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Brian L. Tracy

University of Colorado at Boulder

Katrina S. Maluf

University of Colorado at Boulder

Jennifer L. Stephenson

University of Colorado

Sandra K. Hunter

Marquette University, sandra.hunter@marquette.edu

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Variability of Motor Unit Discharge and Force Fluctuations Across a Range of Muscle Forces in Older Adults

Brian L. Tracy

Department of Integrative Physiology, University of Colorado, Boulder, Colorado

Katrina S. Maluf

Department of Integrative Physiology, University of Colorado, Boulder, Colorado

Jennifer L. Stephenson

Department of Integrative Physiology, University of Colorado, Boulder, Colorado

Sandra K. Hunter

Department of Integrative Physiology, University of Colorado, Boulder, Colorado

Roger M. Enoka

Department of Integrative Physiology, University of Colorado, Boulder, Colorado

Abstract

Variability of motor unit discharge is a likely contributor to the greater force fluctuations observed in old adults at low muscle forces. We sought to determine whether the variability of motor unit discharge rate underlies the fluctuations in force during steady contractions across a range of forces in young ($n = 11$) and old ($n = 14$) adults. The coefficient of variation (CV) for discharge rate and force were measured during a force-matching task as the first dorsal interosseous muscle performed isometric contractions. The recruitment thresholds of the 78 motor units ranged from 0.04% to 34% of maximal voluntary contraction (MVC) force. The CV for discharge rate ranged from 7.6% to 46.2% and was greater ($P < 0.05$) for old adults ($21.5\% \pm 7.7\%$) than young adults ($17.3\% \pm 8.1\%$). Although the CV for force was similar for young and old subjects ($2.53\% \pm 1.6\%$) across all target forces, it was greater for old adults at the lowest forces. Furthermore, there was a positive relation ($r^2 = 0.20$, $P < 0.001$) between the CV for force and the CV for discharge rate across the range of recruitment thresholds. This relation was significant for old adults ($r^2 = 0.30$, $P < 0.001$), but not for young adults ($r^2 = 0.06$, $P > 0.05$). Thus, the normalized variability (CV) of motor unit discharge was greater in old adults and was related to the amplitude of force fluctuations across a broader range of forces than previously examined. These findings underscore the contribution of variability of motor unit activity to motor output in normal human aging. *Muscle Nerve*, 2005

The adaptations that occur in the nervous system with advancing age result in many impairments in elderly adults, including a reduced ability to exert constant forces and perform steady movements. The decline in steadiness of a single hand muscle in old adults, for example, has been associated with a reduction in performance on a test of manual dexterity.¹² Such associations are consistent with the hypothesis that fluctuations in muscle force during a voluntary contraction influence the precision that can be achieved during goal-directed tasks.^{8,9} The fluctuations in force, at least during brief isometric contractions, are influenced by the variability in motor unit discharge rate. Moritz et al.,¹⁵ for example, found that variation in force fluctuations across the operating range of the first dorsal interosseous muscle (2%–95% of maximal force) was strongly influenced by the coefficient of variation (CV) for discharge rate.

Old adults exhibit greater force fluctuations than young adults at low contraction intensities for some muscle groups, and these fluctuations are associated with increased discharge-rate variability of the active motor units. For example, Laidlaw et al. found that the CV for force was greater for old (9.6%) than young adults (4.1%) during weak isometric contractions ($\leq 10\%$ of maximal force) and that this difference was associated with a greater CV for motor unit discharge for the old adults (31% vs. 7%).¹³ Additionally, the CV for discharge rate was positively related to the CV for force ($r^2 = 0.50$), which indicated that the subjects with the greatest variability in motor unit discharge exhibited the greatest force fluctuations. Subsequent studies found that the variability in the simulated force was directly related to the variability of motor unit discharge in a computational model,¹⁸ and that a training-induced reduction in fluctuations in motor unit discharge rate also decreased the fluctuations in the force exerted by the first dorsal interosseous muscle.¹² These findings suggest that variability of motor unit discharge contributes to the amplitude of force fluctuations during steady contractions.

