

Effect of Velocity and Mechanical History on the Forces of Motor Units in the Cat Medial Gastrocnemius Muscle

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SUMMARY AND CONCLUSIONS

1. Two fundamental aspects of the dynamic behavior of motor units of the cat medial gastrocnemius (MG) muscle were measured. Force-velocity (FV) relationships were measured with the use of constant velocity shortening and lengthening movements. Effects of mechanical history were assessed via comparisons of forces immediately after or during slow movements with standard isometric forces. Isometric force-length (FL) relations were also measured, and the effect of different stimulation rates on both FV and FL data was assessed.

2. Prior or concurrent movement greatly potentiated motor-unit force, but this movement potentiation was highly dependent on the amplitude of the unit's force. The smallest twitch forces of type S units (<10 mN) were potentiated more than threefold, but no potentiation occurred for unit forces >200 mN. It was tentatively concluded that movement potentiation may play little role in normal movements because it does not occur at forces >1% of maximal isometric force of the MG.

3. During shortening, the normalized FV relations of type S units were relatively steeper than those of type FR or FF units. For lengthening, there was no evident relation between FV steepness and motor-unit type.

4. Stimulation rate affected both the FV and FL relationships of the motor units. The peak of the FL relationship (L_o) clearly shifted to shorter muscle lengths as stimulation rate was increased. The steepness of the FV relationship for shortening was decreased by increasing stimulation rate, but this effect was modest.

5. The shift in motor-unit L_o and the differences in motor-unit FV relationships were hypothesized to play significant roles during normal motor behavior. Realistic computer simulations of FL and FV functions for a population of motor units undergoing normal steady-state recruitment and rate modulation supported these hypotheses. As the level of simulated neural drive increased, the population L_o shifted to considerably shorter lengths, and the normalized FV function became much less steep. The significance of these results for models of muscle are discussed.

Studies of whole muscles and single muscle fibers have clearly shown that the force output of muscle is dependent not only on muscle length (Gordon et al. 1966; Partridge and Benton 1981) but also on dynamic parameters such as rate of change of muscle length (i.e., velocity) (Hill 1938; Partridge and Benton 1981) and prior mechanical history (Julian and Morgan 1981; Partridge and Benton 1981). The kinematic conditions that exist in normal movement in the cat include a very wide range of dynamic conditions, including large variations in velocities (Abrahams and Loeb 1985; Goslow et al. 1973). Thus, to understand the importance of differences in motor-unit mechanical properties, it is necessary to consider dynamic mechanical conditions.

In this paper our goal was to test the hypothesis that two important components of the dynamic behavior of single motor units, the effects of velocity and of mechanical history, vary as a function of motor-unit type. The effects of velocity on motor-unit force were measured with the use of constant velocity shortening and lengthening movements. The effects of mechanical history were assessed by comparison of single-unit forces in the standard isometric state to the forces immediately after or during slow movements. In cat medial gastrocnemius (MG) motor units, we found that the twitch forces of the smallest units, including all type S units and the smaller type FR units, were greatly potentiated by prior or concurrent slow movements. The type S units were also much more sensitive to the effects of shortening velocity, having significantly steeper force-velocity (FV) relationships than FR or FF units. The implications of these differences for motor control and for current models of muscle are discussed. A preliminary account of some of these results have been previously reported (Heckman et al. 1988).

INTRODUCTION

The neural activation of a muscle consists of recruitment and rate modulation of the population of single motor units that compose the muscle. In the cat, there are large differences in the isometric mechanical properties of the different motor-unit types within single muscles (Burke et al. 1973; Burke 1981; Henneman and Mendell 1981; McDonagh et al. 1980; Wuerker et al. 1965). However, as yet, the mechanical properties of single motor units have only rarely been studied under nonisometric conditions (e.g., Devasahayam and Sandercock 1992; Petit et al. 1990; Powers and Binder 1991). This is a highly restrictive limitation on our understanding of the full range of motor-unit behav-

METHODS

Preparation

Data were obtained from 10 male and female adult cats. All cats were anesthetized with pentobarbital sodium throughout the experiment. Anesthesia was maintained at a deep level, as judged by the absence of withdrawal reflexes. At the end of the experiment, cats were killed with a high dose of pentobarbital. The MG muscle, distal tendon, and nerve were carefully isolated. The maximal physiological length range was determined by measuring the length of MG at the extremes of the possible rotation of the ankle joint (the knee joint was fixed at $\sim 100^\circ$ extension). Then the calcaneus was cut, leaving a bone chip connected to the MG tendon to allow secure attachment to the muscle puller. A conven-

tional laminectomy was performed from S₁ to L₄, and the ipsilateral S₁ and L₇ dorsal and ventral roots were cut near their entry to the cord.

The spinal area was covered by a mineral oil pool. The muscle was bathed in normal saline to assure that the tendon stayed moist throughout the duration of the experiments, which lasted as long as 40 h. In addition, a small section of saline-soaked gauze was wrapped around the distal part of the tendon and secured lightly by suture ties. In preliminary experiments we found that maintaining adequate tendon moisture was absolutely essential for obtaining consistent passive behavior during the constant velocity movements. Even slight drying of the tendon greatly altered the passive response to stretch and prevented accurate separation of the small unit force from the total active plus passive force. Core and hindlimb temperatures were maintained at 37–38°C by a heated water blanket and radiant heat.

Single units were obtained by splitting ventral root filaments, with the use of the criteria (McPhedran et al. 1965) of all-or-none force and electromyographic (EMG; recorded by epimysial patch electrodes) responses.

Experimental protocols

A force transducer with a linear range of up to 5 N was found to provide a reasonable compromise between sensitivity (to accurately measure single-unit forces) and dynamic range (to measure passive forces). The first step in each experiment was then to determine the muscle length at which passive force just reached this 5-N limit at the highest stretch velocity (in most cases, 60 mm/s). This length was typically 2–8 mm shorter than the maximum physiological length but was substantially longer than the optimal length (L_o) for the tetanic force outputs of all units (see RESULTS). The limit in the shortening direction was usually set ~14–16 mm shorter than the lengthening limit. At the short length limit, the motor units generated 5–20% of their L_o output. This total excursion was less than the maximum physiological range in situ, but it did cover the major part of the range over which MG is active in locomotion (Stephens et al. 1975; Walmsley et al. 1978).

FORCE-LENGTH (FL) PROTOCOLS. All muscle lengths were referenced to physiological maximum, although, as noted above, the longest portion of the physiological range was not studied. Isometric FL data were taken at six to eight different lengths in increments of 2 mm. The passive muscle was slowly stretched to the first length to be studied, a delay period ensued, and then the unit was stimulated. The muscle was then slowly stretched 2 mm and the delay and unit stimulus repeated. Additional 2-mm steps each with delay periods and unit stimuli were repeated until the full length range allowed by the maximal puller limits was covered. In most cases two entire sets of FL data were taken, one where unit force was measured after a long delay after cessation of the stretch (10–30 s) and one for a short (100-ms) delay. The long delay was sufficient to allow the passive force to reach a steady level and corresponds to the conventional measurement of isometric motor-unit force; all forces labeled “isometric” in this paper refer to data obtained after a 10 to 30-s delay. As shown in the RESULTS, the short (100-ms) delay was found to potentiate the force of small units. To remove the passive force from the short delay trials, in which motor-unit force was superimposed on a rapidly decaying passive background, trials without stimulation of the motor unit were alternated with trials that included stimulation. The passive trial was then subtracted from the active + passive trial to reveal the motor-unit force. In addition, two experiments were done to obtain data on isometric FL and prior movement potentiation for the whole MG muscle, with the use of a high force range transducer.

