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Discharge Rate Variability Influences the Variation in Force Fluctuations Across the Working Range of a Hand Muscle

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Moritz, Chet T., Benjamin K. Barry, Michael A. Pascoe, and Roger M. Enoka. Discharge rate variability influences the variation in force fluctuations across the working range of a hand muscle. *J Neurophysiol* 93: 2449–2459, 2005. First published December 22, 2004; doi:10.1152/jn.01122.2004. The goal of this study was to improve the ability of a motor unit model to predict experimentally measured force variability across a wide range of forces. Motor unit discharge characteristics were obtained from 38 motor units of the first dorsal interosseus muscle. Motor unit discharges were recorded in separate isometric contractions that ranged from 4 to 85% of the maximal voluntary contraction (MVC) force above recruitment threshold. High-threshold motor units exhibited both greater minimal and peak discharge rates compared with low-threshold units ($P < 0.01$). Minimal discharge rate increased from 7 to 23 pps, and peak discharge rate increased from 14 to 38 pps with an increase in recruitment threshold. Relative discharge rate variability (CV) decreased exponentially for each motor unit from an average of 30 to 13% as index finger force increased above recruitment threshold. In separate experiments, force variability was assessed at eight force levels from 2 to 95% MVC. The CV for force decreased from 4.9 to 1.4% as force increased from 2 to 15% MVC ($P < 0.01$) and remained constant at higher forces (1.2–1.9%; $P = 0.14$). When the motor unit model was revised using these experimental findings, discharge rate variability was the critical factor that resulted in no significant difference between simulated and experimental force variability ($P = 0.22$) at all force levels. These results support the hypothesis that discharge rate variability is a major determinant of the trends in isometric force variability across the working range of a muscle.

INTRODUCTION

The force produced by a muscle during a voluntary contraction depends on the number of active motor units and the rate at which those units discharge action potentials (Adrian and Bronk 1929; Macefield et al. 1996; Seyffarth 1940; Thomas et al. 1991). The relative contribution of these two mechanisms to an increase in muscle force varies across the working range of the muscle. Recruitment dominates at low forces, whereas rate coding is more significant at high forces (De Luca et al. 1982; Kernell and Sjoholm 1975; Milner-Brown et al. 1973a; Monster and Chan 1977; Person and Kudina 1972).

Despite a general consensus on the control scheme by which variation in motor unit activity grades the force exerted by a muscle, some details are uncertain. For example, there is no agreement on the relative distributions of minimal and maximal discharge rates across the motor unit population. Some reports indicate that the minimal rate is constant (Monster and Chan 1977) or decreases with recruitment threshold (Tanji and Kato 1973), whereas other findings suggest that the minimal rate increases with recruitment threshold (Bigland and Lippold 1954; Gydikov and Kosarov 1974). Similarly, maximal discharge rates have been observed to be greater (De Luca et al. 1982; Duchateau and Hainaut 1990; Hoffer et al. 1987; Mellah et al. 1990; Tanji and Kato 1973) and lesser (Bigland and Lippold 1954; Gydikov and Kosarov 1974; Kanosue et al. 1979; Kosarov and Gydikov 1976) in low-threshold units compared with high-threshold units. Nonetheless, maximal discharge rates seem to be insufficient to elicit peak tetanic forces in single motor units during brief isometric contractions (Fuglevand et al. 1999; Macefield et al. 1996; Thomas et al. 1991). Furthermore, the slope of the relation between discharge rate and force has been reported to vary as a function of recruitment threshold in some studies (Freund et al. 1975; Monster and Chan 1977), but not others (Milner-Brown et al. 1973a,b).

Much less is known about the distribution of two other factors that can also influence muscle force: discharge rate variability and correlated discharges. The coefficient of variation (CV) for discharge rate, which has a significant effect on the force fluctuations during steady contractions (Enoka et al. 2003; Laidlaw et al. 2000), is typically reported as a constant value of about 10–20% as muscle force increases (Nordstrom et al. 1992; Semmler and Nordstrom 1998). However, the CV for discharge rate, which is a measure of relative discharge rate variability, declines with an increase in mean discharge rate (Mori 1973; Person and Kudina 1972), and most of the measurements have been limited to low-threshold motor units. Similarly, the proportion of correlated discharges, one measure of which is motor unit synchronization, varies between pairs of motor units and depends on the task that is performed (Datta et al. 1991; Huesler et al. 1998; Milner-Brown et al. 1975; Schmied et al. 2000; Semmler et al. 2002). Some evidence suggests that the coupling is greatest between motor units with similar recruitment thresholds (Schmied et al. 1994), but relatively little is known about high-threshold motor units.

Given the uncertainty over the discharge characteristics across the motor unit pool during voluntary contractions, a reasonable strategy is to determine the extent to which simulations can replicate experimental results. Accordingly, Fuglevand et al. (1993) developed an elegant model of motor unit recruitment and rate coding that was able to match experimentally observed EMG-force relations. However, Taylor et al. (2003) were unable to reproduce the exact variation in force fluctuations as a function of muscle force with the Fuglevand

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model, even when the model was modified to include various forms of correlated discharges. The goal of this study was to measure the variation in the activity of a population of motor units across the operating range of a hand muscle and to use the findings to improve the match between experimentally measured and simulated force variability.

METHODS

This study involved two separate experimental protocols over a wide range of forces: the measurement of single motor unit discharges and the assessment of the fluctuations in force during steady contractions. Single motor unit data were obtained for 38 motor units from 18 subjects (12 men and 6 women) who had a mean age of 25.7 ± 5.7 yr (range: 18–38 yr). Many of the subjects participated in multiple motor unit recording sessions, especially those subjects from whom consistently clear single motor unit recordings were obtained. The fluctuations in force were measured in 20 subjects (10 men and 10 women), with a mean age of 25.0 ± 5.7 yr (range: 19–39 yr). Eight subjects (6 men and 2 women) participated in both experiments. All subjects were righthanded, as verified by the Edinburgh Handedness Inventory (Oldfield 1971), and reported no known neurological disorders. The Human Subjects Committee at the University of Colorado approved the protocol, and informed consent was obtained before participation from each subject.

Force measurement

Subjects were seated with the left shoulder abducted by ~0.79 rad (45°), and the forearm was restrained in a neutral position and resting on a platform. The elbow joint and forearm were immobilized with a vacuum pillow (Tumble Forms, Trenton, Ontario, Canada) and Velcro straps. The left hand was supported with the palm vertical, the third through fifth digits flexed slightly at the metacarpophalangeal joints and restrained in a brace, and the thumb extended vertically and held with a separate brace in the same plane as the palm of the hand at an angle of ~1.1 rad (60°) to the index finger. The index finger was secured to a hinged splint to maintain both interphalangeal joints extended and to constrain finger excursion to the abduction-adduction plane. To maximize the contribution of the first dorsal interosseus muscle to the abduction torque, the index finger was flexed at the metacarophalangeal joint by ~0.1 rad (5°). The abduction force exerted by the index finger was measured with a force transducer that was aligned with the proximal interphalangeal joint. To measure forces from <2% maximal voluntary contraction (MVC) to maximal levels with a sufficiently high signal-to-noise ratio, both low (0.049 V/N) and high (0.472 V/N) sensitivity transducers were used (model 13, Sensotec). Force was digitized with a Power 1401 (CED, Cambridge, UK) at 200 samples/s during the motor unit experiment and at 1,000 samples/s during the force steadiness task, and stored on a computer. To provide visual feedback of the abduction force exerted by the index finger, a 17-in computer monitor was located at eye level in front of the subjects at a distance of 1.6 m.