Although age-related differences in the steadiness of contractions performed with the first dorsal interosseous muscle are greatest at low muscle forces, the CV for force has also been observed to be greater for old adults at moderate and high forces.^{2,7,14} The purpose of this study was to assess the relation between the variability in motor unit discharge rate and the fluctuations in force during steady contractions across a range of forces in young and old adults. Some of these data have been presented in abstract form.¹⁶

METHODS

Eleven young adults (22.3 ± 3.5 years; range, 19–30 years; 7 men, 4 women) and 14 old adults (74.9 ± 5.7 years; range, 65–82 years; 8 men, 5 women) were oriented to the procedures and provided informed consent prior to

participating in the study. The young and old subjects were of similar body mass (73.1 ± 16 vs. 75.2 ± 17 kg), height (177 ± 7 vs. 171 ± 14 cm), and body mass index (23.4 ± 3.6 vs. 25.5 ± 3.5 kg/m²). Subjects had no symptoms or signs of neurological disease, were free of medications known to influence the dependent measures, and reported less than 3 h per week of low-to-moderate intensity exercise with no strength training for at least 1 year. All subjects were right handed. The Human Research Committee at the University of Colorado in Boulder approved the procedures.

Each subject participated in one to three experimental sessions that each lasted about 2.5 h. In each session, the recruitment threshold of a motor unit was determined and its discharge rate during constant-force contractions was then recorded. The protocol yielded data for 1–4 motor units in a single session, with a total of 34 motor units from young subjects and 44 motor units from old subjects.

Experimental Arrangement.

The protocol required subjects to perform isometric contractions with the first dorsal interosseous muscle that resulted in an abduction force being exerted by the index finger. Subjects were seated in an adjustable chair, and the left arm was fastened into a customized device on a platform designed to restrain movements of the forearm, wrist, and fingers.¹⁰ The upper arm was vertical and slightly abducted from the trunk with the elbow at a right angle. The forearm was pronated, the thumb was placed behind a rigid stop in an extended position, and the index finger was extended in a neutral position. A padded splint was fastened on the index finger with small straps. The vertical surface of the splint had a shallow indentation (~ 0.5 mm) that was placed over a button load cell (Sensotec Model 13, Columbus, Ohio). The measurement axis of the load cell was aligned with the proximal interphalangeal joint of the index finger. The sensitivity of the load cell differed for the maximal force tasks (0–223 N linear range) and the constant-force tasks (0–9.8 N linear range). The flexion force exerted by the index finger was monitored with a second load cell so that out-of-plane actions produced during contraction of the first dorsal interosseous muscle were minimized. The flexion force did not differ between old and young subjects (1.81% vs. 1.78% MVC force, $P = 0.96$), across recruitment thresholds, or between target forces ($P > 0.05$).

Motor unit action potentials were recorded with a pair of 25- or 50- μ m diameter fine wires inserted into the first dorsal interosseous with a sterile 30-gauge needle. A 4-mm silver–silver chloride surface electrode was placed over the fifth metacarpophalangeal joint and served as the reference electrode. Intramuscular electromyographic (EMG) and force signals were amplified and filtered using Coulbourn V-series bioamplifiers and transducer couplers (Coulbourn Instruments, Allentown, Pennsylvania). Analog-to-digital conversion and computer recording of digital signals were performed using the 1401 plus A/D device and Spike2, version 4 software (Cambridge Electronic Design, Cambridge, United Kingdom). Intramuscular EMG and force were digitized at 20k and 1k samples/s, respectively. Bandpass filter settings for the intramuscular EMG were approximately 0.6–2.4 kHz and were adjusted as necessary during an experiment to optimize the signal-to-noise ratio for a particular motor unit action potential.

Experimental Tasks.

The protocol comprised four tasks: a maximal voluntary contraction (MVC), identification of a motor unit potential, measurement of the recruitment threshold for a motor unit, and the performance of constant-force tasks. For the MVC task, subjects performed a 3-s ramp increase in index finger abduction force during an isometric contraction and then maintained the maximal force for 2–4 s. Unacceptable trials were discarded. Subjects rested for at least 1 min between trials to minimize fatigue. Trials were performed until two maximal force values were within 3% of each other. This was accomplished in three to five trials, which does not produce fatigue that can be detected as a decline in MVC force.