FV PROTOCOLS. FV data were obtained by subjecting the muscle to constant velocity lengthening and shortening movements (cf. Joyce et al. 1969). The muscle puller was a servo-controlled stepping motor (Aerotech) driven by a PDP-11 computer (Rindos 1988). The acceleration time to achieve a constant 100 mm/s was <40 ms. Unlike the procedure of Joyce et al. (1969), stimuli were not applied to the motor units until *after* the movement had achieved the desired constant velocity to minimize the yielding behavior of the units (Cordo and Rymer 1982) in the hope of simplifying the description of their mechanical output. At each velocity, paired trials with and without stimulation of the unit were applied. The trial without stimulation was subtracted from the previous trial with stimulation to remove the contribution of passive force. The passive force during constant velocity ramps was relatively large so that this was a critical step (see RESULTS, Fig. 4). Six velocities were applied in each direction, ranging from 4 to 60 mm/s. Above 60 mm/s the small mechanical oscillations produced by the puller became large enough to severely distort the unit force outputs (see RESULTS, Fig. 4). This velocity range is far short of maximum unloaded shortening velocity of MG (Spector et al. 1980) but did cover a significant portion of the speeds MG undergoes in locomotion [studies of unrestrained locomotion in the cat indicate that peak velocities in MG for slow to moderate speed locomotion are ~60 mm/s (Goslow et al. 1973; Weytjens and Loeb 1987)].

In most units, three different stimulation patterns were applied: a single twitch and two constant rate trains (1 moderate and 1 high rate). Train durations were 300–1,000 ms for putative slow-twitch units (isometric contraction time, >40 ms) and 100–500 ms for putative fast-twitch units (contraction time, <40 ms). The interspike intervals for the medium rates were 1.5–2.0 times the twitch contraction time (measured from the time of initial divergence from the baseline to the time of the peak of the twitch). In each case the force output for these medium rates produced an unfused tetanus. The high rate was 30–50 Hz for slow-twitch units and 50–100 Hz for fast-twitch units. These rates were based on the known differences in slow versus fast motor-unit rate-force relationships (Botterman et al. 1986; Kernell et al. 1983) and were intended to produce relatively high forces with minimal fatigue. In all cases the high rates produced forces with very little ripple. Thus these high rate forces were used as a measure of the maximal forces of the units and are referred to here as “near-tetanic” rates and forces.

Collection of a complete data set for a single unit required at least 60 trials in which the unit received a twitch or train stimulus (8 lengths for FL data, 12 velocities for FV data, for a total of 20 for each of the 3 stimulation patterns). Several steps were taken to avoid activation history effects and to minimize fatigue. Rest periods between trials with stimulation of the unit were set at ~1 min for putative S units and ~2 min for putative F units. Passive trials were run during these rests. Twitch FL and FV data were collected first, usually followed next by near-tetanic rate data and then by medium rate data. For putative F units, we also allowed longer rest periods of up to 10 min between sets of FL and FV data. Finally, before any medium or high stimulation rate trials were begun, a reference stimulus was defined to allow fatigue and potentiation to be monitored. This reference stimulus typically consisted of 5–10 pulses at 20–50 Hz, depending on putative motor-unit type. It was monitored throughout the medium and high rate trials. If the reference fell below 85% of its initial value, study of the unit was discontinued.

Because of the numerous trials and lengthy rest periods, data collection for a single unit took as long as 2–4 h, and experiments often lasted 20–40 h. To monitor the viability of the preparation, one ventral root division was set aside and stimulated in its entirety. This produced a reference twitch generated by a substantial fraction of the muscle's motor units. Muscle length was set short

enough to assure that the peak force of the twitch did not exceed the linear range of the load cell. Experiments were terminated if this viability test showed a decrease of $>10\%$ from the initial test.

At the end of the data collection for each unit, fatigue and sag tests were performed to allow typing of the motor units (Burke et al. 1973). However, our measurements of some of the motor-unit parameters underlying these criteria were somewhat nonstandard. Maximal forces were taken from the previously collected near-tetanic data at L_0 and thus may have slightly underestimated the true maximum. Because the unit had already undergone a large number of stimuli, the sag and fatigue tests done at the end of the data collection were often performed on units that were already partially fatigued. However, misclassification of units in our small sample seemed unlikely. The S-FR separation was very distinct in terms of contraction times. The FF-FR separation was clear because the maximal forces of all but one of the FF units exceeded the normal range of FR units in this muscle (Burke 1981), and even this FF unit had a fatigue index of <0.1 .

Data processing

The output from the strain gauge amplifier was low-pass filtered (-3 dB at 200 Hz, 12 dB/octave) and digitized (12-bit resolution, 500 samples/s) by the same PDP-11 that controlled the muscle puller. All analyses were done off-line on the digitized records. Velocities were expressed in millimeters per second to facilitate comparison with velocities that occur in MG during locomotion in freely moving cats (Goslow et al. 1973; Weytjens and Loeb 1987). Velocities were also estimated in fiber lengths per second by assuming that all MG fibers were 18.5 mm long. This figure is based on the combined average values of 18.9 mm from the data of Spector et al. (1980) and 18.1 mm from the data of Walmsley and Proske (1981). Series compliance in tendon and aponeurotic sheet was ignored for the low forces to which these experiments were limited. Peak unit forces were measured for both twitches and constant rate trains. The peaks for trains were measured within limited time windows: the first 200–400 ms for S units and the first 100–200 ms for FR and FF units. The longer duration trains sometimes used at low velocities could not be used at high velocities because the puller excursion would have exceeded the maximal physiological range of the muscle. We also measured contraction times for the twitch data. These were taken at the twitch L_0 , which was often at the long muscle length limit of the puller (see RESULTS).

RESULTS

FL relations

Figure 1 shows the FL relationships for three different motor units, one of each type. Three stimulation levels are shown for each unit: twitch (■ in A–C), a medium rate (□), and a near-tetanic rate (◆). As noted in METHODS, muscle lengths were specified with respect to physiological maximum. In all cases it is apparent that the optimal length (L_0) for force production shifted to shorter lengths as stimulation level was increased. The effect of stimulation rate on these single-unit FL relations resembled that seen by Rack and Westbury (1969) for the whole soleus muscle. The twitch L_0 was substantially longer than the near-tetanic L_0 for all 15 units studied (4.7 ± 1.9 mm, mean \pm SD). In 10 of the 15 units, intermediate stimulation rates were also studied. In only five of these was the L_0 for intermediate rate shorter than that for the twitch but longer than that for the near-tetanic stimulation (as illustrated in Figs. 4, A and

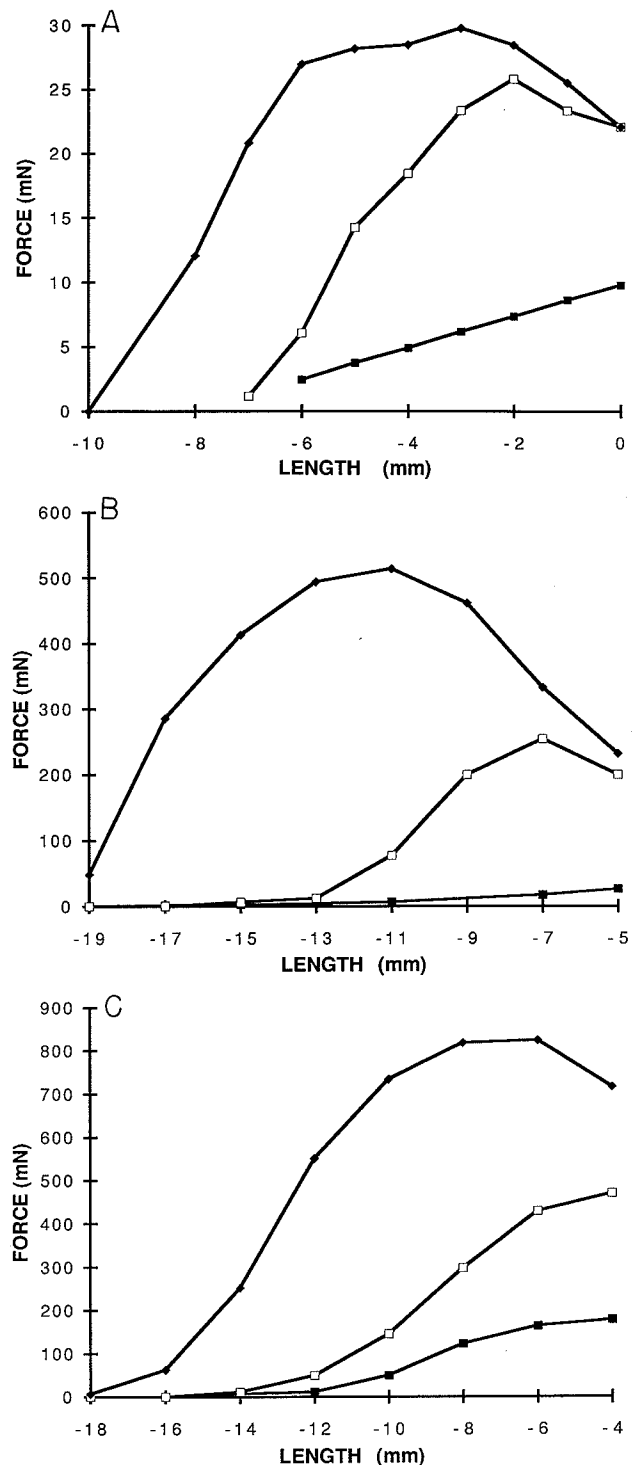


FIG. 1. Force-length (FL) relationships at 3 different stimulation levels (twitch, ■; medium rate train, □; near-tetanic rate train, ◆). A: S unit; stimulation rates of 10 and 30 Hz. B: FR unit; stimulation rates of 20 and 50 Hz. C: FF unit; stimulation rates of 30 and 100 Hz.

