenon is evident in Figure 2A and B, which display motor unit data recorded in the same contraction. Note how the distance between the curves at lower force levels decreases at higher force values, as a result of the convergence in firing rates. Figure 6 displays the firing rates as a function of time in a 20% MVC in part A and in an attempted 100% MVC in part B in order to provide another point of view into the behavior of firing rates at maximal force levels. Notice the separation among the firing rate curves of different motor units in part A, while the firing rate curves in part B are much closer, with the firing rates of the last three units essentially superimposed on each other.

DISCUSSION

In this study, the firing rate behavior of motor units in the TA muscle was studied as the isometric force was increased linearly with time up to 100% MVC. The following discussion elaborates on the main findings and attempts to place them in perspective with each other and other reports in literature.

"Onion Skin" Phenomenon: Firing Rate Dependence on Recruitment Threshold. It has been noted earlier that at any given instant in the contraction firing rates of motor units adhered to a hierarchy determined by their recruitment thresholds. This observation, which has been reported earlier,[8,10,17,24,26,27] contradicts the teleological argument occasionally advanced in the literature[4,13,18,25,29] (among others) which maintains that since the later-recruited motor units have higher-amplitude, shorter-duration twitch responses, they would be expected to fire faster in order for their twitches to fuse and to contribute an average force similar to that of the earlier motor units with longer-duration twitches. Our results show that this is not so. The lower firing rates of higher-threshold motor