After measurement of MVC force, a pair of fine wire electrodes was inserted into the muscle under antiseptic conditions and connected to the recording equipment. Subjects were instructed to increase the abduction force slowly until a single motor unit was identified using auditory and visual feedback. Electrode position and intramuscular EMG filter settings were adjusted to maximize the amplitude of the individual action potential relative to the background muscle activity. The approximate force at which the motor unit began discharging action potentials regularly was noted.

Subsequently, three recruitment threshold trials were performed to determine the reliability of the onset of motor unit discharge across repeated contractions. The recruitment threshold was determined by having the subject increase the abduction force slowly with visual feedback until the identified motor unit began discharging action potentials regularly. The rate of force increase did not differ across the three trials ($P > 0.05$) and was similar ($P = 0.35$) for the young ($1.93\% \pm 1.8\%$ MVC/s) and old subjects ($2.45\% \pm 2.2\%$ MVC/s). At least 1 min of rest was given between the three trials. Because the first few discharges during a recruitment threshold trial often displayed widely varying interspike intervals (ISIs), the force at which the discharge became regular was determined from visual inspection of the record and this force was identified as the recruitment threshold. Visual inspection also indicated that the following 10 ISIs provided a stable value for the calculation of discharge rate during the ramp task when force was still slowly increasing. Therefore, the discharge rate at recruitment was measured as the average ISI for the next 11 discharges.

A target force was then set at 3% of MVC force above the average recruitment threshold of the motor unit. Subjects received visual feedback in the form of a horizontal line on a 17-in monitor approximately 1 m away. Subjects increased the abduction force to the target line and matched the target as steadily as possible (Fig. 1). The target force was held for 10–25 s for each trial, with longer trials performed at lower forces. To minimize fatigue, two trials were performed with a rest of at least 1 min between trials. If the discharge of the identified motor unit became irregular or ceased, another trial was performed at a slightly higher target force. Subjects received only visual feedback of force during the constant-force task and did not receive auditory feedback of motor unit discharge.

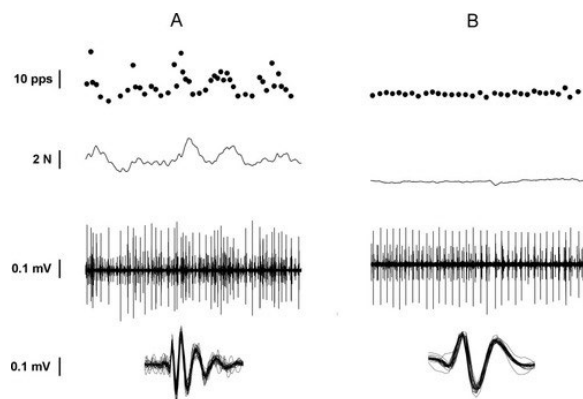


Figure 1 Representative data for two motor units that discharged with high (**A**) and low (**B**) coefficients of variation (CV) for discharge rate. Top trace: instantaneous discharge rate (pulses per second, pps); second trace: index finger abduction force; third trace: intramuscular recording of motor unit potentials; fourth trace: superimposed motor unit potentials. Motor unit (**A**) had a recruitment threshold of 10.3 N, the target force was 11.7 N, the CV for force was 4.3%, and the CV for discharge rate was 37.8%. Motor unit (**B**) had a recruitment threshold of 7.1 N, the target force was 9.7 N, the CV for force was 1.2%, and the CV for discharge rate was 12.8%.

Experimental Measurements.

Measurements were performed offline using Spike2, version 4 (Cambridge Electronic Design, Cambridge, United Kingdom). The peak force (N) measured during the MVC trial was taken as the measurement of maximal force. The fluctuations in index finger force were characterized by the measurement of absolute (SD of force), and relative [CV of force; $CV = (SD \text{ of force} / \text{mean force}) \cdot 100$] force fluctuations during a 10-s segment in the middle of the constant-force task. Motor unit discharge was measured over the same interval. The average of the two trials was calculated for each dependent variable.