EMG measurement

Single motor unit potentials were recorded from the first dorsal interosseus muscle using Formvar-insulated, stainless-steel wires (diameter: 50 or 25 μm, California Fine Wire, Grover Beach, CA) that were fastened together at the recording tip with nontoxic glue and inserted into the muscle belly using a 27-gauge hypodermic needle. The needle was removed after the wires were inserted. The insulation was only absent from the recording tip of each wire, and three or four wires were included in each recording electrode to permit alternative bipolar configurations. The quality of the single motor unit recordings was optimized by using different pairs of recording wires and by making slight adjustments in the location of the electrode. The EMG signal was amplified ×5,000 and band-pass filtered between 300 Hz and 8.5 kHz (S-series, Coulbourn Instruments, Allentown, PA). The motor unit signal was sampled at 20,000 samples/s with a Power 1401 (CED) and stored on a computer.

Single motor unit potentials were identified on-line using both a dual-window discriminator (S-series, Coulbourn Instruments) and Spike2 software (CED). A reference surface electrode for the single motor unit recordings was placed over the styloid process of the ulna (silver-silver chloride, 4 mm diam).

Experimental protocol

At the beginning of both experimental protocols, subjects performed several trials of the MVC task to determine the maximal force capacity of the first dorsal interosseus muscle. Participants were provided with verbal encouragement as they increased force from zero to maximum over a 3-s period and then held this maximal level for a further 1–2 s. Visual feedback of abduction force exerted by the index finger was provided on the computer monitor, and the subject's hand was closely observed by one of the experimenters to ensure that the task was performed correctly. The peak value from three or four trials was taken as the MVC force, provided it was within 5% of the peak value for another trial.

MOTOR UNIT EXPERIMENT. The goal of the motor unit experiment was to identify the potentials of a single motor unit that could be discriminated during brief contractions at multiple forces. Subjects were asked to perform three tasks during this experiment: *1*) a graded minimal rate task with audio feedback of discharge rate, *2*) a ramp contraction in which the force increased gradually and continuously, and *3*) a discrete isometric force task with many target forces.

The experiment began by the subject gradually increasing contraction intensity as the investigators observed the intramuscular EMG signal for the appearance of a candidate motor unit. The subject was provided with visual feedback of index finger force and audio feedback of the discharge for the motor unit being tracked. Once a unit was identified, the subject was instructed to increase the force gradually until the motor unit became active and to reduce the force slowly to identify the minimal rate at which the unit could discharge action potentials repetitively. This task, which is referred to as the graded minimal rate task, was repeated three times, with each trial lasting between 5 and 20 s.

The recruitment threshold of the motor unit was characterized as the force at which the unit began to discharge action potentials repetitively during a ramp increase in index finger force. The target force level for the ramp contractions was set at twice the force associated with the graded minimal rate task. The ramp contractions were performed two to three times.

Subsequently, an additional ramp contraction was performed to determine the peak force at which the discharge of the motor unit could be discriminated. Once the upper limit was identified, a series of about 10 target forces was determined across the range that the unit could be discriminated. The actual number of target forces varied, however, due to both the variable number of trials needed to identify the minimal discharge rate and changes that occurred in the recording conditions during the experiment. Successive target forces were presented on the visual display, and participants were instructed to exert an index finger force to match the target and to do so without either exceeding the target force or generating a rapid contraction. Subjects were required to maintain the target force for 2–10 s, with briefer durations for the high forces. There was a rest period of ≥30 s between trials. The force targets were presented in an ascending order, except that, around the recruitment threshold, the target forces were adjusted up and down in small increments (<1% MVC force) to identify the force associated with the minimal discharge rate. The minimal rate obtained with this protocol is referred to as the discrete minimal discharge rate. After the series of contractions to the target forces, MVCs were performed to verify that the observed discharge rates were not influenced by fatigue.

FORCE STEADINESS TASK. Subjects performed isometric contractions with the first dorsal interosseus muscle so that the index finger exerted an abduction force to match a series of eight target forces. Subjects practiced the task a few times at a moderate intensity before beginning the series. The target forces were presented in random order with two attempts at each of 2, 5, 15, 30, 50, 70, 85, and 95% of MVC force. Subjects were instructed to increase the abduction force to match the target indicated on the visual display and to hold that force as steadily as possible for 6 s or as close to 6 s as possible. Visual feedback of target force and the index finger force was provided for the first 3 s of each contraction, but was removed for the final 3 s. The entire force trace was shown to the participant after the completion of each trial. The gain of the force display was adjusted so that the target-force line was always at the same position on the monitor relative to zero force. Although the variation in gain likely influenced the subjects' perception of variability, only nonvisual feedback data from each trial were included in the analysis. A minimum rest interval of 30 s was provided between each trial, with considerably longer rest periods after high-force contractions.

Motor unit model

A model of motor unit recruitment and rate coding, originally developed by Fuglevand et al. (1993), was used to simulate the isometric force produced by a pool of motor units with characteristics resembling the first dorsal interosseus muscle (Taylor et al. 2002, 2003; Yao et al. 2000). The model was implemented in Matlab version 6.1 (Mathworks, Natwick, MA). A detailed description of the simulation has been published previously (Fuglevand et al. 1993; Taylor et al. 2002, 2003).

In brief, the model comprised a pool of motor units with systematic variation in recruitment threshold, minimal and maximal discharge rates, and twitch force. Relative discharge variability remained constant, typically at a nominal value of 20%. In this study, the number of motor units included in the pool was increased from 120 to 180, as suggested by motorneuron labeling data obtained from monkeys (Jenny and Inukai 1983). Motor unit recruitment and discharge rate were determined by an excitation function that acted on all the units in the pool. Motor unit 1 was the first recruited, had the smallest twitch force [1 arbitrary unit (au)], and had the longest twitch time (90 ms). In contrast, motor unit 180 was the last recruited, had the largest twitch force (100 au), and had the briefest contraction time (30 ms). Each motor unit generated a twitch force in response to a single discharge and a tetanic force when the activation involved multiple discharges. The amplitude of each tetanus was defined by a gain function that depended on discharge rate. The simulated muscle force was calculated as the sum of all the motor unit forces. Muscle force at each level of excitation was normalized to the force produced when all motor units were recruited and discharging at their maximal rates (analogous to the MVC).