B). In the other five, the intermediate rate L_0 s and the twitch L_0 s were the same, being at the longest length studied (as illustrated in Fig. 4C). In fact, for 11 of the 15 units, no clear twitch maximum was reached within the range of the longer limit on muscle puller excursion (which was still 2–8 mm shorter than physiological maximum; see METHODS).

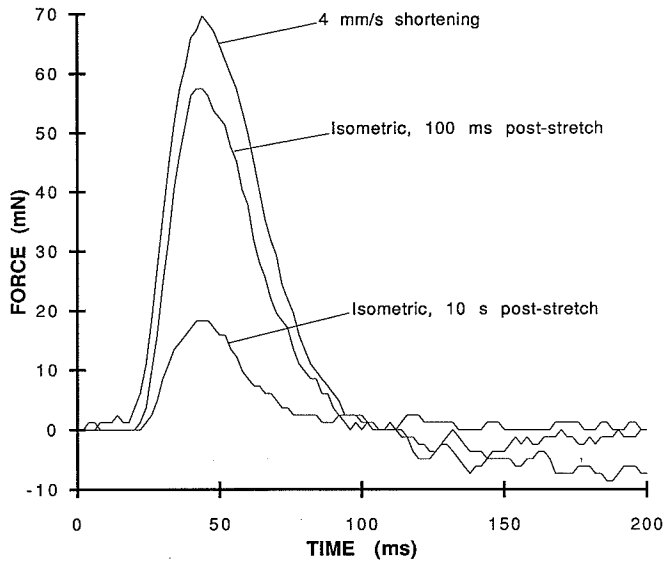


FIG. 2. Effect of movement potentiation on the twitch force of an FR unit. *Bottom trace*: isometric twitch measured 10 s after cessation of stretch. *Middle trace*: isometric twitch measured just after (100 ms) cessation of stretch. *Top trace*: twitch during slow shortening (4 mm/s) past the same length as for the *bottom 2 traces* (-8 mm with respect to physiological maximum).

Thus our ability to detect differences in the twitch versus intermediate rate L_0 s was limited by the lack of data at the longest portion of the physiological range. The twitch - near-tetanic difference in L_0 was not systematically related to either contraction time or maximal force (t test, $P > 0.05$). Finally, there was no significant relationship between the near-tetanic L_0 s and either contraction time or maximal force (cf. Stephens et al. 1975).

Movement potentiation

Figure 2 shows the typical effects of movement on the twitch force of a motor unit (type FR). The *bottom trace* shows the standard isometric twitch, measured after muscle length had remained constant for 10 s. The *middle trace* shows the twitch force immediately (100 ms) after a 2-mm stretch at 10 mm/s. The resulting isometric force was nearly three times as large as the standard isometric twitch. The *top trace* shows that the twitch force was even bigger during slow shortening (4 mm/s; peak force occurred at the same length as for the isometric twitches). Thus both prior and concurrent movement greatly increased the force output of this motor unit.

This movement potentiation was studied across a full range of muscle lengths in five units and was found to be roughly the same percentage increase at all lengths. An analysis of the time course of the movement potentiation in two units showed that it rapidly decayed after stretch, with a roughly exponential time course with a time constant of ~ 2 s. By ~ 10 s poststretch, the effect had decayed to zero.

We found that the effect of movement was strongly related to the amplitude of the unit force. Figure 3 shows the degree of movement potentiation (expressed as the ratio between the potentiated force and the standard isometric force) plotted versus the standard isometric force for the entire sample of motor units. In each case the motor-unit

force was measured at a single length at the near-tetanic L_0 . The filled diamonds show the data for prior movement potentiation of the twitches of 22 units; the open diamonds the concurrent movement (4-mm/s shortening) potentiation of the twitches of 15 units, and the open squares show the concurrent movement (4-mm/s shortening) potentiation of the tetanic forces of the same 15 units (4 of which are off scale to the right; these showed little or no potentiation). The relationship for all the data in Fig. 8 was clearly statistically significant ($r = 0.87$, $P \ll 0.001$; regression based on log transformations of the data). The important point is that movement potentiation was seen only when the active force was < 200 mN, regardless of how the force was generated. Consistent with this, results of two experiments showed that the twitch of the whole MG muscle ($\sim 20,000$ mN) showed no detectable signs of movement potentiation.

FV relations

SUBTRACTION OF PASSIVE FORCES. The chief difficulty in obtaining single-unit FV data was separating the small motor-unit forces (30–1,000 mN) from the large passive background during stretching and shortening (as large as 5,000 mN, see below). Figure 4 shows the raw data for a type FR unit (isometric tetanic force of ~ 300 mN). In 4A, the thin lines indicate the total force during stimulation of the unit (50 Hz for 100 ms in all cases), whereas the thick traces show the passive responses. The velocities are, from *top* to *bottom*, 60, 8, -8 , and -60 mm/s (negative velocities indicate shortening). The changes in whole muscle length associated with these velocities are shown in Fig. 4B. The motor-unit forces were resolved simply by subtracting the passive trials from the active trials. The motor-unit forces obtained in this way for the data in Fig. 4A are shown in Fig. 4C. Note that the records for the slower velocities were quite good, but, at ± 60 mm/s, oscillations (shortening, see

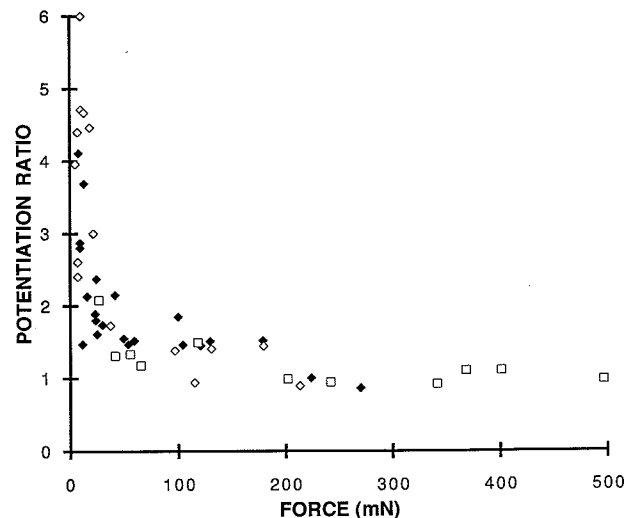


FIG. 3. Amount of movement potentiation expressed as the ratio between the potentiated force and the unpotentiated force. Filled diamonds, prior movement potentiation of the twitches of 22 units; open diamonds, concurrent movement (4-mm/s shortening) potentiation of the twitches of 15 units; open squares, concurrent movement (4-mm/s shortening) of the near-tetanic forces of 15 units (the x-axis has been expanded to allow better discrimination in the low force area so the near-tetanic forces of the largest 4 units are off scale to the right).

