ABSTRACT: The purpose of this study was to compare the steadiness and discharge rate of motor units during submaximal contractions performed by young and old adults. Subjects performed isometric and slow shortening and lengthening contractions with the first dorsal interosseous muscle. The steadiness of the isometric and slow anisometric contractions was less for the old subjects compared with young subjects, especially at the lower target forces and with the lightest loads. Furthermore, the steadiness of the lengthening contractions was less compared with the shortening contractions for the old subjects. Although the mean discharge rates of motor units were not different for the two groups of subjects, the variability of the discharge rates was greater for the old subjects during the isometric and anisometric contractions. We conclude that a more variable discharge by single motor units probably contributes to the reduced ability of old adults to perform steady muscle contractions.


STEADINESS IS REDUCED AND MOTOR UNIT DISCHARGE IS MORE VARIABLE IN OLD ADULTS

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When an individual performs a steady contraction with the first dorsal interosseous muscle, the abduction force exerted by the index finger is not constant, but rather it fluctuates about an average value. For isometric contractions, the standard deviation of the fluctuations for both young and old adults increases as a function of the average force exerted by the finger.15,19 When differences in muscle strength are taken into account, however, the normalized force fluctuations are greater for the old adults, especially at the lowest forces.15

Our initial explanation for the reduced steadiness exhibited by the old adults during isometric contractions was based on differences in motor unit size.1 Because motor units tend to be recruited in order of ascending size and initial discharge rates are low, Christakos5 was able to demonstrate with computer simulations that the fluctuations in the force during an isometric contraction are due to the unfused tetani of the most recently recruited motor units. Consequently, differences in motor unit forces among individuals, such as those due to the enlargement of motor unit territories with aging,25,33 should be associated with differences in the magnitude of force fluctuations. Consistent with this explanation, Galganski et al.15 found that old adults had both greater normalized force fluctuations and greater peak-to-peak forces for low-threshold motor units when discharging at minimum rates.

When old adults participated in a strength-training program, however, we found that the magnitude of the normalized force fluctuations decreased without a change in the distribution of average peak-to-peak forces for low-threshold motor units.19 This suggests that the enhanced force fluctuations exhibited by old adults may be attributable to more than the unfused contractions of the most recently recruited motor units. For example, the force fluctuations may include the effects of alternating activity between the agonist and antagonist muscles, which occurs at about 8–10 Hz in slow finger movements.40,41 Furthermore, it has been proposed that the steadiness of a contraction is maximized when the discharge of motor units is regular (low variability) but not synchronized.37

Abbreviations: AEMG, average electromyogram; CV, coefficient of variation; EMG, electromyogram; LVDT, linear variable displacement transducer; MVC, maximum voluntary contractions

Key words: aging; finger movement; first dorsal interosseous; motor unit

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As an alternative test of the association between motor unit force and steadiness, we measured steadiness in tasks that involved different motor unit behaviors. The purpose of the study was to compare the steadiness and discharge rate of motor units during isometric and anisometric contractions performed with the first dorsal interosseous muscle by young and old adults. We anticipated that these comparisons would enable us to determine the feature of the motor output that is most responsible for differences in steadiness among individuals. Because the gradation of force in the first dorsal interosseous muscle relies more on modulation of the discharge rate during anisometric contractions, we expected to find that the discharge rate variability would be greater and performance would be less steady for the anisometric contractions compared with the isometric contractions. Furthermore, we expected to find an age-related association between the variability of motor unit discharge and the steadiness of the performance. A preliminary account of our findings has been published.

METHODS

Experiments were performed on the left hand (non-dominant) of eight young (four women and four men; mean age ± SEM, 26.6 ± 0.57 years; range, 24–27 years) and 14 old (eight women and six men; mean age ± SEM, 73.4 ± 1.63 years; range, 64–83 years) human subjects with no known neuromuscular disorders and their vision corrected to normal levels. In order to gain a representative sample of motor unit activity from individuals, each subject participated in four experimental sessions. The Institutional Review Board of The Cleveland Clinic Foundation approved all procedures, and the subjects gave their informed consent prior to participation in the study.