Several simulation parameters were modified to reflect the experimental findings from this study. First, the recruitment range of the motor unit pool was expanded from 40% (Taylor et al. 2003) to an upper limit of 60% MVC. Second, the minimal discharge rate was increased linearly with recruitment threshold from 7.6 to 17.9 pps (see Fig. 4). The maximal discharge rate was also increased linearly, with recruitment threshold from 17.6 to 34.8 pps. In previous versions of the model, the minimal discharge rate was 8 pps for all motor units, and the maximal discharge rate decreased from 35 pps for the first recruited unit to 25 pps for the last recruited unit. Third, the CV for the interspike interval (ISI) observed in the experiments was implemented in two ways: *1*) the mean CV for the ISI observed in the experiments (19.8%) was used for all motor units, and *2*) the CV for the ISI decreased for each motor unit as the force increased. The force-dependent reduction in the CV for the ISI (CV_{ISI}) was modeled as an exponential function to reproduce the decline observed experimentally (30–10%) as force increased above recruitment threshold ($\Delta Force$)

$$CV_{ISI} = 10 + 20e^{(-\Delta Force/2.5)} \tag{1}$$

The relation between CV_{ISI} and force for each motor unit was well predicted by individual exponential regressions of the form used in *Eq. 1* ($r^2 = 0.72 \pm 0.07$). All simulations were run 20 times so that the variability assigned to each parameter could influence the variability in the simulated forces.

Data analysis

Discrimination of single motor unit potentials was verified off-line by visual inspection of each potential and by using the template-matching features of the Spike2 software (Version 5.02, CED). ISIs $>$250 ms ($<$4 pps; $n = 120$, 0.37% of discharges) or $<$20 ms ($>$50 pps; $n = 223$, 0.67% of discharges) were excluded from the calculations of discharge rate. Long ISIs ($<$4 pps) were likely due to brief cessation of motor unit discharge, whereas very short intervals ($>$50 pps) exceed the rates normally observed during these types of contractions for human motor units (Bigland and Lippold 1954; De Luca et al. 1982; Kanosue et al. 1979; Tanji and Kato 1973) and were likely due to discrimination error or double discharges. To determine the region over which to calculate the mean and CV for discharge rate during each contraction, the force plateau was identified as beginning when the force rose to within 90% of the target force and ended 1 s before the force dropped below 90% of the target force. The force and discharge rate measurements were made over the intervening interval.

The recruitment threshold of each motor unit was determined by moving a 0.5-s window forward in time in 1-ms steps for the data from the ramp task until the CV for discharge rate for the potentials within the window was $<$50%. The force corresponding to the first discharge within this window was taken as the recruitment threshold of the motor unit.

The minimal discharge rate of each motor unit was measured in two tasks: *1*) a graded decrease in force until a minimal rate was achieved and *2*) discrete increments in target force around the recruitment threshold of the motor unit. The minimal discharge rate during the graded test corresponded to the lowest rate measured during a 2-s interval when the CV was $<$50%. The minimal rate during the discrete test was identified by moving a 2-s window forward in 1-ms steps and noting the rate when both the CV for discharge rate was $<$50% and $\geq$1 discharge occurred both before and after the 2-s window. Data for the graded decrease in force with audio feedback were only obtained for 29 of the 38 total motor units because the graded decrease was added to the protocol after 9 units had been recorded.

The average slope of the relation between discharge rate and force was approximated for each motor unit by fitting a linear regression to the data for three or more target forces occurring before the first plateau in discharge rate.

The abduction force exerted by the index finger at each target level during the steadiness contractions was quantified for a 1-s period commencing 500 ms after visual feedback of the force was removed. To minimize the contribution of slight errors in target-matching performance, the 1-s epoch was linearly detrended prior to the assessment of the CV for force. The mean force was calculated over this 1-s region for the two trials at each target level. The CV for force for the trial with the mean force closer to the desired target force was used in the analysis. Similarly, the CV for the simulated force was calculated after it had been detrended.

Statistical analysis

Repeated-measures ANOVAs were used to compare the forces and discharge rates obtained during the ramp, graded, and discrete tasks. The relations between recruitment threshold and the minimal and peak discharge rates observed during the brief contractions at different target forces were characterized with linear regression analyses. Similarly, regression analyses were used to determine the association between recruitment threshold and the slope of the relation between discharge rate and force.

A two-factor, repeated-measures ANOVA with Bonferroni posthoc tests was used to compare the simulated and experimental measures of the CV for force (between-subject factor) at each of the eight target levels (repeated-measures factor). Regressions were also performed on the average CV for force at each target level to quantify the improvement in the model's ability to match the experimental data, with the r^2 value used as an index of improvement. All statistical procedures were performed with SPSS version 11.5 and SigmaPlot version 8.0 (SYSTAT Software). α was set at 0.05, and all reported values are means and 95% CIs.

RESULTS

Recordings were obtained from 38 motor units at 10.0 ± 1.0 (mean ± CI) different force levels (Table 1). On average, it was possible to discriminate 87 ± 10 discharges during the 5.9 ± 0.9-s contraction at each force level. Motor units were followed for an average increase of 23% MVC force (range, 4–85% MVC) above recruitment threshold (Table 1).

Recruitment threshold

The discrete target force at which motor units began to discharge action potentials repetitively was similar to the recruitment threshold of the units. Figure 1*A* shows that the recruitment thresholds obtained during ramp increases in force did not differ from the forces measured during the graded minimal rate task ($P = 0.202$) and the discrete minimal rate task ($P = 0.784$). In contrast, motor units discharged more slowly (7.5 ± 1.6 pps; a decrease of 2.7 ± 1.0 pps; $P < 0.001$)