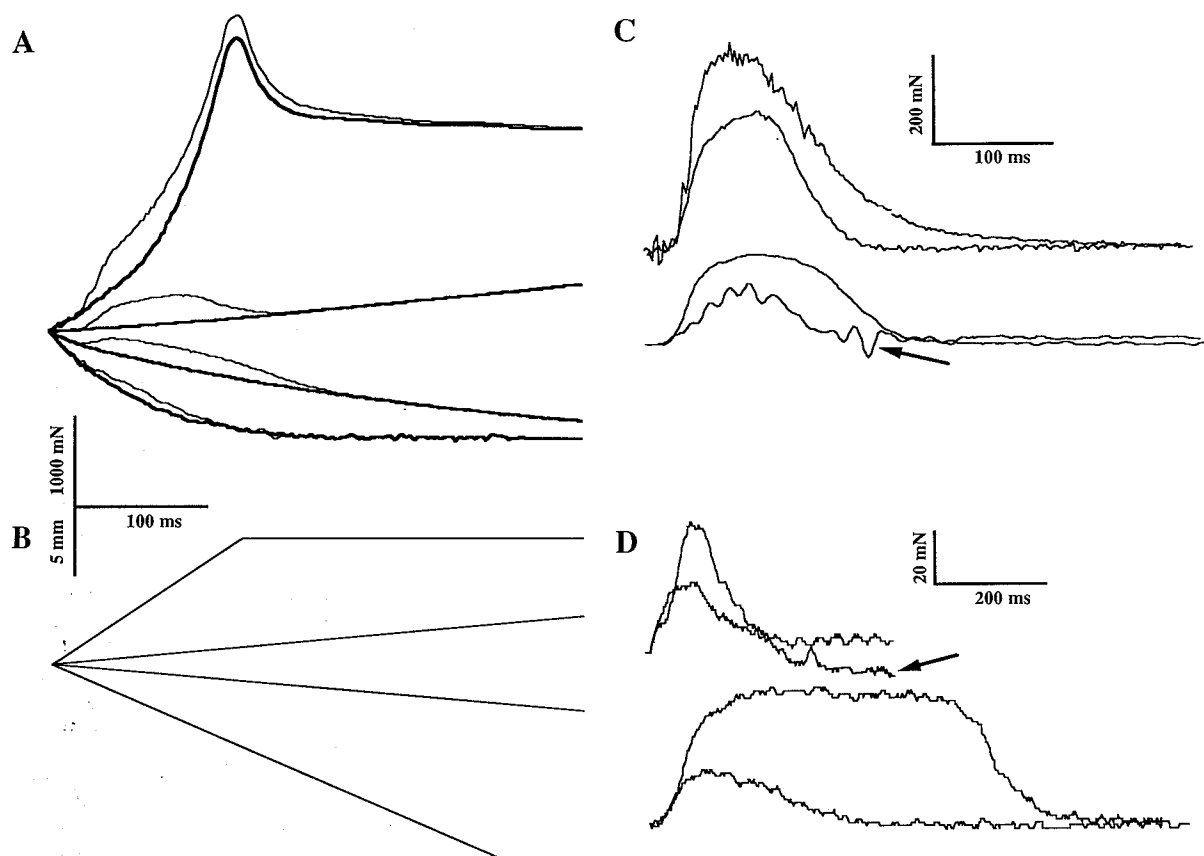


FIG. 4. Raw data trials for the force-velocity (FV) relationship of 2 units. *A*: thin traces show the forces of an FR motor unit (stimulation at 50 Hz for 100 ms in all cases) during 4 different constant velocity ramps (from *top* to *bottom*: 60, 8, -8, and -60 mm/s, respectively). Thick traces show the passive responses for the same ramps. *B*: length changes for the ramps shown in *A*. *C*: single-unit forces obtained by subtraction of thick from thin traces in *A*. Arrow indicates an oscillation error in this process (see text). *D*: single-unit forces for an S unit after the same subtraction process (velocities of 20 and 4 mm/s for a single twitch and -4 and -20 mm/s for 40-Hz, 550-ms trains). Arrow indicates a baseline error.

arrow) and noise (lengthening) appeared. These effects were apparently due to the puller motor (see METHODS). Finally, Fig. 4*D* shows a similar set of records for an S unit (isometric tetanic force of ~ 50 mN) at 20 and 4 mm/s for a twitch and -4 and -20 mm/s for a near-tetanic stimulus. Note that the twitch during 20 mm/s lengthening shows a slanting baseline (see arrow). Slanting baselines were the most common form of distortion for lengthening trials. In shortening, the passive force was usually more repeatable, but here, as the unit force decreased with increasing shortening velocity, A/D resolution (least significant bit = 1.24 mN; the individual A/D steps are clearly visible in the records in Fig. 4*D*) and mechanical noise from the puller became limiting factors (Fig. 4*C*).

The main criterion for acceptance of data was the flatness of the baseline for the motor-unit force after passive force subtraction. Trials in which the baseline slant caused the initial and final forces of the trial to diverge by $>20\%$ of the peak force output of the unit during that same trial were rejected (the arrow in Fig. 4*D* shows a just acceptable baseline slant). This criterion resulted in rejection of as much as 50% of the data for twitches of type S units. These problems were less serious with the larger force outputs of S units during tetanic stimulation ($\sim 30\%$ of the data rejected) and, as indicated by Fig. 4*C*, even less so for FR and FF units ($<20\%$ rejected). Baseline slants in accepted data

were removed before measurements were made by subtraction of a straight line fit to the initial and final points of the trace. FV data were collected from 30 units. After data selection based on the baseline flatness criterion, reasonably complete sets of data remained for 15 units, 5 of each type. This sample was, however, biased toward the larger units within each type, which tended to be selected preferentially because of the difficulty in separating active and passive forces. The smallest S units (those with tetanic forces of <30 mN) were all rejected.

To allow comparisons of the relative shapes of FV relationships in different motor units, the peak forces were normalized. However, because of the movement potentiation of the forces of S units and small FR units (see Figs. 2 and 3), the isometric forces could not be used as the basis for this normalization. Therefore all FV data were normalized with respect to the peak force at the slowest velocity in the appropriate direction (4 mm/s in all cases). No data were collected below this velocity so that the shape of the FV relationship at the slowest velocities was unknown. A normalized FV relation for the smallest S unit in our sample (isometric force of ~ 30 mN) is shown in Fig. 5 ($\Delta - - - \Delta$). This FV relation was somewhat oddly shaped, especially for lengthening. As discussed next, this was because of the effect of the muscle length in addition to that of velocity.

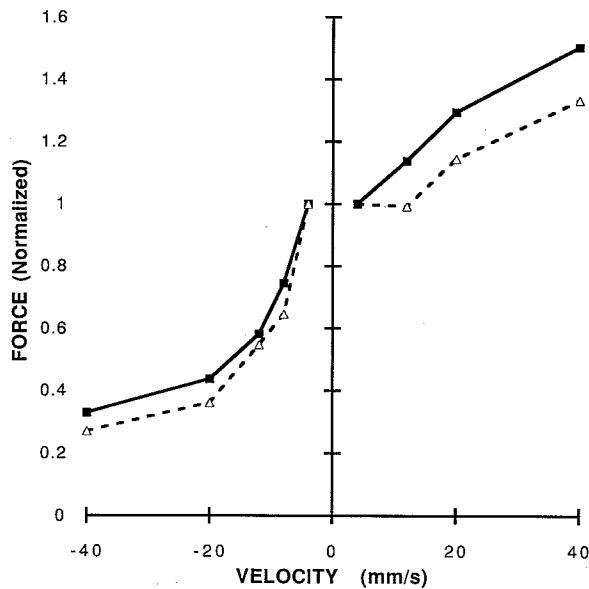


FIG. 5. Force-velocity (FV) relationship for near-tetanic stimulation of the smallest S unit in our sample. Negative velocities indicate shortening. Normalized data (Δ --- Δ) and length-corrected normalized data (\blacksquare — \blacksquare). Note the discontinuity about the y-axis produced by the normalization (see text).

CORRECTIONS FOR THE EFFECT OF LENGTH. In our protocol, stimulation for a unit in a given direction was always initiated at the same length. This meant that there was a considerable difference between the lengths at which motor-unit forces were measured for low versus high velocities. For example, if the peak force of a motor unit occurred 100 ms after movement onset and the muscle was shortening at 40 mm/s, muscle length would have decreased by 4 mm with respect to the initial length. If this ramp was initiated at the muscle's L_0 , the 4-mm movement would correspond to roughly a 20–40% reduction in force because of the FL relationship (Stephens et al. 1975; Walmsley and Proske 1981) in addition to the decrease expected from the FV relationship. Thus it was necessary to correct the data for the effect of changes in length.