Experimental Setup. The experiments were conducted with each subject seated and facing an oscilloscope, which was positioned 1.2 m away, at the level of the subject’s eyes. The index finger was placed in an individualized polyvinyl silicone mold and strapped inside an L-shaped delryn splint. The splint was placed along the lateral and ventral surfaces of the index finger to keep the interphalangeal joints extended. The left arm was abducted so that the elbow joint was positioned directly below the shoulder and flexed to a right angle, with the hand and forearm prone and resting on a manipulandum. The forearm and hand were immobilized in the manipulandum by several restraints: (1) an L-shaped splint with two straps over the forearm; (2) an L-shaped splint with two straps over the forearm; (3) a brace placed against the lateral aspect of the hand, eliminating ulnar deviation; (4) a brace for the thumb that maintained an angle between the first and second metacarpals at ~90°; (5) a strap over the third to fifth fingers; and (6) a brace that eliminated flexion at the metacarpophalangeal joint of the index finger.

Mechanical Recording. Isometric Contractions. With the hand positioned in the manipulandum so that the index finger was abducted 5° from the neutral position, a force transducer (Sensotec model no. 13, Columbus, Ohio) attached to the delryn splint detected the abduction force at the proximal interphalangeal joint. The sensitivity of the force transducer used during the high-force tasks was 0.053 V/N (linear range, 0–220 N), whereas more sensitive force transducers (0.54 V/N, linear range 0–22 N; 1.01 V/N, linear range 0–9.81 N) were used for the low-force tasks.

Anisometric Contractions. A low-friction, linear variable differential transducer (LVDT; Novotechnik, Stuttgart, Germany) was used to detect the abduction displacement of the index finger about the first metacarpophalangeal joint. The LVDT was mounted on an extended delryn platform and positioned perpendicular to the index finger when abducted 5°. This configuration minimized the error in the linear recording of angular motion. The LVDT was attached to the delryn splint with a low-friction ball-and-socket joint, allowing for free movement of the index finger through its range of motion. The LVDT was calibrated for each subject and session over a 10° range of motion.

Electrical Recording. The electromyogram (EMG) of the left first dorsal interosseous muscle was recorded with bipolar surface electrodes (4 mm in diameter; silver–silver chloride) that were positioned ~8 mm center-to-center apart on the skin overlying the midbelly of the muscle. A common electrode (4 mm in diameter; silver–silver chloride) was placed over a bony aspect on the dorsal surface of the hand. The surface EMG signals were amplified (1000–10,000 times), band-pass filtered (20–800 Hz), and displayed on an oscilloscope.

Motor unit activity was recorded with two bipolar intramuscular electrodes inserted into the first dorsal interosseous muscle (Fig. 1). One of the electrodes consisted of three Formvar-insulated stainless steel wires (two 25-µm and one 50-µm diameter; California Fine Wire, Grover Beach, California). The
other electrode consisted of two Formvar-insulated, stainless steel wires (one 25 µm and one 50 µm in diameter), and a single enamel-insulated, 10-µm diameter stainless steel wire (H.P. Reid, Palm Coast, Florida). For both electrodes, the three wires were glued together with medical-grade cyanoacrylate at the recording end and coiled around a 0.13-mm diameter steel mandrel for ~3-mm with a custom-coiling apparatus. This assembly was then threaded through a disposable 27-gauge needle that was inserted into the first dorsal interosseous muscle and then removed, leaving the wire electrode in the muscle. The location of the electrode could be altered by fine manual adjustments, and recordings were made with the pair of wires that optimized the detection of the action potentials for a single motor unit. The signals from these electrodes were amplified (1000–10,000 times), band-pass filtered (0.3–10 kHz), and displayed on an oscilloscope. Motor units were identified on-line by the shape of the extracellular action potential detected by the intramuscular electrodes using an amplitude window discriminator (DIS-1; BAK Electronics, Inc., Rockville, Maryland).