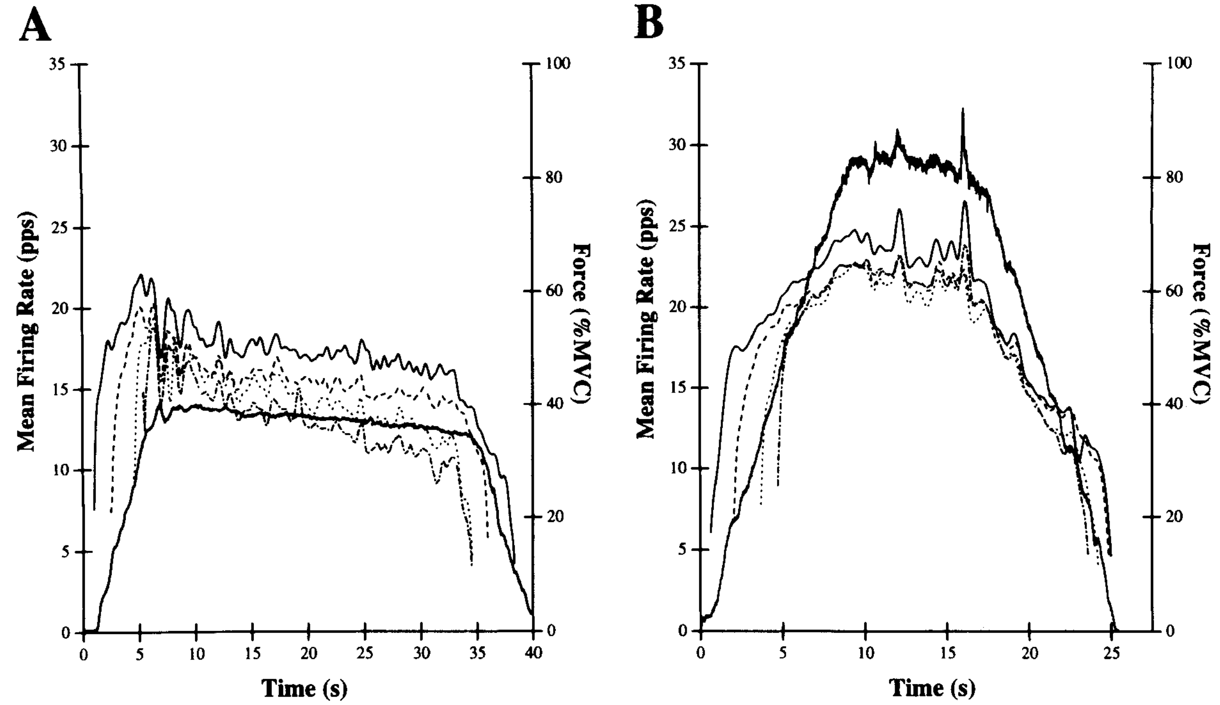

FIGURE 6. The convergence of firing rates at maximal levels. The firing rates are presented as a function of time in **(A)** a 20% MVC and **(B)** a 80% MVC. Notice that the firing rate curves of different motor units in the 20% MVC are separated from each other, while the firing rate curves in the 80% MVC have converged to the same value. The heavy dark lines correspond to the force from the tibialis anterior muscle.

units have the advantage of minimizing fatigue. It is known that the higher-threshold units fatigue faster than those with lower thresholds.[4] Hence, higher firing rates would cause the higher-threshold motor units to fatigue early in the contraction and would diminish their contribution to the force output. In actuality, it appears that the central nervous system may be optimizing a combination of force and the time in which it can be sustained, as opposed to maximizing the force at a given instant. Based on a minimum-metabolic-energy principle, Hatze and Buys[14] predicted the onion skin behavior, i.e., that the motor units with fast-twitch fibers would fire at lower rates than those with slow-twitch fibers, for forces up to 50% MVC.

Dependence of Initial Firing Rate on Recruitment Threshold. A positive correlation was observed between the initial firing rates of motor units and their recruitment thresholds. It is important to note that even though higher-threshold motor units begin firing at higher rates than the lower-threshold motor units, at the instant of their recruitment, as in every other moment in the contraction, their firing rates are lower than the firing rates of lower-threshold units at that instant. Hence, the positive correlation between the initial firing rates and recruitment threshold does not represent a contradiction to the onion skin phenomenon, which predicts a negative correlation between the firing rate at any given instant and recruitment threshold.

Clamann[5] also reported a positive correlation between initial firing rate and recruitment threshold, whereas others[22,24] observed no correlation between these variables. These conflicting results may be indicative of the weak correlation between initial firing rate and recruitment threshold and the "noisy" nature of the system. The discrepancy in the reports may also be due to the technical difficulties. Recruitment threshold calculations, specifically at low force levels, are particularly prone to estimation errors. Differences in experimental techniques and in the definition of various parameters may also contribute to discrepancies in results.

When motor units became active they were observed to fire in an unstable manner. It was not unusual for motor units to start firing, stop, and then fire again when the force output of the muscle fluctuated close to their recruitment values. The unstable firing of motor units upon recruitment and their stopping and starting firing were problematic in the estimation of firing rates. The long interfiring intervals introduced by the pauses in firing caused underestimation of the firing rates when the overall force output of the muscle was close to the recruitment threshold of a given motor unit. An example of this phenomenon can be seen in Figure 2D. The motor unit that is marked with an arrow was firing in an unstable manner, which resulted in a negative bias in the estimate for its initial firing rate. This bias causes the illusion that the positive correlation between the initial firing rate and the recruitment threshold is violated.

The unstable firing patterns that were observed when motor units were recruited, or when the contraction level was close to their recruitment thresholds, can be intuitively explained by considering the net excitation to the motoneuron. If the excitation fluctuates around the value that forms the threshold for the motoneuron to be activated, a slight fluctuation in the net excitation received will determine if the motor unit will be recruited. A similar amount of fluctuation would likely cause only a minor change in the firing rate of a motor unit receiving excitation far beyond its threshold. These unstable initial firings of motor units have been reported by others.[22,26,27]

It was stated that the unstable firings of motor units could result in biased estimates for firing rates. However, we wish to remark that not all deviations from the general rules and relationships set forth here indicate errors in estimation or measurement. The control system in question is admittedly random in nature, resulting in "noisy" signals. The origin of the "noise" in the system is both physiological and experimental. Hence, it is expected that some of the motor units behave in ways differing from the general observations. In fact, the purpose of establishing general relationships between various parameters is not to construct deterministic formulas whereby one parameter can be predicted with respect to another, but rather to shed light on the general properties and mechanisms underlying the activation of motor units.