To accomplish this length correction, the length at which the unit force was measured and the length at which the unit's stimulation was initiated were compared with the unit's previously measured isometric FL relationship. The relative forces at these two lengths predicted by the FL relationship were used for the length correction. To illustrate this, again consider the case of the 40-mm/s ramp with stimulation initiated at L_0 , where the peak motor-unit force occurred at a length that was 4 mm shorter than L_0 . If the isometric force at the shorter length was 80% of the isometric force at the initial length (i.e., L_0), then the peak force of the unit measured during the constant velocity ramp was multiplied by a factor of $1/0.8$ ($=1.25$) to give the length-corrected value. Note that this process assumes that the FV and FL relations are independent. To date, velocity and length interactions have not been directly investigated. However, the biophysical mechanisms generally proposed to account for the two different functions (e.g., Gordon et al. 1966; Huxley 1957; Iwamoto et al. 1990) suggest that they should be relatively independent.

The FV relation in Fig. 5 indicated by the filled squares

and thick line illustrates the typical effect of the length correction on the FV relation. Without the length correction, the normalized data (Δ) would have overestimated the effect of velocity for shortening and underestimated it for lengthening. In addition, the shape of the relationship would have been distorted. For example, failing to take length into account would have implied that the +8-mm/s force was actually less than the +4-mm/s force. Such distortions in the FV data without the length corrections were evident for all motor units studied.

FV RELATIONSHIP AS A FUNCTION OF MOTOR-UNIT TYPE. Figure 6A shows the normalized, length-corrected FV relationships for three different units, one of each type. (In Figs. 6–8, motor-unit type is indicated as follows: type S, \blacksquare ; FR, \diamond ; FF, Δ). In all three cases the stimulation rate was near-tetanic. In shortening, the FV relationships for the FF and the FR units were similar, but that for the S unit was considerably steeper. In lengthening, this was not the case, with the S unit relationship falling roughly between those of the FF and FR units. We quantified the relative steepness of the near-tetanic FV functions for all 15 motor units in the shortening direction by comparing the slopes of the functions at low velocities. These FV slopes were calculated as the differences between two FV data points, those at -4 and at -20 mm/s. Similarly, for lengthening, slopes were calculated from the $+4$ - and $+20$ -mm/s data points. The upper velocity of 20 mm/s in each direction was chosen for this purpose because it was the highest one for which good data were available for 14 of 15 motor units [20 mm/s is ~ 1.1 fiber lengths/s and corresponds to the velocity achieved in MG during a slow walk (Weytjens and Loeb 1987)]. At 40 mm/s or above, even with near-tetanic stimuli, the lengthening data for three or more of the S units were of poor quality and were rejected (see METHODS for acceptance criterion). However, near-tetanic data were available for all units at -20 mm/s and all but one S unit at $+20$ mm/s.

Figure 7A shows the FV slopes for all 15 motor units

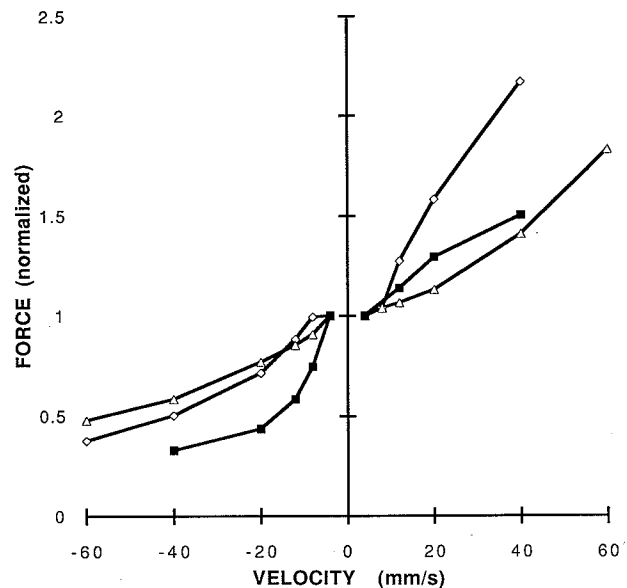


FIG. 6. Comparison of normalized, length-corrected force-velocity relationships for a type S unit (\blacksquare), a type FR unit (\diamond), and a type FF unit (Δ).

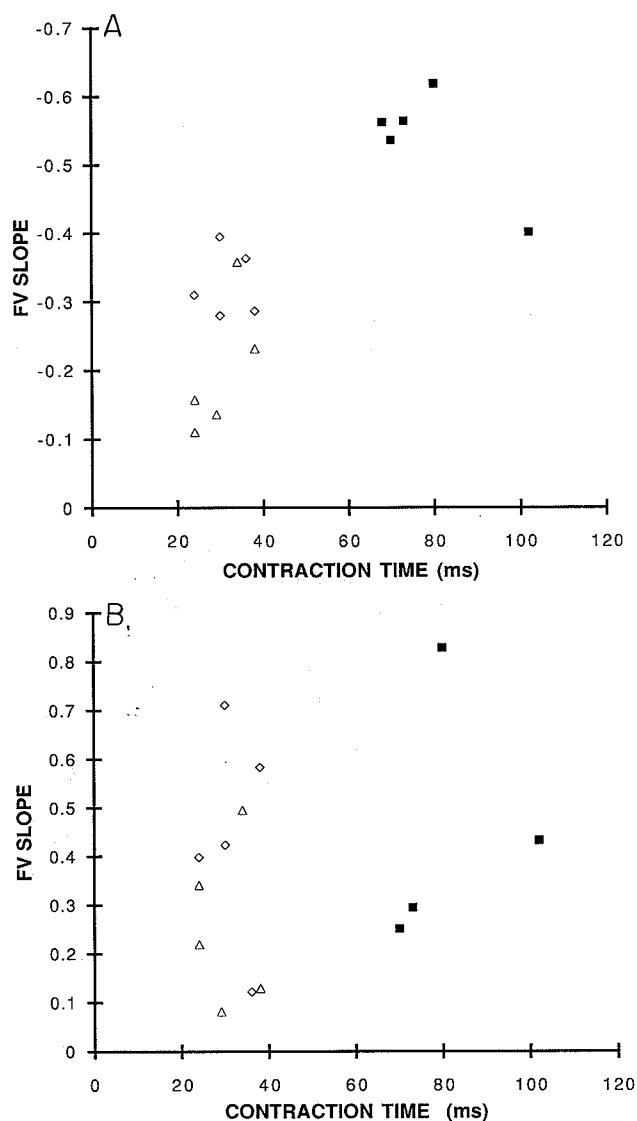


FIG. 7. *A*: relationship between the slope of the force-velocity relations during shortening (see text) and contraction time (normalized, length-corrected data, $n = 15$, $r = -0.75$, $P < 0.001$, $y = -0.005x + 0.874$). Motor-unit type symbols as in Fig. 6. *B*: same relationship during lengthening ($n = 14$, $r = 0.24$, $P \geq 0.05$).

during shortening at -20 mm/s plotted versus twitch contraction time. Only near-tetanic data are included. The relationship was quite steep and was statistically significant ($r = -0.75$, $P < 0.001$). Using the next higher velocity of shortening (-40 mm/s) and -4 mm/s to calculate FV slopes also produced a relationship with contraction time that was statistically significant (all units had acceptable data during shortening at this speed; $r = 0.79$, $P < 0.001$). Both the FV slopes for -20 and -40 mm/s were also correlated with the near-tetanic unit isometric forces (-20 : $r = 0.58$, $P < 0.001$; -40 : $r = 0.75$, $P < 0.001$).

In addition, there was a statistically significant relationship between the FV slope for -20 mm/s and motor-unit type [1-way analysis of variance (ANOVA), $F < 0.001$]. The motor-unit type clusters seen in Fig. 7*A* show that the fast versus slow-twitch distinction was very clear. Consistent with this, multiple comparison tests among the three type groups showed that both the FF-S and FR-S differ-

ences in slope were statistically significant (Tukey tests, $P < 0.01$). However, the FF-FR differences were not (Tukey test, $P > 0.05$).

Figure 7*B* shows the slopes of the FV relationships during lengthening ($+20$ compared with $+4$ mm/s) for 14 of the 15 units. There was not a statistically significant relationship between FV slope and contraction time ($r = 0.24$, $P \geq 0.05$), nor was there one between FV slope and near-tetanic isometric force ($r = 0.40$, $P > 0.05$). Thus there was no clear relationship between normalized FV behavior during stretching and motor-unit properties.