The individual discharges of a motor unit were discriminated with an amplitude and shape-recognition algorithm of the Spike2 software, and were confirmed manually on a spike-by-spike basis. The ISIs for the appropriate segment of data were calculated. Because ISIs >250 ms and <20 ms likely do not represent normal variability of motor unit discharge, intervals corresponding to discharge frequencies <4 pps and >50 pps were discarded. This criterion resulted in a negligible and similar removal of ISIs for the young and elderly subjects (0.16% and 0.25% of ISIs, $P = 0.64$). The number of discharges analyzed and the mean, SD, and CV of the ISIs were calculated using a custom Matlab program (The Mathworks, Natick, Massachusetts). The values of the dependent variables from two trials for a particular motor unit were averaged.

Multiple motor units were often detected during the constant-force tasks, especially at higher target forces. Motor units other than that identified as the target motor unit during the measurement of recruitment threshold could often be reliably identified and discriminated. Therefore, the recruitment threshold of these motor units was estimated as the force at which the motor unit began to discharge action potentials regularly during the ramp increase in force immediately preceding the constant-force contractions. The discharge behavior during the constant-force contractions was determined in this manner for 11 of the 75 motor units studied. This strategy resulted in motor unit recordings being obtained at a range of forces above recruitment threshold.

Data Analysis.

Repeated-measures analysis of variance (ANOVA) and intraclass correlation coefficients were used to quantify the reliability of recruitment threshold values across three trials. Univariate ANOVA was used to compare muscle strength, force fluctuations, and motor unit discharge variability between age groups. Linear regression was used to examine relations between motor unit discharge variability and recruitment threshold, target force, and CV for force. When the distributions of motor unit discharge measures deviated from normal, the natural log of the values was calculated and the statistical comparisons were performed on the transformed values. To identify any systematic differences in the relation between discharge rate variability and force fluctuations, motor units were separated into four quartiles based on recruitment threshold (0%–4%, 4.1%–8.8%, 8.9%–19%, and 19.1%–34% MVC force).

RESULTS

The recruitment threshold of the motor units ranged from 0.04% to 34% of MVC force (mean, $11.3\% \pm 10\%$ MVC) for young subjects and from 1.0% to 31% of MVC force (mean, $11.6\% \pm 10\%$ MVC) for old subjects. The average recruitment threshold of the motor units did not differ significantly across the three trials ($9.3\% \pm 7.7\%$, $8.1\% \pm 7.7\%$, and $8.7\% \pm 8.3\%$ MVC) for young and old subjects and the intraclass correlation coefficients between the three trials ranged from 0.89 to 0.91 ($\alpha = 0.96$). The discharge rate at recruitment, calculated as the inverse of the mean ISI, was 10.7 ± 2.8 pps for young subjects and 12.2 ± 3.5 pps for old subjects ($P < 0.05$), which resulted in a value of 11.6 ± 3.3 pps for all subjects combined. The discharge rate at recruitment was slightly greater in motor units with higher recruitment thresholds, as indicated by a weak but significant positive relation between discharge rate at recruitment and recruitment threshold ($r^2 = 0.13$, $P < 0.001$).

MVC force averaged 38.0 ± 11.0 N and was not significantly different between young (40.3 ± 11 N) and old (36.1 ± 11 N) subjects. The range of target forces for the brief constant-force contractions was 2%–41% and 3%–50% of MVC force for the young and old subjects, respectively. Although the mean target force during the constant-force trials was similar for young ($5.25\% \pm 4.0\%$ MVC) and old ($6.38\% \pm 3.8\%$ MVC) subjects, the SD of force was greater ($P < 0.05$) for old (0.16 ± 0.13 N) than young adults (0.12 ± 0.11 N). In contrast, the average CV for force ($2.53\% \pm 1.59\%$) was similar for the young and old adults. When the fluctuations in finger force were compared for target forces in 5% MVC force bins, the SD of force was greater for the old adults for the first three bins (0%–5%, 5.1%–10%, and 10.1%–15% MVC force), whereas the CV for force was greater only for the first bin (0%–5% MVC force). For the first bin, the SD of force was 0.78 ± 0.05 N for the old adults and 0.22 ± 0.06 N for the young adults, and the CV for force was $8.12\% \pm 2.6\%$ and $2.60\% \pm 1.30\%$, respectively.