Convergence of Firing Rates at Maximal Force Levels. At near-maximal force levels, the firing rates of motor units active in a contraction were observed to converge toward the same maximal value. It is known that the high-threshold, fast-twitch motor units are more susceptible to fatigue.[4] Hence, in lower force level contractions, such as those one commonly performs in daily life, high-threshold units are activated at lower firing rates than the low-threshold units, thus minimizing fatigue. Only when faced with the requirement to generate unusually high levels of force, approaching maximal voluntary effort, does the system opt to operate these units as high firing rates, thus producing higher force at the expense of fatigue. In extreme cases, the system reserves the ability to activate the high-threshold motor units at even higher firing rates than the low-threshold ones. This would result in the maximal fusing of the twitches of the high-threshold motor units and the production of extraordinary force levels for brief periods, in other words, the reserve capacity discussed previously.

A clear example of the property of convergence of firing rates at maximal force levels is provided in Figure 6A and B, but it appears obsured in Figure 2D. In this figure, even at 100% MVC, the firing rates of motor units seem to be ordered with respect to their recruitment thresholds, and there is no convergence of the firing rates to the same value. This is due to the fact that combining data from different contractions and even from different subjects, as in Figure 2D, overlooks very important factors such as the actual rate of increase of force, the history of the force output of the muscle, and intersubject variability. The ideal analysis would be based on a multitude of motor units whose activities were observed in the same contraction. However, due to technical limitations, currently it is not possible to correctly identify the firings of a substantial number of motor units in a single contraction. This is especially true at the high force levels that are of interest here, as at these levels the large number of active motor units and the high firing rates increase both the similarity between motor unit action potential shapes and the occurrence of superposition of motor unit action potentials. Hence, in the lack of a large set of data, we resort to considering the combined data from different contractions and subjects since they, nonetheless, provide insight into the basic trends and properties governing motor unit firing behavior.

Firing Rate/Force Relationship—General Characteristics. It was remarked earlier that the curves displayed in Figure 2 suggest that there are basically three parts to the activation profile of a motor unit in the TA muscle. The first region of the activation profile involves the immediate vicinity of the force value at which motor unit becomes recruited. In this region the motor unit is newly recruited and increases its firing rate sharply in response to a desire to increase force. The second region is one in which firing rates increase steadily and essentially linearly with increasing force. It is possible that in this region the force twitches of the motor unit begin fusing and hence a given increase in force can be achieved by a smaller increase in firing rate than before the twitches' fusing. Although this region starts below 15 pps for low-threshold units, which may seem to be too low for substantial fusing of twitches, recent work by Thomas et al.[28] has shown that in situ motor units begin to fuse between 5 and 8 Hz in the human thenar muscle.

In the third region of the force/firing rate relationship, firing rates increased sharply with increasing force. Although the border between the first and second regions differed from one motor unit to the next (depending on its recruitment threshold and presumably twitch characteristics), the border between the second and third regions appeared to be considerably constant. In all cases, the third region of sharp firing rate increase started around 70% MVC. This value coincides with force level beyond which no new recruitment was observed. It is conceivable that in order to increase the force output beyond the level at which all the motor units are recruited, the motor units need to increase their firing rates faster as the other means of force generation, i.e., recruitment, is no longer available.

The general shape of our firing rate/force curves, obtained from the firing rate of single motor unit versus the total force output of the muscle, was similar in shape to the force/frequency characteristics of single motor units by Thomas et al.[28] In experiments where they stimulated a single motor axon in situ and investigated the force produced by that single motor unit, they obtained curves that, if plotted with our convention, would represent an initial region of high slope, followed by a longer region of lower slope, and a final region of high slope.