**Experimental Procedures.** Each of the 22 subjects was asked to participate in five tasks in each experiment: (1) assessment of isometric strength with maximum voluntary contractions (MVCs), (2) char-
acterization of the state of the neuromuscular system with evoked responses (twitches and M waves), (3) measurement of the recruitment threshold of identified motor units, (4) performance of the isometric constant-force task, and (5) execution of the anisometric constant-load task. The isometric tasks were performed with the index finger abducted to 5° from the neutral position. The recruitment-threshold, constant-force, and constant-load tasks were repeated as a group whenever different motor units could be reliably identified and tested.

**MVC.** The MVC task involved a gradual increase in the abduction force exerted by the index finger from baseline to maximum in 3–4 s and then sustained at maximum for 1–2 s. Subjects monitored the index finger force on an oscilloscope. The timing of the task was based on a verbal count given at 1-s intervals, with vigorous encouragement from the investigators when the force trace began to plateau. After several practice trials, subjects performed two MVCs. Subsequent trials were performed if the difference in peak force between the first two MVCs exceeded 5%. The trial with the highest peak force was chosen for analysis. Subjects rested for 60–90 s between consecutive trials.

**Evoked Responses.** The M waves and twitch forces were elicited in the first dorsal interosseous muscle by percutaneous stimulation of the ulnar nerve at the wrist. Three responses were evoked in a relaxed muscle by supramaximal electrical stimuli (0.1 ms in duration) that were provided by a Grass S-8800 stimulator (Grass Instrument Co., Quincy, Massachusetts). The shocks were delivered through a bipolar electrode that was placed on the ventromedial aspect of the forearm, 3–5 cm proximal to the wrist joint. The cathode was positioned at the location that maximized the peak-to-peak amplitude of the M wave. It was held firmly in place, and the stimulus intensity was increased to a supramaximal level. The responses were elicited once every 3 s. Twitch force was monitored during this process to ensure that the measurements were not affected by previous activation of the muscle.

**Recruitment Threshold.** This task was used to determine the isometric abduction force exerted by the index finger when a single motor unit discharged action potentials at a relatively constant, low rate. The subject gradually increased the abduction force to a level where a single recruited motor unit could be identified by its shape and amplitude. This procedure was repeated three times for each motor unit, with the average of the three trials used for the subsequent tasks. Recruitment thresholds were categorized into bins relative to the MVC force (i.e., 0–1%, 2.5–3.5%, 5–6%, and 7.5–8.5%). Subsequently, the target force or load used during the constant-force and constant-load tasks was set at 2.5% MVC above the recruitment threshold in increments of 2.5% from 2.5 to 10% MVC force. For example, if an identified motor unit had a recruitment threshold of 3% MVC force, the target force and load were set at 5% MVC for the constant-force and constant-load contractions, respectively. Only motor units with recruitment thresholds within the specified ranges were included in the analysis. The use of low forces was necessary to ensure an adequate yield with our discrimination procedures.

The distributions of recruitment thresholds for the motor units recorded relative to the target forces and loads are shown in Figure 2. The target force exceeded the recruitment threshold by a mean (±SEM) of 2.50 ± 0.01% MVC force for the young subjects and by 2.55 ± 0.01% MVC force for the old subjects. These values were not statistically different for the two groups of subjects.

**Constant-Force Task.** The subject was instructed to gradually increase the isometric abduction force to the target force displayed on the oscilloscope and to hold the force steady at the target force for 30 s (Fig. 1). The sensitivity of the force display was set relative to the target force level so that the baseline to target force level was 3–4 vertical divisions on the oscilloscope. The subject performed one trial for each identified motor unit.

**Constant-Load Task.** A weight that matched the target force of the constant-force task was attached to a line connected to the splint at the proximal interphalangeal joint, providing a load in the adduction

![FIGURE 2. The target force at which individual motor units were recorded is plotted relative to the recruitment threshold. For all loads, there were no age-related differences in the relationship between the two variables. Across both age groups, the target force was 2.52 ± 0.003% above the recruitment threshold, and the linear regression was significant (target force = 2.48 + [1.03 \cdot recruitment threshold], r = 0.98; P < 0.0001).](image_url)
direction. For the first dorsal interosseous muscle, the MVC force is generally ~3 times greater than the maximum load lifted in old adults and ~2 times greater in young adults.