The average number of action potentials discriminated during the constant-force contractions (148 ± 46) was similar for young and old subjects. The mean discharge rate during the constant-force contractions was also similar for young and old subjects (13.2 ± 2.7 vs. 14.5 ± 2.8 pps). There was a weak but significant positive relation between the mean discharge rate during the constant-force contractions and recruitment threshold ($r^2 = 0.09$, $P < 0.001$; Fig. 2A).

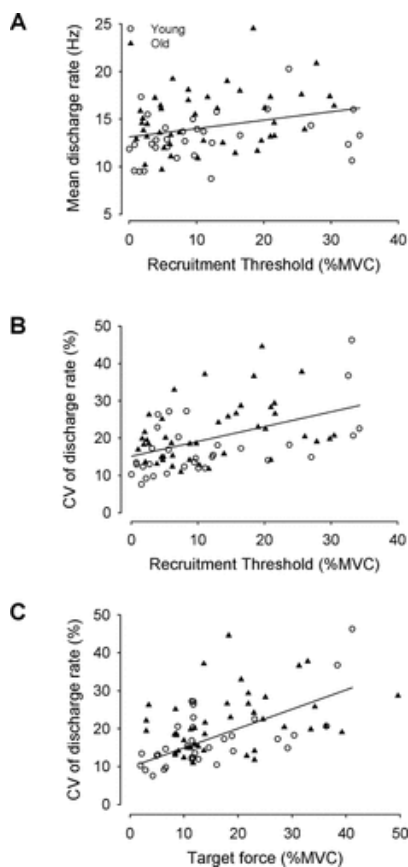


Figure 2 Associations between discharge rate and force during the constant-force contractions. **(A)** Mean discharge rate (pps) and recruitment threshold. **(B)** Coefficient of variation (CV) for interspike interval and recruitment threshold. **(C)** CV for interspike interval and target force.

The CV for discharge rate ranged from 7.6% to 46.2% and was greater ($P < 0.05$) for old ($21.5\% \pm 7.7\%$) than young subjects ($17.3\% \pm 8.1\%$), based on a comparison of the log-transformed values. There was a positive relation between CV for discharge rate and recruitment threshold ($r^2 = 0.22$, $P < 0.001$), which indicated that the relative discharge rate variability was greater for the higher threshold motor units (Fig. 2B). This relation was

similar for young and old subjects. The CV for discharge rate was also positively related with the target force during the constant-force contraction, with no difference between young and old subjects ($r^2 = 0.26$, $P < 0.001$, Fig. 2C).

For all motor units combined, the CV for force during the constant-force contractions was positively related with the CV for discharge rate ($r^2 = 0.20$, $P < 0.001$, Fig. 3A). This relation was evident across a range of recruitment thresholds, and was significant within each recruitment threshold quartile (0%–4% quartile: $r^2 = 0.22$; 4.1%–8.8% quartile: $r^2 = 0.17$; 8.9%–19% quartile: $r^2 = 0.49$; 19.1%–34% quartile: $r^2 = 0.39$; all $P < 0.05$ except for the 4.1%–8.8% quartile with $P = 0.08$, Fig. 3A). The relation between the CV for force and the CV for discharge rate was significant for old subjects ($r^2 = 0.30$, $P < 0.001$, Fig. 3C), but not for young subjects ($r^2 = 0.06$, $P > 0.05$, Fig. 3B).