EFFECT OF STIMULATION RATE. Figure 8 shows the relationship between the steepness of the normalized FV relationship during shortening at -20 mm/s and stimulation level (classified into 3 categories: twitch, medium rate, and near-tetanic rate). There were statistically significant differences according to stimulation level (1-way ANOVA, $F < 0.05$) and thus there existed a tendency for the normalized FV relationship for shortening to become steeper as stimulation level increased. However, multiple comparison tests showed that only the twitch - near-tetanic difference was significant (Tukey tests, $P < 0.05$), whereas the medium rate group was not significantly different from either the twitch or near-tetanic group. Unfortunately, there is a lack of data for the medium rate level (only 7 units had good medium rate data, because this data was often taken last; see METHODS). In contrast, for lengthening, there was no statistically significant relationship between stimulation level and FV slope at $+20$ mm/s (1-way ANOVA, $F > 0.05$).

NONNORMALIZED COMPARISONS. Finally, nonnormalized FV data were analyzed to determine whether the very wide differences in the force outputs of MG motor units during isometric conditions (Burke 1981; Henneman and Mendell 1981) were also apparent during constant velocity movements. The average values for the motor-unit forces measured at -20 , -4 , $+4$, and $+20$ mm/s were calculated for the S, FR, and FF groups, and these were compared with

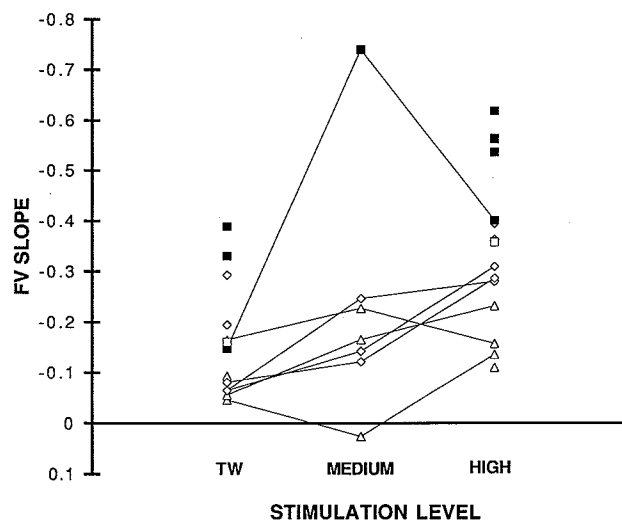


FIG. 8. Effect of the 3 different categories of stimulation on force-velocity slope during shortening. Motor-unit type symbols as in Fig. 6. Lines connect the data points obtained for the same unit. The relationship is significant (1-way analysis of variance, $F < 0.05$).

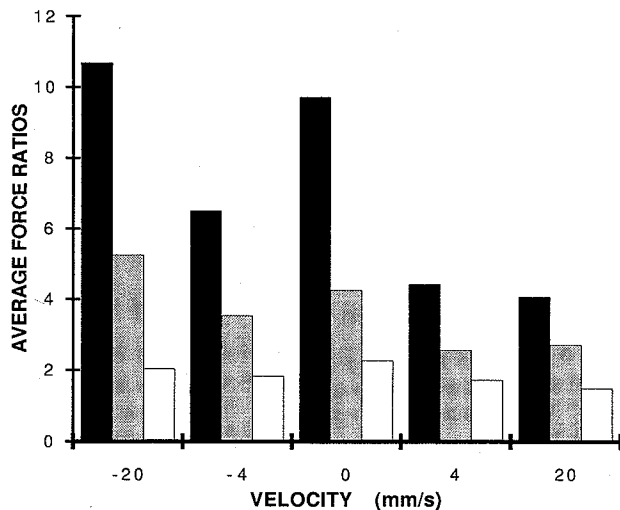


FIG. 9. Ranges of the differences in nonnormalized forces between the 3 types of motor units. Shown are nonnormalized but length-corrected averages for each group during both shortening and lengthening at 4 and 20 mm/s (negative velocities are shortening) and during isometric conditions (0 velocity). Darkest bars, range of FF to S forces (FF/S); medium dark bars, FR/S; lightest bars, FF/FR.

the average values for the isometric forces (0 mm/s). Stimulation rate was near-tetanic in all cases. The differences between each group were expressed as ratios (e.g., FF/S) to show the range of the differences in the force amplitudes at the various velocities between the motor-unit types. These ratios are plotted in Fig. 9.

Overall, the type-specific differences in the isometric state (center set of bars) were greater than during slow movement (± 4 mm/s; sets of bars flanking center). This is probably due to movement potentiation (see DISCUSSION). However, the differences during faster shortening (-20 mm/s, *left set of bars*) were, if anything, larger than during the isometric state. This reflects the greater steepness of the FV relationship for S versus F units, because at -20 mm/s the S forces had on average decreased to $\sim 50\%$ of their -4 -mm/s value, whereas the F unit forces had only decreased to $\sim 75\%$ (see Fig. 10A). Overall, the differences between motor-unit types were quite large for all velocities, with the FF-S range being greater than fourfold at all four velocities.

DISCUSSION

The results presented above provide the first systematic analysis of the FV relations of single motor units in the cat. These FV data showed that type S units in the MG muscle were much more sensitive to the effects of shortening velocity than were FR or FF units. These differences are consistent with the different whole-muscle FV relationships during shortening obtained for soleus (virtually 100% type S) (Burke 1981) and MG (75% fast twitch) (Burke 1981) by Spector et al. (1980). The important implication of these results is that the velocity dependence of a normally activated MG muscle, which has a heterogeneous population of units, will vary strongly as a function of recruitment level (see below).

Devasahayam and Sandercock (1992) have recently analyzed the FV relations of single motor units in the rat soleus

muscle, focusing only on shortening and tetanic stimulation. They found a poor correlation between contraction time and the velocity at which the motor units developed their maximum power (=force \times velocity). However, the motor units in the soleus in the rat do not have as wide a range of contraction times (18–36 ms in the sample of Devasahayam and Sandercock 1992) as do the motor units in the cat MG (22–100 ms in the present sample). The relationship between contraction time and FV slope in our data is consistent with previous work on single fibers isolated from different motor-unit types, which have shown that the characteristics of both myosin ATPase and troponin T are correlated with maximal velocity of shortening (Bottinelli et al. 1991; Edman et al. 1988; Greaser et al. 1988).

Mechanism of movement potentiation

Prior or concurrent movement had a great effect on the forces generated by motor units. The amplitude of this effect decreased with peak amplitude of motor-unit force (Fig. 3). There was no effect on the whole-muscle twitch (nor has previous research on whole muscle reported any such effect). The limitation to low force levels suggests that movement-dependent potentiation is due to interactions between active and passive muscle fibers (cf. Trotter 1990), rather than to crossbridge mechanisms. This interpretation is supported by the data of Edman (1980) and of Powers and Binder (1991). Edman studied isolated, single frog muscle fibers and found that passive shortening did not effect subsequent force generation. Powers and Binder (1991) studied the nonlinear summation known to exist among pairs or small groups of motor-unit forces (Clamann and Schelhorn 1988; Emonet-Dénand et al. 1990) and found that imposed movements reduced this nonlinearity. This finding suggested that movement affects how muscle fibers interact with each other, because nonlinear summation had previously been attributed to frictional interactions between active and passive fibers (Clamann and Schelhorn 1988; Emonet-Dénand et al. 1990). Powers and Binder (1991) hypothesized that the movement effects were due to a reduction in the viscosity of the substance linking adjacent muscle fibers, i.e., of the endomysium.

Substances with a viscosity that decreases with movement (shear) are called thixotropic (Hiemenz 1986). Muscle thixotropy (see also Hagbarth et al. 1985; Lakie et al. 1984; Wiegner 1987) also provides a simple explanation for movement-dependent potentiation, as follows (Weytjens 1992). Because of its viscosity, the endomysium of neighboring passive fibers generates an opposing force. The amplitude of this opposing force depends on the relative number of active fibers and the actual viscosity of the endomysium. If the endomysium is thixotropic, its viscosity decreases as a result of the shear experienced during the ramp stretches or releases. At the end of the ramp changes in muscle length, when conditions are stationary, it slowly increases again. Because the viscosity of the endomysium 0.1 s after the end of the ramp stretch is smaller than it is 10 s after the end of the movement, the opposing forces are smaller, and, consequently, the measured twitch forces are "potentiated." This mechanism also explains why the potentiation depends on twitch amplitude, i.e., on the number

of active muscle fibers, and why the whole-muscle twitch does not potentiate (no opposing force).