TABLE 1. *Characteristics of the motor unit data*

MU NO.	Minimum Force, % MVC	Peak Force, % MVC	Range, % MVC	Minimum DR, pps	Peak DR, pps	Number of Targets	Mean Target Duration, s	Number of Discharges
1	0.3	14.8	14.5	8.0	15.8	12	9.36	101
2	**0.5**	**8.4**	**8.0**	**6.8**	**16.4**	**6**	**10.58**	**116**
3	0.5	8.6	8.1	6.9	13.8	14	9.82	105
4	**1.0**	**7.8**	**6.8**	**11.2**	**14.1**	**10**	**10.89**	**137**
5	1.1	9.3	8.2	8.1	15.7	6	7.89	91
6	**1.2**	**12.6**	**11.4**	**6.7**	**16.1**	**17**	**5.93**	**60**
7	**1.2**	**19.4**	**18.1**	**6.5**	**14.1**	**15**	**6.78**	**69**
8	**2.3**	**87.1**	**84.9**	**8.3**	**21.8**	**16**	**8.68**	**133**
9	**2.6**	**23.4**	**20.8**	**9.9**	**17.7**	**13**	**10.56**	**149**
10	3.0	32.6	29.6	8.8	30.3	9	10.06	162
11	4.2	17.0	12.7	6.9	16.5	9	3.96	47
12	4.5	9.0	4.5	9.3	17.5	8	6.78	85
13	6.8	15.4	8.6	11.4	17.7	9	9.72	141
14	9.2	24.6	15.4	6.8	19.8	11	7.12	79
15	9.8	20.5	10.7	11.7	16.5	10	5.53	77
16	10.4	42.8	32.5	8.2	22.1	11	4.73	75
17	10.9	27.3	16.4	10.1	15.0	7	7.00	91
18	**11.4**	**39.6**	**28.2**	**11.2**	**30.7**	**11**	**3.54**	**77**
19	**12.4**	**39.8**	**27.5**	**10.7**	**22.5**	**9**	**5.90**	**101**
20	13.2	38.1	24.9	10.2	26.5	11	4.98	91
21	14.3	22.0	7.7	9.1	19.2	9	4.37	60
22	14.4	40.6	26.2	6.8	19.0	9	4.53	53
23	**15.1**	**32.6**	**17.5**	**9.0**	**22.0**	**7**	**5.16**	**82**
24	15.5	32.0	16.5	13.7	20.0	10	6.80	110
25	**16.1**	**49.3**	**33.3**	**11.7**	**27.4**	**12**	**3.32**	**64**
26	16.4	60.0	43.6	9.5	27.8	11	4.28	62
27	20.5	27.6	7.1	10.6	21.9	6	5.53	91
28	**21.1**	**80.3**	**59.2**	**10.9**	**17.7**	**13**	**6.76**	**97**
29	22.5	38.2	15.7	13.3	23.4	8	3.36	58
30	22.7	34.0	11.3	11.5	23.3	11	3.93	67
31	24.2	44.3	20.0	11.9	22.8	7	6.17	106
32	28.2	66.9	38.7	7.0	23.3	13	4.32	69
33	32.4	74.3	41.9	9.3	33.8	9	4.58	100
34	43.4	74.1	30.8	14.8	30.9	8	3.20	69
35	44.2	70.9	26.7	9.6	28.2	7	2.49	41
36	48.7	60.8	12.0	13.4	21.9	5	1.33	23
37	55.0	90.5	35.5	21.0	35.5	10	2.11	64
38	**60.9**	**95.2**	**34.3**	**22.5**	**32.2**	**7**	**3.35**	**95**
Mean	**16.4**	**39.3**	**22.9**	**10.3**	**22.3**	**10**	**5.93**	**86.8**
CI	**5.3**	**8.4**	**5.3**	**1.2**	**2.2**	**1**	**0.85**	**10.0**

Mean values and 95% CI are for all units. The data comprise the ranges for force and DR observed for each motor unit during the discrete task, the number of target forces and the mean duration of each contraction, and the average number of discharges analyzed at each force target. Motor units in bold are those 12 units that exhibited a clear plateau in peak discharge rate and had exceptionally large signal-to-noise ratios. DR, discharge rate.

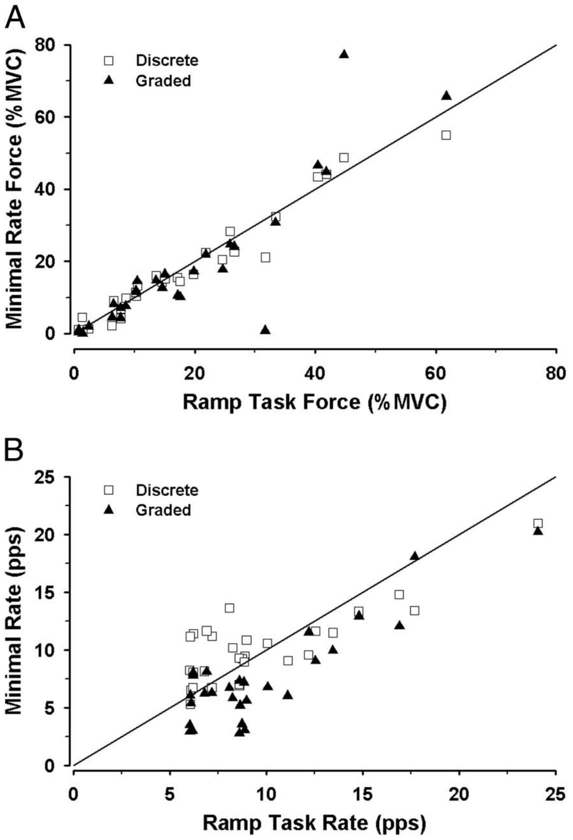

FIG. 1. Relations between forces and discharge rates observed for 29 motor units during ramp task, graded minimal rate task, and discrete minimal rate task. *A*: forces measured during the 3 tasks. Clustering of data about the line of identity indicates similar relations for graded (P = 0.202) and discrete (P = 0.784) minimal rate tasks compared with ramp task. *B*: minimal discharge rates observed during the 3 tasks. Minimal discharge rates recorded during discrete minimal rate task did not differ from the line of identity with ramp task (P = 0.514), whereas discharge rates were lower for graded minimal rate task ($P < 0.001$).

during the graded minimal rate task when subjects were given audio feedback (Fig. 1*B*). There was no difference (P = 0.514) in minimal discharge rate during the ramp task (9.7 ± 1.7 pps) and the discrete minimal rate task (10.2 ± 1.2 pps).

Discharge rate

Motor unit discharge rate increased with index finger force for all units (Fig. 2). Twelve of the 38 motor units exhibited a clear plateau in discharge rate. The slope of the relation between discharge rate and force was not related to recruitment threshold ($r^2 = 0.08$; $P = 0.124$) and had an average value of 0.99 ± 0.24 pps/%MVC.

Minimal and peak discharge rates measured during the discrete tasks both increased with recruitment threshold. Figure 3 shows representative data from three motor units spanning the range of recruitment thresholds observed in this study. Minimal discharge rates increased from 6.5 to 22.7 pps as recruitment threshold increased. Similarly, peak discharge rates increased from 13.8 at lower thresholds to 37.8 pps at higher thresholds (Table 1). Minimal and peak discharge rates for all motor units are summarized in Fig. 4. Regression analyses revealed a positive linear trend in both minimal (r^2 = 0.57, $P < 0.001$) and peak ($r^2 = 0.49$, $P < 0.001$) discharge rate as a function of recruitment threshold. A similar regression was obtained for the peak discharge rates ($r^2 = 0.53$, $P <$ 0.001) of a subset of the 12 motor units that showed a clear plateau in discharge rate.

Discharge rate variability

Relative discharge rate variability (CV) decreased exponentially as force increased above recruitment threshold for each motor unit (Fig. 5, *A* and *B*). The CV for the ISIs for each motor unit declined as an exponential function of index finger force ($r^2 = 0.72 \pm 0.07$). The CV for ISIs ranged from peak values of 30.0 ± 3.5% to minimal values of 13.4 ± 1.1% for all motor units. The exponential decrease in the CV was most evident for the 12 motor units that exhibited clear plateaus in discharge rate (Fig. 5*B*), although the CV often reached minimal values before the plateau in discharge rate. The mean CV for ISIs for all trials was 19.8 ± 2.5%. Absolute discharge rate variability (SD) also decreased exponentially with an increase in force (Fig. 5*C*).