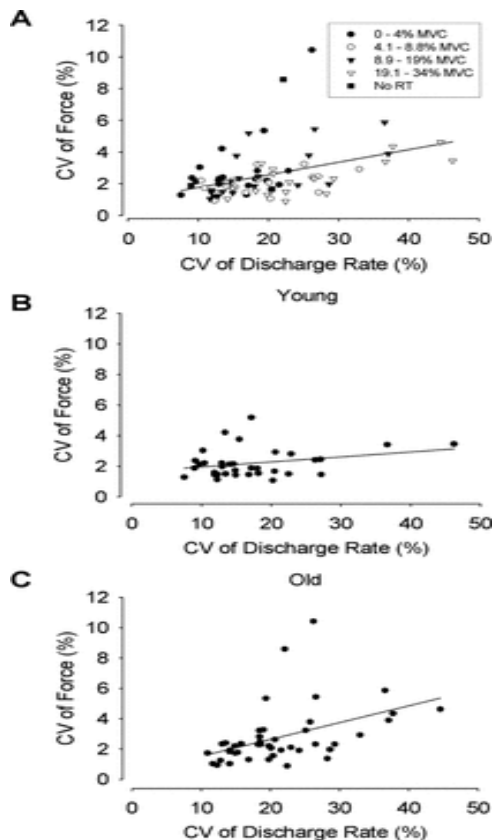


Figure 3 Associations between the coefficients of variation (CV) for force and discharge rate (interspike interval) during the constant-force contractions. **(A)** Data for all subjects as distributed across the recruitment-threshold quartiles (0%–4%, 4.1%–8.8%, 8.9%–19%, and 19.1%–34% MVC quartiles; three motor units included without measurable recruitment thresholds (no RT). **(B)** Young subjects. **(C)** Old subjects.

DISCUSSION

Our main findings were that steady, isometric contractions with the first dorsal interosseous muscle involved greater fluctuations in force for old subjects at low target forces, a greater CV for motor unit discharge for old subjects, and a positive relation between the relative variability in motor unit discharge and the relative force fluctuations for old, but not young subjects.

Force Fluctuations and Discharge Rate Variability.

When the fluctuations in force were categorized into 5% MVC target-force bins for comparison with previous studies, the CV for force was greater for the old than young adults only for the 0%–5% MVC bin and not for

higher target forces. Similar to previous comparisons of force fluctuations between young and old adults, the difference in CV for force was greatest at low target forces.^{2, 7, 10, 13} However, these prior studies all found a statistically greater CV for force for the old adults at forces that extended up to 75% MVC force. The difference in normalized force fluctuations has been observed whether^{7, 13} or not^{2, 10, 14} there was a difference in MVC force between young and old adults. In the current study, the observation that the SD of force ($P < 0.05$), but not the CV for force ($P = 0.16$), was greater for the old adults across all target forces is probably due to the trend toward statistical significance ($P = 0.09$) for the difference in target force between the young and old subjects.

The main finding of this study was the existence of a statistically significant association between the relative (CV) force fluctuations and discharge rate variability for old but not young adults. Although this association has been reported previously,¹³ the motor unit sample was limited to those with recruitment thresholds less than 8% of maximum. The present data extend these findings in old adults to motor units with recruitment thresholds up to 34% of MVC force, which likely includes about 85% of the motor units in this muscle.⁵ These results are consistent with the experimental observations that both the force fluctuations and the CV for discharge rate decreased after a training intervention,¹² and that the CV for discharge rate decreased after a practice session that improved the ability to track sinusoidal variations in force.¹¹ The results also support the findings of a simulation study in which increases in the CV for discharge rate caused increases in the fluctuations in force.¹⁷ For the elderly adults, the functional impact of these adaptations can be observed when attempts are made to exert steady forces or to move precisely during daily activities.^{8, 9}

Collectively, these results raise the question of why the association between the relative fluctuations in discharge rate and force are significant for old adults, but not young adults. One possibility is a difference in the target force relative to the recruitment threshold for the respective samples of motor units. Because discharge rate increases as the force increases above the recruitment threshold of a motor unit, the fluctuations in motor unit force will decline and contribute less to the fluctuations in net force.^{1, 3, 6} Consequently, the fluctuations in motor unit forces will be greater when there is less of a difference between the target force and the recruitment threshold of the motor units. Although the target force was often adjusted to optimize the motor unit recordings, the difference between the target force and recruitment threshold was similar ($P > 0.05$) for the young adults ($1.5\% \pm 2.1\%$ MVC force) and the old adults ($2.2\% \pm 1.9\%$ MVC force) and could not have contributed to the difference in the association for the two groups of subjects.

Strength of the Association.