Firing Rate/Force Relationship as a Function of Recruitment Threshold. Two observations reported above, the onion skin phenomenon which states that at submaximal force levels the higher-threshold motor units maintain lower firing rates, at any given instant, compared to the lower-threshold ones, and the convergence of all motor unit firing rates to the same value at maximal force levels, lead to the following deduction: For the same increase in force, higher-threshold units must increase their firing rates faster than their lower-threshold counterparts in order to reach the same maximal firing rate at maximal force levels, even though they have lower firing rates at submaximal forces. This conclusion is in fact supported by the data in Figure 3. In this figure motor units with higher recruitment thresholds display higher slopes, or higher sensitivities to increased excitation, making it possible for the onion skin and convergence phenomena to coexist. This observation agrees with the findings of higher sensitivity of later-recruited motor units to volitional changes in motoneuron pool excitability[24] and steeper slope of the force rate relationship for the larger motor units.[23]

The Model. All the findings in this study spport the notion of a hierarchy among the motor units that underlies the harmonious operation of the units in producing a desired force output. The response of motor units to a given input appears to be determined by their rank in this hierarchy as specified by their recruitment threshold. That is, various parameters that define this response, such as the initial firing rate or the firing rate at a given force level, are not independent but are strongly interrelated via the rank (recruitment threshold) of the motor unit. This hierarchical arrangement relieves the central nervous system from the burden of controlling the activation of individual motor units in regulating muscle force. Thus, a common drive to the motoneuron pool, indicative of the targeted force at any given instant, can be used to drive all the motor units in the pool. The notion of recruitment rank as the main defining variable for the behavior of a motor unit was discussed by Henneman and colleagues.[15,16] Indirect proof for the existence of "common drive" was provided in our earlier work,[6,11] and the concept was more recently elaborated on in detail.[8]

The model in Figure 7 summarizes the findings of this study in the context of the common drive concept. Part A represents a block diagram of the generation of motor unit firing rates starting with a targeted force level. Every motor unit belonging to the motoneuron pool receives the common drive. Other inputs received by a given motor unit but not shared by others are represented as noise in this model. The firing rate response of each motor unit to the combined excitation it receives is determined by its intrinsic excitation/firing rate properties. These properties are not randomly distributed, but highly ordered according to the recruitment threshold or rank of the motor unit. Part B of the figure employs the example of a drive that linearly increases with time, to demonstrate the ordered firing responses of motor units. Even though all motor units are receiving essentially the same drive, because of their ordered excitation/firing rate properties, they respond with different firing patterns. As the net drive is increased, smaller motor units with low recruitment thresholds are the first to surpass their thresholds and begin firing according to their drive firing rate profiles. With increasing drive, the next unit in the hierarchy becomes recruited and begins firing. However, its firing rate, as governed by its drive/firing rate curve, is lower than that of the earlier-recruited one. Further increases in drive level will recruit other motor units and cause increases in the firing rates of the already-active units, with the