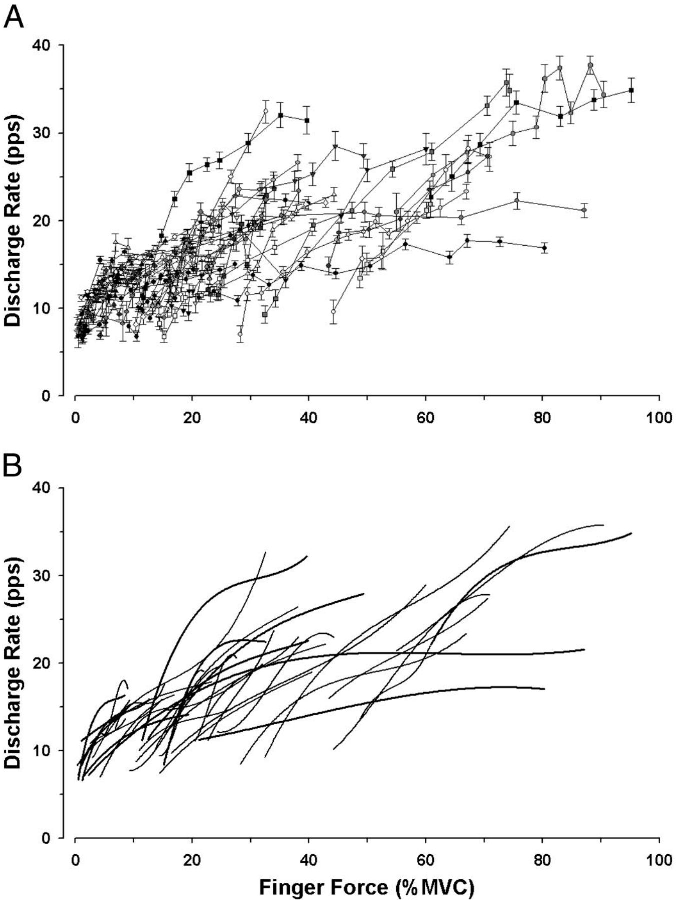

FIG. 2. Variation in the discharge rate of 38 motor units during the discrete task with increases in the abduction force exerted by the index finger. *A*: each symbol represents a different motor unit, and each data point corresponds to mean ± CI of the discharge rate during an isometric contraction. Data were obtained for an average of 10.0 ± 1.0 target forces for each motor unit, with each contraction lasting 5.9 ± 0.9 s. Range of forces that the discharge of each motor unit could be discriminated is reported in Table 1. *B*: 3rd-order regressions for data in *A*. Bold lines in *B* represent 12 motor units that exhibited a clear plateau in peak discharge rate.

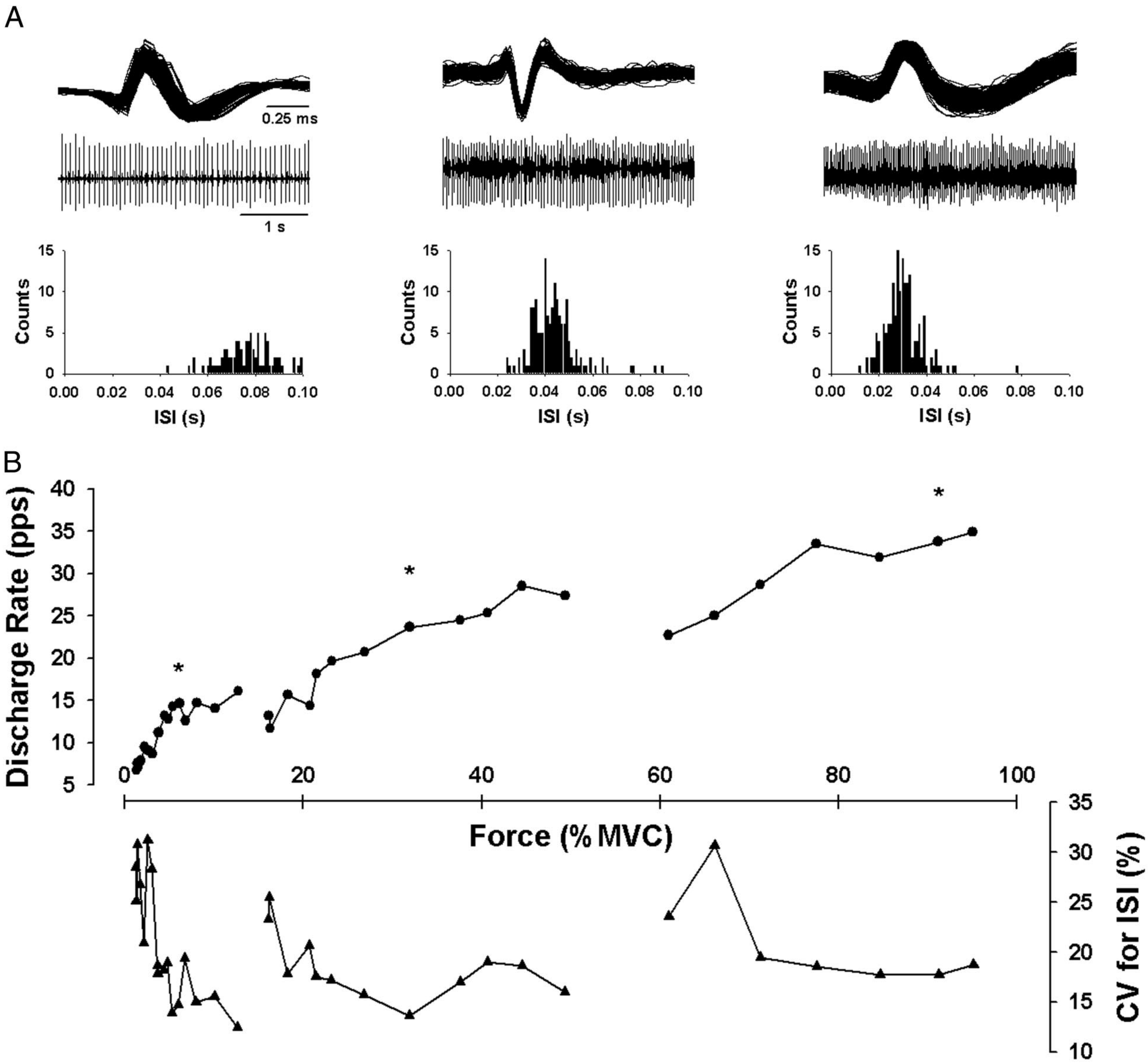

FIG. 3. Representative data for 3 motor units that had low, medium, and high recruitment thresholds. These correspond to motor units 6, 25, and 38 in Table 1. Figure shows discharge data for each motor unit across the range of target forces that its action potential could be discriminated. *A*: discrimination of action potentials for each of the 3 motor units during a single isometric contraction. The 3 rows show superimposed action potentials (*top*), trains of action potentials (*middle*), and histograms of the interspike intervals (ISIs; *bottom*). *B*: mean discharge rate and CV for ISIs for the 3 units. *Target forces at which recordings shown in *A* were obtained.