Three to five trials with each load were performed with the index finger moving through a 10° range of motion from the neutral position. The subjects raised and lowered the weight during 6 s of abduction and 6 s of adduction, respectively (Fig. 1). A triangular template was displayed on the oscilloscope and the subjects were given practice trials to become familiar with the timing and amplitude of the movement. The subjects were instructed to match the desired finger-displacement template as closely as possible.

**Data Analysis.** All data collected during the experiments, excluding the single motor unit records, were recorded and stored in digital format (Sony PC 116 DAT recorder; Sony Magnescale, Inc., Montvale, New Jersey, band-width DC to 5 kHz) and analyzed off-line using the Spike2 data analysis system (Cambridge Electronic Design Ltd., Cambridge, UK) with custom-designed software. The force and position data were sampled at 200 Hz, whereas the surface EMG data were sampled at 2 kHz. Records of motor unit action potentials were sampled on-line at 20 kHz with the use of a microcomputer and an A/D processor (1401plus, Cambridge Electronic Design Ltd.; band-width DC to 30 kHz).

Motor unit discrimination was accomplished off-line with the use of a computer-based spike-sorting algorithm (Spike2; Cambridge Electronic Design Ltd., Cambridge, UK). As we have done previously, we used wave-form shape and amplitude to distinguish the action potentials of single motor units.

All discriminated motor unit records were then reviewed on a spike-by-spike basis to ensure that only the action potentials of the identified motor units were included in the analysis. The discriminated records were analyzed with custom-designed software. First, instantaneous discharge rate records were created for each motor unit (Fig. 1) and the mean discharge rate was determined. Then, least-squares regression was used to determine whether there were any average increases or decreases in the discharge rate during the epoch of interest. The slope of the regression line was subtracted from the data to remove any trend. The standard deviation of the discharge rate was calculated from the detrended data. This procedure resulted in a more conservative measure of variability for all motor unit records, because the changes in discharge rate were smaller when measured perpendicular to the regression line. To normalize the variability of the motor unit discharge rate, the standard deviation was divided by the mean discharge rate and expressed as the coefficient of variation.

**Dependent Variables.** The dependent variables for the MVC task were peak force and the average of the full-wave rectified EMG (AEMG) for a 0.5-s window centered at the peak force. For the evoked responses, the dependent variables were peak twitch force, time to peak twitch force (contraction time), and one-half relaxation time. The AEMG for the MVC was normalized to the maximum M-wave amplitude to allow for comparisons between subjects and across sessions. The EMG amplitudes from the other tasks were normalized to the AEMG for the MVC because the intraclass correlations were higher compared with normalizing to the M-wave amplitude.

The dependent variables for the constant-force task were: (1) standard deviation of the force fluctuations within a 20-s window, (2) coefficient of variation (standard deviation/mean force • 100) of the force fluctuations about the actual mean force, (3) AEMG in a 2-s window when the force was relatively constant, and (4) motor unit activity within the 20-s window. For these analyses, trials with similar target forces (2.5%, 5%, 7.5%, and 10% MVC) were averaged within and across sessions for each subject.

For the constant-load task, the average slope of the position-time record during both the lifting and lowering phases were subtracted from the data, and steadiness was expressed as the variation in position. Least-squares regression was used to determine the average velocity so that the slope of the regression line could be subtracted from the data to remove the trend (average velocity) from the position data. The detrending procedure resulted in a more conservative measure of fluctuations in position. The measurements for this task included: (1) peak abduction position, (2) average movement velocity and standard deviation of the detrended position data for the entire lifting (abduction) and lowering (adduction) phases (~6 s each) and for the middle 4 s of each phase, and (3) motor unit activity during the lifting and lowering phases of the task. Most of the analysis focused on the middle 4 s of each phase. Additionally, separate analyses were performed on the steadiest performance (smallest standard deviation) of each phase, for each subject and load condition.