Although our hypothesis provides a parsimonious explanation for our data, it does not, in its current form, resolve why movement-dependent potentiation is sensitive to motor-unit force, but nonlinear summation is not (Powers and Binder 1991). Nor does it explain why the extent to which motor-unit forces sum nonlinearly is different in different muscles (Emonet-Dénand et al. 1990). Thus there is a need for comparative, multimuscle studies of the microarchitecture and mechanical behavior of the endomysium.

Significance of movement potentiation

If maintenance of isometric conditions for long periods of time reduces the force generated by a motor unit at the tendon, it follows that the standard isometric measurement of the smallest motor-unit forces may greatly underestimate their true force-generating capacities. In this sense the isometric state can be considered "abnormal" compared with most natural behaviors. An important implication of this finding is that *in situ* measurements of isometric forces would lead to large underestimates of the specific tensions of S units. This may account for the discrepancy between the data of Lucas et al. (1987), who found no significant differences in specific tension between slow and fast isolated, skinned muscle fibers, and Burke and colleagues (Burke 1981), who estimated specific tensions based on measurements of motor-unit force measurements and number of fibers per motor unit.

Movement potentiation itself may have very little functional significance during most normal movements. Although movement potentiation is profound in some of our experimental conditions, it vanishes as unit forces exceed 200 mN (see Fig. 8), which is much less than 1% of the maximal force of MG (~100,000 mN). Thus movement potentiation should be unimportant in normal movements, where many units are active and the aggregate force levels often greatly exceed 1% of maximum. Nonetheless, even if movement potentiation is confined to very small force levels, it could still be important in precisely controlled low force movements such as those of the intrinsic muscles of the hand. In this regard it is interesting to note that finely coordinated movements are rarely initiated from long periods of isometric rest. Instead, we tend to stretch and make practice motions before performing highly precise movements, which may in part reflect the need to remove the effects of the abnormally low forces of the isometric state. Finally, it should also be noted that movement potentiation has not yet been examined when the forces of several small motor units are combined. If the mechanism outlined above is correct, than multiple small units should exhibit little potentiation as long as their summed force exceeds 200 mN. However, this has not yet been directly tested.

Sources of error in the FV data

All FV data were normalized with respect to the force at the slowest velocity measured, 4 mm/s. Thus the decrease in force with shortening and the increase with lengthening from zero velocity will have been somewhat underesti-

ated. Comparison with the whole-muscle data of Spector et al. (1980) and Joyce et al. (1969) suggests that force at 4 mm/s shortening of the whole MG muscle is >90% of the isometric value, but, for soleus, a slow-twitch muscle, it may be as low as 80%. This suggests that the present data may underestimate the differences between the FV functions of type S versus type FR and FF units. Future work needs to investigate even slower velocities (≤ 1 mm/s) to avoid this problem, but this in turn must be predicated on a more quantitative understanding of the transition between the unpotentiated resting state and very slow motion.

Another significant problem is that it is now known that muscle fiber lengths may substantially diverge from whole-muscle length because of the effect of tendon compliance (Griffiths and Hoffer 1987; Griffiths 1991). Fiber lengths have not yet been measured for single motor units during constant velocity movements. The forces of the motor units in this study are quite small compared with the whole-muscle forces analyzed by Griffiths (1991), and for the present we assume that the corresponding divergence's in fiber and whole-muscle length are also small.

Effect of stimulation rate on FL and FV relations

Rack and Westbury (1969) showed that, for the whole soleus muscle, the optimal length for FL relations shifted to shorter lengths as stimulation rate increased. The single-unit FL relations in our data showed that the same effect exists for single motor units. However, our data were limited by two factors. First, only 1–2 intermediate rates were studied in only 10 of the 15 units; more data would be helpful. Second, the 5-N limit on our force transducer meant that the longest portion of the physiological range was not studied. Nonetheless, the twitch versus tetanus difference in L_{0s} was quite clear and is consistent with previous data from a much larger sample of single MG FL functions obtained by Stephens et al. (1975). It seems reasonable to conclude that single motor units behave much like the entire soleus muscle in this regard.

Our data also indicate that there may be a small interaction between stimulation rate and the FV relation during shortening, where the relationship became steeper as stimulation level increased. As noted in the RESULTS, this interaction was largely due to the difference between twitch and near-tetanic behaviors, because our data on medium rates was incomplete.

Motor-unit FV relations during lengthening

We found that, in contrast to shortening, there was no significant relationship between motor-unit type and FV behavior during lengthening. A major reason for this may be that the mechanisms underlying FV relationships during shortening and lengthening are quite different (Joyce et al. 1969). For lengthening, the differences between slow- and fast-twitch muscle may be modest if there is no population of attached crossbridges before stretch onset (see the following paragraph). It is possible that small differences were masked by measurement error. Although our data acceptance criterion were designed to minimize errors in the separation of active unit forces from the passive background

(see METHODS), the inherently larger passive forces during lengthening as compared with shortening may well have increased measurement error.

Recently, Petit et al. (1990) have shown that, during 0.5-mm stretches, the stiffness of S units is considerably greater than that of FR or FF units. No such differences were seen in the present study, but our protocol differed from that of Petit et al. (1990) in one important respect: the muscle was passive at the initiation of stretch, so that the motor unit had no population of already attached crossbridges at the time of stretch onset. Note that, if the resting muscle had attached crossbridges (Hill 1968) before stretch, this behavior would have been subtracted out along with the rest of the passive trace.

Motor-unit FV relations during shortening and recruitment order

It is important to study mechanical properties at the level of the single unit instead of in single muscle fibers or in whole muscles, because the motor unit is the fundamental element of motor control. Because motor units are normally recruited in an orderly fashion beginning with low force, slow-twitch units (Burke 1981; Henneman and Mendell 1981; Zajac and Faden 1985), the mechanical characteristics of the muscle can vary as a function of neural drive. For the isometric state, the functional implications of the differences in motor-unit force and fatigability were pointed out by Henneman and colleagues almost 30 years ago (Henneman and Olson 1965).

One important functional role of the FV relationship is that it provides a viscosity, which will act independently of reflexes to stabilize the velocity of a moving muscle against unexpected disturbances. Although the FV relationship is nonlinear, the important point remains that the steeper the relationship, the greater the viscosity, and the greater the contribution to stability. The steeper slopes of the normalized FV relations in the shortening direction for S versus FR and FF units means that the shape of the FV function will change as a function of recruitment level, becoming less steep as FR and FF units are recruited. This may be useful to help counteract the relatively greater effects of passive elasticity in muscle at low levels of neural activation.

Significance for muscle models

Most models of muscle mechanics employ a variant of the Hill model, with three independent multiplicative terms for FV, FL, and neural activation (e.g., Winters and Stark 1987; Zajac 1989). Such models have been designed to eliminate the normal process of recruitment and rate modulation to simplify the behavior of the model. In the following, we consider whether this simplification is justified in light of our data on single-unit FL and FV relations.

COMPUTER SIMULATION OF THE EFFECT OF RATE MODULATION ON FL FUNCTIONS IN A POPULATION OF MOTOR UNITS. Our data showed that rate modulation can be expected to shift L_0 to shorter lengths in single units whose rates are being increased. However, it must be kept in mind that recruitment and rate modulation form a rather complex overlap-

ping pattern in that low-threshold units can undergo considerable rate modulation before higher threshold units are recruited (Burke 1981; Hoffer et al. 1987; Mendell and Henneman 1981; Monster and Chan 1977). Thus the L_0 s of the low-threshold units would be shifting to shorter lengths, whereas those of the newly recruited high-threshold units would still be at longer lengths. The net outcome is difficult to predict, but an overall shift of L_0 to shorter lengths as neural drive increases would probably occur.