Force variability and simulations

The CV for force decreased rapidly and then plateaued as force increased when 20 subjects produced steady contractions ranging from 2 to 95% MVC (Fig. 6*A*). The CV for force was significantly greater at 2 and 5% MVC than for the remaining force levels ($P = 0.001$). There was also a trend for an increase in the CV for force between 15 and 50% MVC ($P = 0.140$).

The original parameters of the motor unit model did not reproduce the rapid decrease in the CV for force observed in the subjects (Fig. 6*B*). Therefore the model was progressively revised with the values observed in the current experiments. Figure 6, *A* and *C,* shows the result when the minimal and maximal discharge rates observed experimentally were included in the model (see Fig. 4), and the CV for ISI was set to the mean value observed for all trials (19.8%). With these adjustments, the model was still significantly different from the subjects at five of the eight force levels ($P = 0.004$), with a modest regression between the subject and model data ($r^2 = 0.60$, $P = 0.025$). Figure 6, *E–G,* shows the results with the addition of a decreasing exponential function for the CV of ISI (*Eq. 1*). With this adjustment, the model and subject force variability were not significantly different ($P = 0.220$) at any force level, and the regression improved dramatically ($r^2 = 0.91$, $P < 0.001$).

DISCUSSION

The main findings of this study were that relative discharge rate variability decreased exponentially with an increase in index finger force and that adding this change in discharge rate variability to the motor unit model dramatically improved the ability of the model to produce simulated force fluctuations that predicted those observed experimentally. In addition, low-

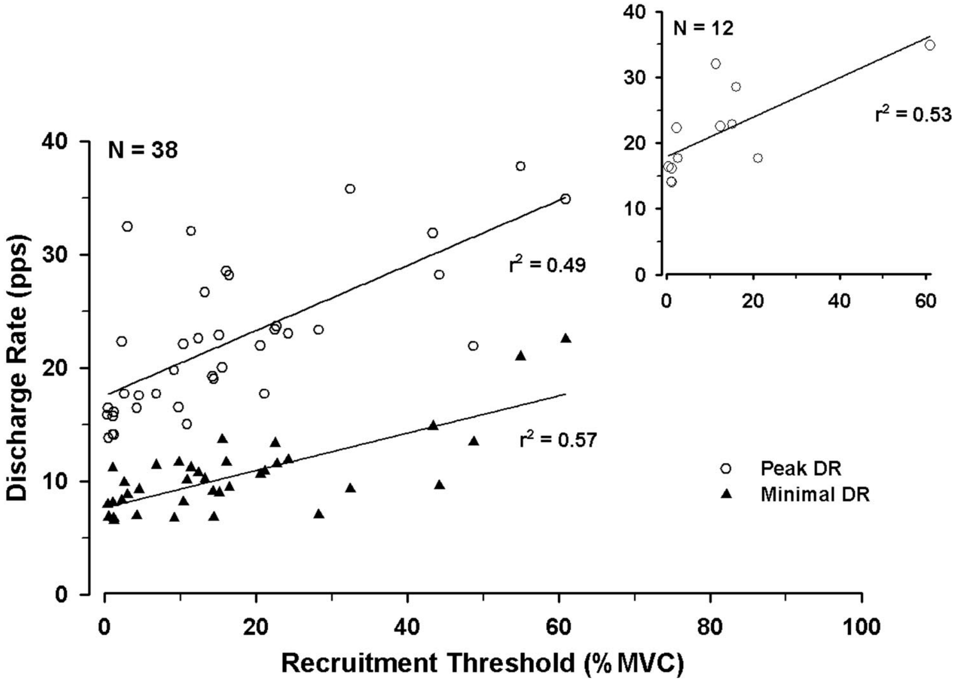

FIG. 4. Minimal and peak discharge rates as measured during the discrete task for 38 motor units as a function of recruitment threshold. Peak discharge rate represents the greatest rate that could be discriminated reliably, which may not have corresponded to the maximal discharge rate. *Inset*: peak discharge rate for 12 motor units that exhibited a clear plateau in peak discharge rate (Fig. 2). Both minimal discharge rate ($r^2 = 0.57$; $y = 0.1645x + 7.646$) and peak discharge rate ($r^2 = 0.49$; $y = 0.2871x + 17.55$) increased significantly across recruitment threshold ($P < 0.001$).

threshold motor units exhibited lower minimal and lower peak discharge rates than high-threshold motor units. Finally, the observed upper limit of motor unit recruitment in the first dorsal interosseus muscle was 60% MVC force.

Force variability

The CV for finger force observed in the subjects declined rapidly from 2 to 15% MVC and then remained relatively constant as the abduction force increased during a series of brief isometric contractions. This trend was similar to that observed in other studies on the first dorsal interosseus (Burnett et al. 2000; Galganski et al. 1993; Laidlaw et al. 1999, 2000) and quadriceps femoris (Christou et al. 2002; Tracy and Enoka 2002) muscles.

Discharge rate variability

The exponential decrease in the CV for ISI with an increase in index finger force for individual motor units (Fig. 5) seems to be a novel finding. One previous study reported that the CV for ISI initially decreased as force rose, but later increased at high forces (Tanji and Kato 1973). Other studies have observed a relation between absolute discharge rate variability (SD) and mean discharge rate when the data for all motor units were combined (Mori 1973; Person and Kudina 1972). When discharge rate variability from these studies was expressed as the CV for ISI, there was an approximate linear decrease in this CV with an increase in mean discharge rate. This trend is similar to that observed in the current study for the *combined* motor unit data, which contrasts with the exponential decrease in the CV for ISI with an increase in index finger force for *individual* motor units.

The addition of an exponential decrease in the CV for ISI to the motor unit model was the critical change that matched the force fluctuations observed experimentally during steady contractions with those simulated with a model of motor unit recruitment and rate coding. This observation is consistent with prior experimental (Kornatz et al. 2002; Laidlaw et al. 2000) and simulation (Enoka et al. 2003) results that have identified discharge rate variability as a key contributor to force fluctuations, especially at low forces. In the model, the exponential function (*Eq. 1*) caused the CV for ISI to decrease from 30 to 10% as force increased by 10% MVC above the recruitment threshold for each motor unit. The force-dependent decline in relative discharge rate variability contrasts with prior modeling work in which the CV for discharge rate was assumed to remain constant (Fuglevand et al. 1993; Hamilton et al. 2004; Taylor et al. 2003; Yao et al. 2000).