**Statistical Analysis.** A two-factor analysis of variance (ANOVA) with a repeated-measures design (one factor between and one within) was used to compare the dependent variables for the MVC and evoked responses between groups (young versus old), across sessions, and the group-by-session inter-
action. A two-factor ANOVA (one factor between and one within) was used to compare the constant-force and constant-load dependent variables between groups, across forces/loads, and the group-by-force/load interaction. A three-factor ANOVA with a repeated-measures design (one factor between and two within) was applied to the constant-load data to compare the dependent variables between groups, across sessions and contraction type, and the interactions. An alpha level of 0.05 was chosen for all initial statistical comparisons, with multiple comparisons performed when necessary to determine between-group and between-contraction-type differences. For the multiple comparisons, the significance levels were adjusted with the Bonferroni/Dunn correction. Unless stated otherwise, all results are reported as mean ± SEM.

RESULTS

The main finding of the present study was that old adults had a reduced ability to perform steady isometric and anisometric muscle contractions, which was associated with greater variability of motor unit discharge. Examples are shown in Figure 1 from trials where a young and an old subject performed a constant-force isometric contraction and made slow, steady movements with the index finger. These records indicate that the fluctuations in force and position and the variability of motor unit discharge for these tasks were greater for the old subject, especially during the lengthening contraction.

Age-Related Differences in MVC Force and Evoked Responses. There were no age-related differences in the reliability of the MVC and evoked responses across sessions. The intraclass correlation coefficients for MVC force and normalized AEMG across sessions for all subjects were 0.95 and 0.82, respectively. This meant that only 5% and 18% of the variance in these variables was due to within-subject variance across the four sessions and not due to differences between the performance of subjects. For the evoked responses, the intraclass correlation coefficients were 0.82, 0.78, and 0.70 for twitch force, contraction time, and one-half relaxation time, respectively.

The MVC force of the young subjects was 45% greater than for the old subjects (Table 1). This difference was accounted for by a significantly greater MVC force exerted by the young women compared with old women and a marginal difference between the men. A gender comparison indicated that the men were stronger than the women. However, there were no age-related or gender differences in the absolute or normalized AEMG (% M-wave amplitude) or the evoked responses.

Age-Related Differences in Isometric Steadiness. The old subjects had greater difficulty performing steady submaximal isometric contractions. Although the actual forces were greater for the young subjects at all target levels (Fig. 3A), the absolute magnitude of the force fluctuations (standard deviation) was not significantly different at any of the target forces (Fig. 3B). In contrast, the normalized force fluctuations (coefficient of variation) were greater for the old subjects at all target forces (Fig. 3C), with the greatest differences occurring at the lower forces. Additionally, although there was no effect of target force on the normalized fluctuations for the young subjects, the coefficient of variation for the old group was greater at the 2.5% force compared with the 7.5% and 10% forces.

The normalized AEMG for first dorsal interosseous increased linearly with target force for the old subjects but not the young subjects (Table 2). Furthermore, the normalized AEMG was greater for the old subjects compared with the young subjects at all target forces.

Before comparing the discharge rate of motor units across conditions and groups, the linear change in discharge rate was subtracted from each

| Table 1. Comparison of the MVC and evoked responses for the young and old groups. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                  | MVC force (N)   | MVC AEMG (mV)   | MVC AEMG (% M wave) | Twitch force (N) | Contraction time (ms) | One-half relaxation time (ms) | M wave amplitude (mV) |
| Young            | 32.9 ± 3.97*    | 0.67 ± 0.13     | 6.22 ± 0.78         | 1.97 ± 0.30      | 78.6 ± 5.14          | 66.0 ± 4.03          | 10.5 ± 1.06       |
| Men              | 43.0 ± 4.96†    | 0.84 ± 0.22     | 7.11 ± 1.17         | 2.11 ± 0.41      | 75.0 ± 1.52          | 60.5 ± 3.20          | 11.9 ± 2.05       |
| Women            | 26.8 ± 3.45‡    | 0.57 ± 0.16     | 5.68 ± 1.06         | 1.89 ± 0.50      | 80.8 ± 6.69          | 69.3 ± 3.66          | 9.6 ± 1.19        |
| Old              | 22.7 ± 2.29     | 0.41 ± 0.04     | 5.09 ± 0.44         | 1.71 ± 0.20      | 79.7 ± 2.04          | 76.2 ± 5.31          | 8.49 ± 0.83       |
| Men              | 30.3 ± 3.57†    | 0.44 ± 0.07     | 5.98 ± 0.94         | 2.10 ± 0.33      | 79.7 ± 0.58          | 75.7 ± 4.95          | 7.98 ± 1.74       |
| Women            | 18.1 ± 1.17     | 0.39 ± 0.05     | 4.60 ± 0.41         | 1.50 ± 0.19      | 79.7 ± 3.21          | 76.5 ± 7.27          | 8.77 ± 0.94       |