To test this hypothesis, we took advantage of recently developed realistic computer simulations of the steady-state recruitment and rate outputs of the MG motoneuron pool (Heckman and Binder 1991). The recruitment and rate modulation in these simulated outputs overlap extensively for the initial 50% of the force range, just as seen in data from human subjects (e.g., Monster and Chan 1977). In addition, the thresholds and the maximal forces of the 100 motor units that compose the simulated motor-unit population match that of the experimental data very closely. FL functions were added to this simulation, with each unit's function having an identical 6-mm shift in L_0 as its stimulation rate increased to reach maximal force (cf. Fig. 1). Application of various levels of synaptic input (specified as effective synaptic current equally distributed to all simulated motor units) generated the appropriate recruitment and rate modulation patterns for the pool of simulated units (see Heckman and Binder 1991 for details of this simulation process). At each level the whole-muscle FL function was specified simply as the linear sum of the FL functions of the recruited units.

It is important to realize that the simulation was overly simplified in several respects: the motor units within a muscle have considerable diversity in their L_0 s (Bagust et al. 1973; Stephens et al. 1975); force summation includes a nonlinear component (Clamann and Schelhorn 1988; Emonet-Dénand et al. 1990; Powers and Binder 1991); tendon compliance varies as a function of applied force (Zajac 1989); the distributions of synaptic inputs to the motoneurons are not necessarily uniform (Burke 1981; Heckman and Binder 1990); and spindle feedback would clearly have an influence (Houk and Rymer 1981). All of these points are presently being addressed in further simulations, but it was felt that this simple model was sufficient to provide a preliminary evaluation of whether L_0 shifted to shorter lengths as the neural drive to a population of motor units was increased.

Figure 10A shows the resulting set of simulated FL relations for the motor-unit population at five input levels that spanned most of the range of force production. As expected, the effect of the shift in the single-unit L_0 s is readily apparent, especially in comparison with the dashed lines, which show the whole population FL functions that occurred when all motor units had identical FL functions without any rate-dependent shift in L_0 . The dashed lines thus indicate the behavior of a Hill-type model in which a stereotyped FL function is simply scaled by a neural activation function (cf. Winters and Stark 1987; Zajac 1989). At lengths shorter than L_0 , the effect of the shift was to make the population FL functions much steeper and therefore much stiffer. Above L_0 , the negative FL slope was altogether avoided at low input-output levels and substantially

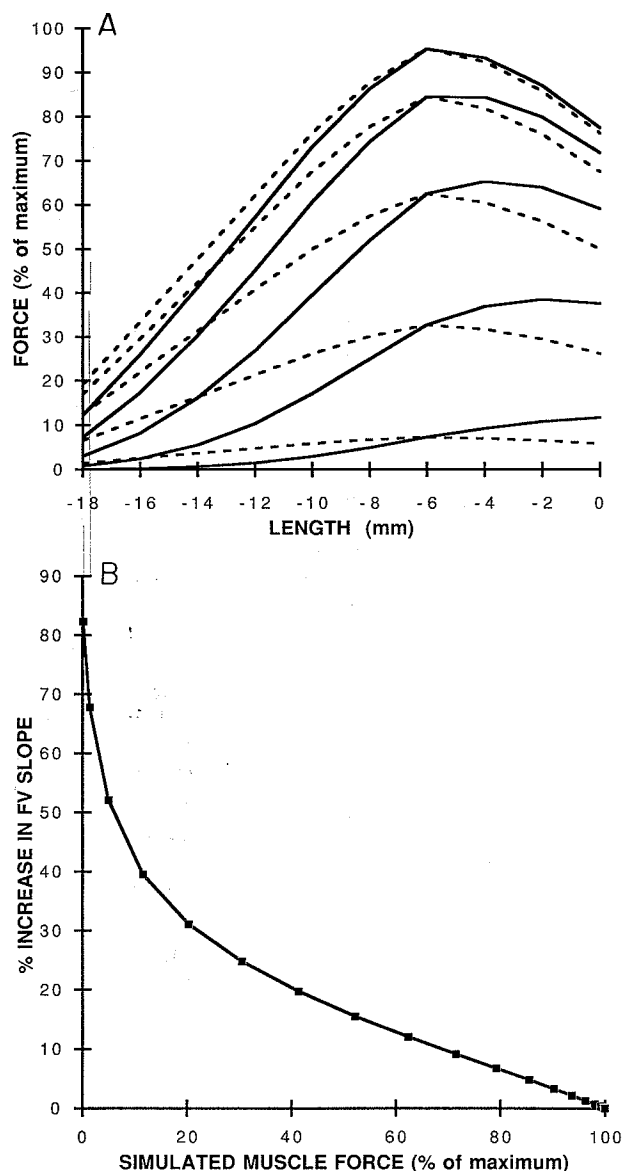


FIG. 10. Computer simulations of the force-length (FL) and force-velocity (FV) behaviors of a population of motor units undergoing realistic recruitment and rate modulation. *A*: simulated FL functions with (solid lines) and without (dashed lines) a rate-dependent shift in the L_0 of each motor unit. *B*: percent increase in FV slope at a low velocity during shortening produced by the type S vs. F differences in FV functions.

decreased at high levels. Both of these effects would tend to enhance the mechanical stability of muscle (cf. Houk and Rymer 1981). Thus we concluded that muscle models that fail to include a rate-dependent shift in L_0 may fail to capture an important aspect of muscle behavior. In this regard it is interesting to note that the compliance of the tendon tends to shift L_0 in the opposite direction (to the right) (Lieber et al. 1992; Zajac 1989), and this may counteract some of the leftward shift shown by the present simulations.

COMPUTER SIMULATIONS OF FV FUNCTIONS IN A POPULATION OF MOTOR UNITS. Just as for the FL relation, the overlapping pattern of recruitment and rate modulation must be taken into account in considering how the FV relation of the population of motor units within a muscle would change as a function of neural drive. Our experimental data

on single-unit FV relations were presented in normalized form to allow comparison of the shapes of the relations (i.e., of their relative slopes). However, it should be emphasized that increases in force caused by increases in the muscle's neural drive would tend to greatly steepen the slope of the nonnormalized FV relation. This is because the FV relation would cross the force axis at higher and higher levels while maintaining a constant velocity axis intercept (a constant FV relation shape means the maximal velocity of shortening does not change). The relatively greater steepness of the FV functions of S versus F units seen in the present data should be linked to a lower maximal velocity for S than F units and therefore would tend to counterbalance the increase in steepness due to increasing force. Or, put another way, the greater steepness for type S units would tend to make the FV function at low input levels steeper than it would be if all motor units had FV functions that were the same as that for the whole muscle.

To accomplish a preliminary test of this hypothesis, we again took advantage of recently developed realistic computer simulations of the steady-state recruitment and rate outputs of the MG motoneuron pool (Heckman and Binder 1991). FV outputs for shortening were added to this simulation, with shapes synthesized from the present data on the regression relations between FV slopes at -20 and -40 mm/s and near-tetanic forces. The same caveats about oversimplification and the need for further work stated above for the FL simulations above apply here as well. In addition, although Fig. 8 did show that rate modulation had a small effect on the shape of the FV function, this was ignored for the sake of simplicity. The simulated population behavior with the heterogeneous FV functions was compared with a homogeneous simulation in which all motor units had precisely the same normalized FV functions, each matching the FV behavior of the whole population at maximal output. This homogeneous case mimicked the behavior of a typical whole-muscle FV experiment (e.g., Joyce et al. 1969). The homogeneous simulation also matches the typical Hill model simulation, in which a standardized FV function is simply scaled by an activation function (e.g., Winters and Stark 1987; Zajac 1989).

In general, the FV simulation results showed that, at low input-output levels, the FV function of the heterogeneous population of motor units was considerably steeper than the homogeneous case. Figure 10*B* illustrates this. The percentage increase in FV slope for low velocities (from 0 to 8 mm/s) generated by the heterogeneous population in comparison with the homogeneous one is plotted for the full range of force outputs. At low forces, where the S units generate a substantial fraction of the total force, the FV slope was nearly doubled. This effect progressively decreased as the recruitment level increased and FF units began to dominate force output. At maximal activation, the differences vanished, because the two populations had matched maximal FV behaviors. These simulation results indicate that the realism of muscle models at low input-output levels could be greatly enhanced by inclusion of the systematic differences in motor-unit FV relations.

This work was supported in part by National Institute of Neurological Disorders and Stroke Grant NS-08210 to C. J. Heckman, a Fullbright-

Hays Award for Research, and a North Atlantic Treaty Organization Research Fellowship to J. L. F. Weytjens.

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Received 16 December 1991; accepted in final form 1 July 1992.

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