The result of adding this relation to the model was that most motor units exhibited high relative discharge rate variability at low force levels (i.e., 2–5% MVC), which enhanced the force fluctuations. Because the number of motor units recruited at each force level also decreased exponentially with an increase in muscle force (Fuglevand et al. 1993), there were fewer motor units recruited at intermediate forces (i.e., 15–50% MVC), and hence most of the active motor units had low relative discharge rate variability and the force fluctuations were depressed. At high forces (i.e., 70–95% MVC), all motor units were recruited and thus both discharge rate variability and force fluctuations were relatively low.

Minimal and peak discharge rates

The results from this study indicated that the minimal and peak discharge rates were significantly greater for high-threshold motor units compared with low-threshold units. This observation is similar to that reported in several experimental studies on hand and elbow muscles (Bigland and Lippold 1954; Gydikov and Kosarov 1974; Kanosue et al. 1979; Kosarov and Gydikov 1976) and the results obtained in some simulation studies. For example, Heckman and Binder (1991) showed that high-threshold motor units require greater discharge rates to produce a fused tetanus for muscle fibers with fast contraction

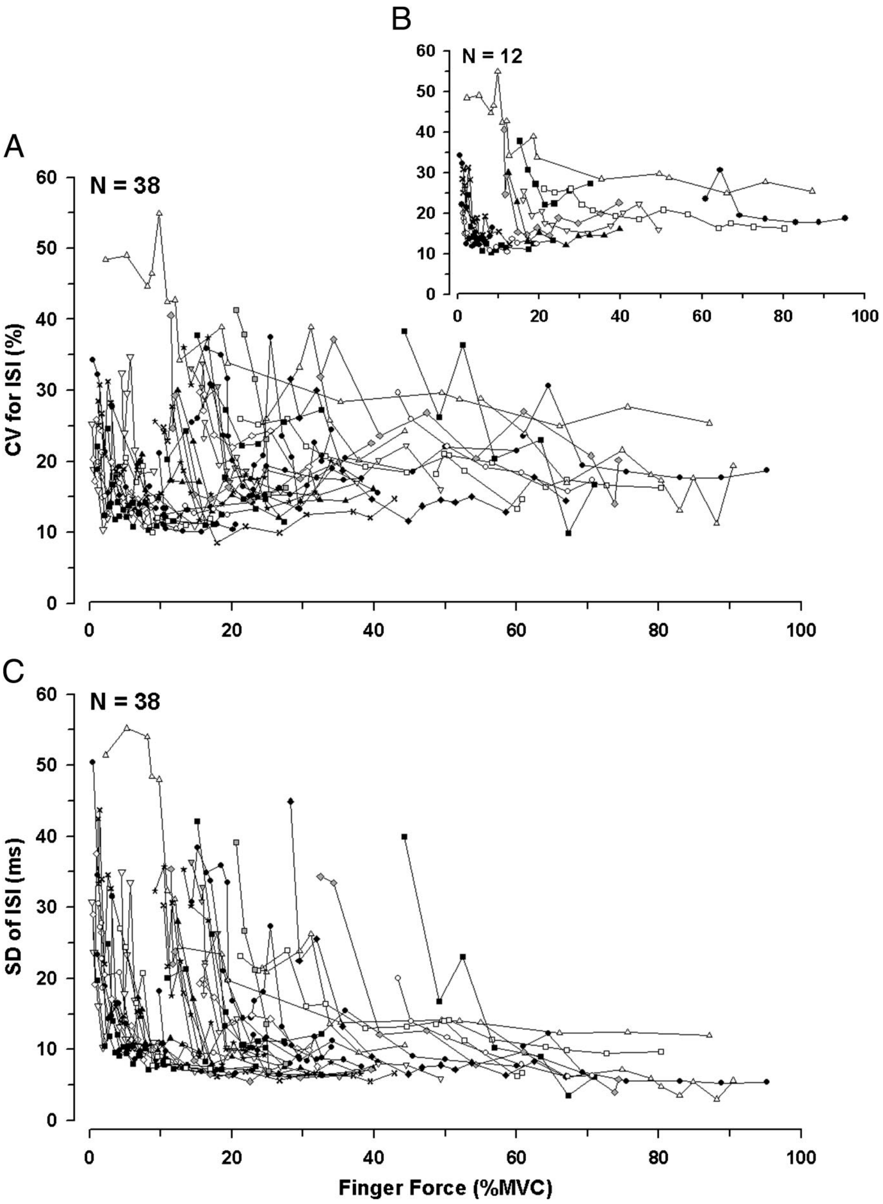

FIG. 5. *A*: reductions in the CV for ISIs during the discrete task for 38 motor units with increases in the abduction force exerted by the index finger. Each symbol represents a different motor unit, and each data point corresponds to mean of the CV for ISIs during an isometric contraction. *B*: CV for ISIs for 12 motor units that exhibited a clear plateau in peak discharge rate (Fig. 2). *C*: SD of ISIs as a function of force for all 38 motor units.

speeds, similar to a previous theoretical argument (Hatze and Buys 1977; Kernell 1992). Furthermore, Taylor and Enoka (2004) found that high-threshold motor neurons reach greater discharge rates (23 pps) compared with low-threshold neurons (17 pps), presumably due to differences in axon diameter and membrane resistance.

This finding, that peak discharge rate is greater for high-threshold motor units, however, contradicts the results obtained in other studies on human hand muscles. Some studies have found a negative correlation between peak discharge rate and recruitment threshold during ramp isometric contractions (De Luca et al. 1982; Duchateau and Hainaut 1990). One explanation for the difference might be that a single ramp contraction in which the intensity increased gradually may have evoked history-dependent effects that are graded across the motor unit pool, such as those that involve persistent inward currents (Gorassini et al. 2002; Heckman et al. 2003). However, Tanji and Kato (1973) also performed a similar protocol with the abductor digiti minimi muscle to that used in this study and observed that two low-threshold motor units achieved greater peak discharge rates compared with the three high-threshold units. Thus the distribution of maximal discharge rates across the motor unit population remains unresolved. Nonetheless, maximal discharge rate seems to have only a minor influence on the variation in force fluctuations across the operating range of a muscle.