Data are means ± SEM: *P < 0.05 young versus old; †P < 0.05 young men versus young women, old men versus old women; ‡P < 0.05 young women versus old women.
record. For the isometric task, the average trend was $-0.03 \pm 0.01$ Hz $\cdot$ s$^{-1}$ for the young subjects and $-0.06 \pm 0.02$ Hz $\cdot$ s$^{-1}$ for the old subjects. These trends were not different from zero, and there were no significant differences between the two groups of subjects. Furthermore, there was no effect of age on the average discharge rate across the different target forces (Table 3). However, both the absolute (standard deviation, SD) and normalized (coefficient of variation, CV) variability of the discharge rate during the isometric contractions were significantly greater for the old subjects at the 2.5% and 5% MVC forces (Table 3). There was a significant positive correlation between the CV for force and the CV of motor unit discharge rate at the lowest forces ($r = 0.71, P < 0.0001$). Additionally, at each force there were a greater number of consecutive discharges with an interspike interval less than 20 ms in the old group (Table 3). However, even when these data were removed, the effects of age on motor unit behavior (mean, SD, and CV of the discharge rate) were unchanged.

When two or more motor units with similar recruitment thresholds (range of differences in recruitment threshold: 0 to 1.0% MVC force; mean $\pm$ SEM: 0.226 $\pm$ 0.002%) were identified during a single contraction, their relative behavior was compared (Fig. 4). There was no effect of age on the differences between the average discharge rates (young: $1.63 \pm 0.37$ Hz versus old: $1.53 \pm 0.31$ Hz) or the trends in discharge rate (young: $0.04 \pm 0.01$ Hz $\cdot$ s$^{-1}$ versus old: $0.10 \pm 0.05$ Hz $\cdot$ s$^{-1}$). However, the old subjects had greater differences within pairs of motor units for both the SD and CV. For the standard deviation (Fig. 4C), the pairwise differences were $0.43 \pm 0.10$ Hz for the young subjects compared with $1.85 \pm 0.51$ Hz for the old subjects. Similarly, the differences in the CV (Fig. 4D) were $2.71 \pm 0.61\%$ for the young subjects compared with $13.77 \pm 3.54\%$ for the old subjects. The pairwise differences for the SD and CV of the discharge rates were greater than zero for the old subjects but not for the young subjects.

**Age-Related Differences in Anisometric Steadiness.** The old subjects were less steady when performing the slow shortening and lengthening contractions (Fig. 1). For all analyses, there were no effects of load on the steadiness of the contractions for either age group. When the data from the middle 4 s were averaged across the three trials (Fig. 5A), the SD of the position fluctuations about the average velocity for both shortening and lengthening contractions was greater for the old subjects compared with the young subjects at each load. For the shortening contractions, the average SD across loads was $0.21 \pm 0.01^\circ$ for the young subjects and $0.29 \pm 0.01^\circ$ for the old subjects. For the lengthening contractions, the average SDs were $0.23 \pm 0.02^\circ$ for the young subjects and $0.46 \pm 0.02^\circ$ for the old subjects. Furthermore, the average SDs for the old subjects were greater for the lengthening contractions com-
compared with their shortening contractions, whereas the young subjects had lower and similar average SDs for the two phases.