The results of the current study demonstrate that the relative variability in discharge rate can influence the force fluctuations during steady isometric contractions, but that other factors also contribute to the variation in force. In an attempt to quantify the influence of discharge rate variability, Moritz et al.¹⁵ compared experimental measurements and computer simulations of motor unit discharge and index finger force across the operating range of the first dorsal interosseous muscle. The CV for force was measured at eight target forces and the relation declined exponentially, as reported previously.^{2, 7} There was also a strong exponential relation ($r^2 = 0.72 \pm 0.07$) between the CV for interspike interval (CV_{ISI}) and force for each motor unit that was characterized for the population by the relation:

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

(1)

where $\Delta Force$ denoted the difference between the target force and recruitment threshold of the motor unit. When this relation was added to a computational model of motor unit recruitment and rate coding,⁶ the variation in simulated force fluctuations across the operating range of the muscle (2% to 95% MVC force) was similar to the profile measured experimentally.

In contrast, the results of the current study indicated that the CV for discharge rate did not explain a significant proportion of the variance in force fluctuations for young adults, and explained only 30% of the variance in force fluctuations for old adults. A key difference between the two protocols was the concurrent measurement of force fluctuations and discharge rate variability in the present study, compared with their measurement in different sessions by Moritz et al.¹⁵ Accordingly, the scattergrams for the current study (Fig. 3B, C) denote the relative variability in discharge rate for single motor units as a function of the fluctuations in force due to the activity of many motor units. The data obtained by Moritz et al.¹⁵ indicate the similarity of the simulated and measured force fluctuations when the simulated force fluctuations included the experimentally determined function (eq. 1) for the CV for discharge rate for all active motor units. Thus, our data demonstrate that measurement of the relative discharge rate variability can predict, within some confidence limits, the relative force fluctuations during brief isometric contractions for old but not young adults.

Because Moritz et al.¹⁵ found that discharge rate variability has a strong influence on the amplitude of the force fluctuations, our current results suggest the measured CV for discharge rate for a single motor unit was weakly related to the relative variability of the other active motor units. Equation (1) indicates that, on average, the CV for motor unit discharge is approximately 30% at recruitment and declines to approximately 10% once target force exceeds motor unit recruitment threshold by 10%. Given that the target force was only ~2% above recruitment threshold in this study, the CV for discharge rate was measured when it was declining rapidly and was likely not indicative of the population level of discharge rate variability.

Studies on the association between motor unit discharge and force fluctuations commonly assume that the force contributed by the most recently recruited motor unit has the greatest influence on force fluctuations.^{3,4,7} Because the most recently recruited motor unit is the largest of the active motor units, according to the size principle, it should contribute the largest force and have the greatest influence on force fluctuations. However, Fuglevand et al.⁶ demonstrated that the relative force contributed by a motor unit to the net muscle force actually declines as recruitment proceeds through the population. Accordingly, Keen et al.¹⁰ found that a training-induced reduction in force fluctuations during brief, isometric contractions with the first dorsal interosseous muscle was not related to the distribution of low-threshold motor unit forces in the muscle. The results of the current study, combined with those of Moritz et al.,¹⁵ underscore that variability in the discharge characteristics of the motor unit population is a better predictor of force fluctuations than variability in the discharge of randomly selected single motor units. Furthermore, our study suggests that variability in the discharge rate of single motor units at forces slightly above recruitment threshold has a greater influence on the relative force fluctuations for old than young adults. The significant change in the discharge rate variability of individual motor units as muscle force increases should thus be accounted for in modeling studies of motor unit discharge and force fluctuations.

In conclusion, the data obtained in this study confirm previous observations that old adults exhibit greater force fluctuations than young adults during weak isometric contractions with the first dorsal interosseous muscle. The relative variability of motor unit discharge was greater in old adults and was related to the amplitude of the fluctuations in force across a range of muscle forces that likely involved most of the motor units in the muscle. Variability in the discharge rate of single motor units at forces slightly above recruitment threshold was not related to the amplitude of the fluctuations in whole muscle force exhibited by young adults.

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Abbreviations:

ANOVA, analysis of variance; CV, coefficient of variation; EMG, electromyogram; ISI, interspike interval; MVC, maximal voluntary contraction

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