Other discharge characteristics

The upper limit of motor unit recruitment observed in this study for first dorsal interosseus was 60% MVC force, which is intermediate between the upper limit of 50% MVC force (De Luca et al. 1982; Kukulka and Clamann 1981) and 75% MVC force (Christou et al. 2004; Thomas et al. 1986) observed by others. Accordingly, the upper limit of motor unit recruitment was set at 60% MVC in the model, compared with the values of 41 and 50% used in previous studies (Moritz et al. 2004; Taylor et al. 2003; Yao et al. 2000). Nonetheless, this adjust-

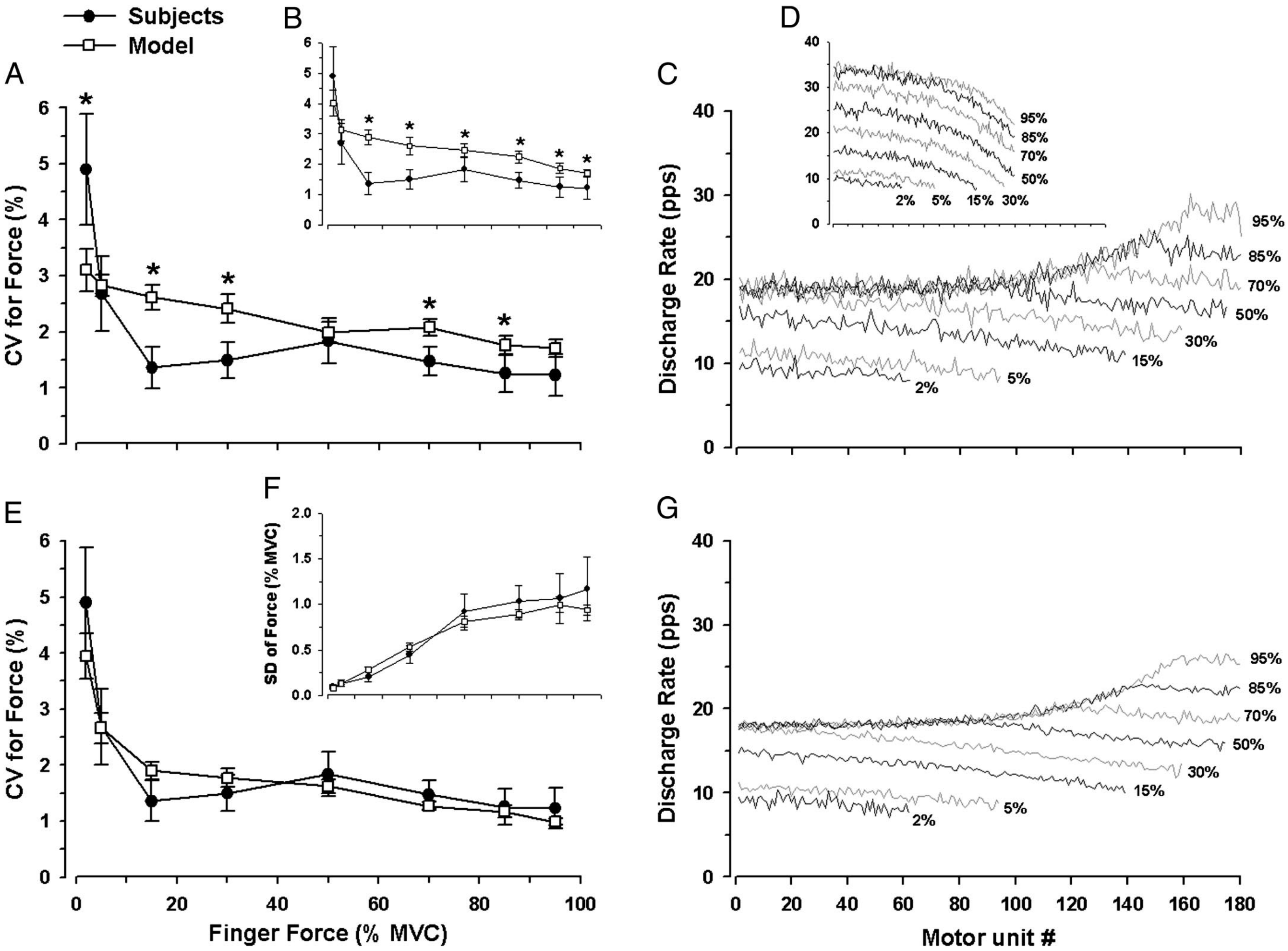

FIG. 6. Associations between experimental and simulated CVs for force across the operating range of the 1st dorsal interosseus muscle. *A*: experimental data were obtained from 20 subjects performing isometric contractions. Model data were generated with the Fuglevand model that was modified by increasing the number of motor units, expanding the upper limit of motor unit recruitment, and adding experimentally observed linear functions for minimal and maximal discharge rates observed. *Significant differences between subject and model data ($P < 0.05$). *B*: comparison of experimental data obtained in this study with simulated data obtained with the original Fuglevand model with 120 motor units all recruited by 41% MVC. *C*: simulated mean discharge rate for each motor unit at 8 target forces (2, 5, 15, 30, 50, 70, 85, and 95% MVC force), showing minimal and maximal discharge rates. *D*: simulated mean discharge rate for each motor unit for the original Fuglevand model, with a minimal discharge rate of 8 pps for all motor units and maximal discharge rates decreasing from 35 to 25 pps across the motor unit pool. *E*: CV for force for subjects and the model with the addition of a decreasing CV for ISI based on experimental observations (Fig. 5). Model and subject CVs for force were not significantly different ($P = 0.220$; $r^2 = 0.91$). *F*: same condition as in *E*, but presented as the SD of force. *G*: simulated mean discharge rate for each motor unit at 8 simulated target forces. CV for ISI decreased from 30 to 10% as force increased. Error bars in *A*, *B*, *E*, and *F* are 95% CIs.

ment of the recruitment range had a negligible effect on the ability of the model to reproduce the experimental force-variability data, which is similar to the findings of Hamilton et al. (2004).

There was no interaction between the slope of the relation for discharge rate and force and recruitment threshold. This result is similar to the findings of Milner-Brown et al. (1973a) for the first dorsal interosseus muscle during ramp increases in force. Several figures in the literature, however, suggest that discharge rate rises more rapidly with increases in force for low-threshold units compared with high-threshold units (Freund et al. 1975; Monster and Chan 1977). The data in this study include a mixture of motor units, equally present at all levels of recruitment threshold, which either increased discharge rate rapidly and reached clear plateaus, or increased discharge rate more gradually over the force range in which they could be discriminated. Thus both the tonic and phasic motor units (Gydikov and Kosarov 1974) were present, although the distinction between these two types of units was less clear in the current data. In addition, some units exhibited the three-phase relation between discharge rate and force that has been observed in tibialis anterior, with an initial steep rise followed by a plateau and ending with another steep rise (Erim et al. 1996).

Notably, the model did not include any form of correlated activity between the motor unit discharges; there was no motor unit synchronization and no common modulation of discharge rate. Consequently, the model was able to replicate the variation in force fluctuations as a function of muscle force without the need for correlated discharges by the active motor units.

This result is consistent with the experimental observation that the magnitude of the fluctuations during steady contractions can differ between individuals despite similar levels of motor unit synchronization (Kornatz et al. 2004).

Summary

Experimental measurements indicated that relative discharge rate variability decreased exponentially with an increase in finger force for each motor unit. When this function was implemented in the motor unit model, the ability of the model to predict the experimentally measured force fluctuations was improved significantly. These results underscore the assertion that discharge rate variability is a key determinant of the variation in the force fluctuations during steady contractions across the working range of a muscle.

GRANTS

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