The analysis of the steadiest performance for the middle 4 s of each phase (Fig. 5B) showed similar differences due to age for all comparisons. The old subjects had greater position fluctuations about the average velocity for both the shortening and lengthening contractions. For the shortening contractions, the average SD across loads was 0.14 ± 0.01° for the young subjects and 0.22 ± 0.01° for the old subjects. For the lengthening contractions, the average standard deviations were 0.17 ± 0.02° for the old subjects and 0.34 ± 0.02° for the old subjects. Furthermore, the SDs of position for the lengthening contractions were greater for the old subjects compared with their shortening contractions, whereas the young subjects had lower and similar SDs for the shortening and lengthening contractions at all loads.

The decline in steadiness with age was not due to differences in the amplitude of the displacement (peak abduction: 10.0 ± 0.12° young versus 10.1 ± 0.10° old) or the average velocity of the movements in either phase (shortening or lengthening contraction) or with any load. However, the between-trial variability (SD) of the average movement velocity with the 2.5% load was greater for the old subjects compared with the young subjects for both the short-

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### Table 2. Surface AEMG* during isometric and anisometric contractions.

<table>
<thead>
<tr>
<th>Force or load</th>
<th>Young</th>
<th>Old</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Isometric</td>
<td>Shorten</td>
</tr>
<tr>
<td>2.5% Force or load</td>
<td>4.99†</td>
<td>10.4†,‡</td>
</tr>
<tr>
<td>(1.06)</td>
<td>(0.64)</td>
<td>(0.28)</td>
</tr>
<tr>
<td>5% Force or load</td>
<td>7.70†</td>
<td>11.3†,‡</td>
</tr>
<tr>
<td>(1.88)</td>
<td>(0.90)</td>
<td>(0.23)</td>
</tr>
<tr>
<td>7.5% Force or load</td>
<td>8.31†</td>
<td>13.8†,‡</td>
</tr>
<tr>
<td>(0.76)</td>
<td>(2.06)</td>
<td>(1.56)</td>
</tr>
<tr>
<td>10% Force or load</td>
<td>9.20†</td>
<td>17.7†,‡</td>
</tr>
<tr>
<td>(1.97)</td>
<td>(2.15)</td>
<td>(2.22)</td>
</tr>
</tbody>
</table>

*Surface AEMG values are normalized to the AEMG for the MVC. Data are means ± SEM: †P < 0.01 young versus old; ‡P < 0.01 shortening versus lengthening.

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### Table 3. Motor unit discharge measures for the isometric contractions and the middle 4 s of each movement phase during anisometric contractions.

<table>
<thead>
<tr>
<th>Force or load</th>
<th>Young</th>
<th>Old</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Isometric</td>
<td>Shorten</td>
</tr>
<tr>
<td>2.5% Force or load</td>
<td>42</td>
<td>54</td>
</tr>
<tr>
<td>Mean (Hz)</td>
<td>11.2</td>
<td>15.7†</td>
</tr>
<tr>
<td>(0.28)</td>
<td>(0.73)</td>
<td>(0.99)</td>
</tr>
<tr>
<td>SD (Hz)</td>
<td>2.00‡</td>
<td>2.69‡</td>
</tr>
<tr>
<td>(0.09)</td>
<td>(0.23)</td>
<td>(0.22)</td>
</tr>
<tr>
<td>CV (%)</td>
<td>18.0‡</td>
<td>17.1‡</td>
</tr>
<tr>
<td>(0.52)</td>
<td>(1.63)</td>
<td>(1.18)</td>
</tr>
<tr>
<td>DD§</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5% Force or load</td>
<td>24</td>
<td>33</td>
</tr>
<tr>
<td>Mean (Hz)</td>
<td>11.6</td>
<td>16.0†</td>
</tr>
<tr>
<td>(0.23)</td>
<td>(0.86)</td>
<td>(1.07)</td>
</tr>
<tr>
<td>SD (Hz)</td>
<td>1.84‡</td>
<td>2.75‡</td>
</tr>
<tr>
<td>(0.02)</td>
<td>(0.22)</td>
<td>(0.15)</td>
</tr>
<tr>
<td>CV (%)</td>
<td>15.9‡</td>
<td>15.4‡</td>
</tr>
<tr>
<td>(0.23)</td>
<td>(0.57)</td>
<td>(1.18)</td>
</tr>
<tr>
<td>DD§</td>
<td>4</td>
<td>0</td>
</tr>
</tbody>
</table>