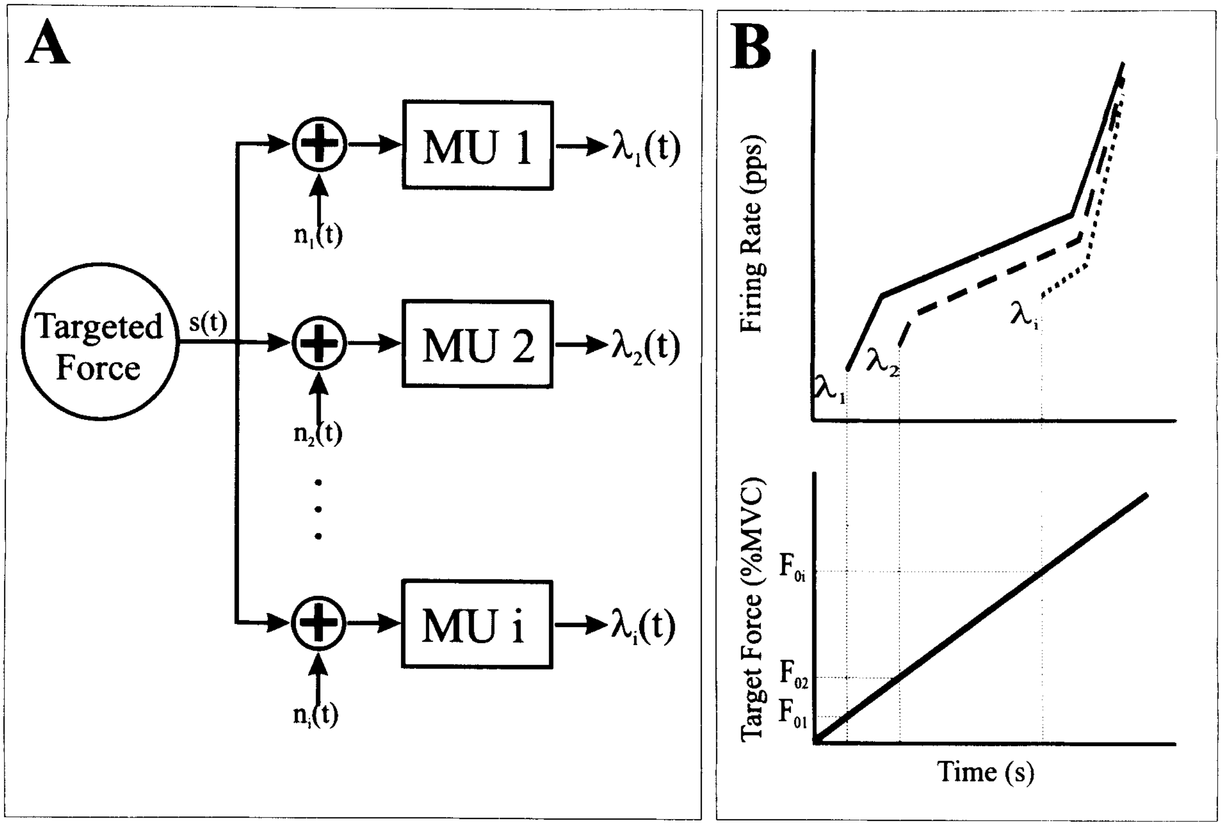

FIGURE 7. **(A)** Model for the regulation of recruitment and firing rates of motor units. Each motor unit receives the common drive [s(t)] in addition to an individual "noise" signal [n(t)] and generates its firing rate [$\lambda(t)$]. **(B)** The response of three motor units with recruitment thresholds F_{01}, F_{02}, and F_{0i} (top panel) when driven by an input that linearly increases with time (bottom panel). As the drive increases, new motor units are recruited and already-active ones increase their firing rates, as dictated by their input–output curves.

reverse relationship between the firing rate and recruitment threshold of a motor unit being preserved.

The model in Figure 7 represents an organization that holds the freedom for the central nervous system to provide a global input to the motoneuron pool corresponding to the intended output of the muscle, as opposed to keeping track of all the motor units and regulating their firings. It is the architecture of the motoneuron pool along with the intrinsic properties of individual motor units, and the gradations therein, that result in the precise activation pattern for each motor unit. These activation patterns, in turn, produce the appropriate force contributions from each motor unit that add up to create the desired muscle force ouput. It should be noted that the model has addressed only contractions where the force linearly increased with time. The force/firing rate curves need to be modified and expanded to include factors such as twitch potentiation, fatigue, nonlinearity, and hysteresis, in order for the model to be applicable to more general cases such as sustained contractions or decreasing force. As it stands, the model encompasses the fundamental relationships and rules that appear to underly the activation of motor units in the production of muscle force that were established in this work and in previous studies.

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