Data are means ± SEM of the group averages calculated from across trial and session averages for each subject. *Number of motor unit records included in the analysis. †P < 0.01 shortening versus lengthening; ‡P < 0.01 young versus old. §Number of consecutive motor unit action potentials (double discharges) with an interspike interval <20 ms.
ening (0.16 ± 0.02° s−1 young versus 0.26 ± 0.02° s−1 old) and lengthening contractions (0.18 ± 0.04° s−1 young versus 0.30 ± 0.03° s−1 old). For the 5% load, only the between-trial variability for the average movement velocity of the lengthening contractions was greater for the old subjects between trials (0.21 ± 0.04° s−1 young versus 0.39 ± 0.05° s−1 old). There were no differences in the between-trial variability of the average movement velocity for the 7.5% and 10% loads.

The amount of muscle activity was also different for the two groups performing the anisometric tasks (Table 2 and Fig. 6). For both age groups, the normalized AEMG for first dorsal interosseous during the shortening and lengthening contractions increased with the load. However, the old subjects had greater AEMG activity for the shortening and lengthening contractions at all loads. Moreover, the ratio of the AEMG activity for the shortening relative to the lengthening contraction with the 2.5% and 5% loads was greater for the young subjects (2.5%, 2.07 ± 1.77; 5%, 2.45 ± 0.84) compared with the old subjects (2.5%, 1.72 ± 1.06; 5%, 1.57 ± 0.60). On average, the AEMG amplitude for the lengthening contractions was not different from the AEMG for the isometric contractions at similar forces for both groups.

Before comparing the discharge rate of motor units across conditions and groups, the linear change in discharge rate was subtracted from each record. For the shortening contractions, the average trend was 0.67 ± 0.30 Hz s−1 for the young subjects and 1.39 ± 0.50 Hz s−1 for the old subjects. For the lengthening contraction, the average trend was −1.03 ± 0.27 Hz s−1 for the young subjects and −0.39 ± 0.27 Hz s−1 for the old subjects. These trends were not significantly different between the two groups of subjects. There was no effect of age on the average discharge rate between the 2.5% and 5% loads (Table 3 and Fig. 7A). However, for both groups, the average discharge rate was lower for the lengthening compared with the shortening contraction. Contrary to the results for the surface AEMG amplitude, there was no difference due to age in the ratio of the average discharge rate for the shortening to lengthening contractions.

The absolute (SD) and normalized (CV) variability of the motor unit discharge rate was significantly
greater for the old subjects at both the 2.5% and 5% MVC loads (Table 3 and Figs. 7B and 7C). Furthermore, the CV for the old subjects was greater for the lengthening compared with the shortening contractions. In contrast, the young subjects had similar CVs for the shortening and lengthening contractions at both loads. Additionally, when the data for the young and old subjects were pooled, there was a significant positive correlation between the SD of the position fluctuations and the CV of motor unit discharge rate at the lowest loads for both shortening and lengthening contractions (shortening: \( r = 0.57, P < 0.0001 \); lengthening: \( r = 0.58, P < 0.0001 \)).

The discharge of consecutive action potentials within 20 ms (double discharges) was exhibited only by the old subjects. The incidence was highest during the shortening contractions, around the transition from the shortening to the lengthening contraction (Table 3). Similarly, when performing the lengthening contractions, the incidence was highest immediately after the transition from the shortening to the lengthening contraction. However, when these data were removed, the results for the variability of motor unit discharge rate did not change.

**DISCUSSION**

The main findings of the study were that old adults were less steady with isometric and anisometric contractions with the first dorsal interosseous muscle. The decrease in steadiness was associated with more surface EMG and greater variability in the discharge rate of motor units. Moreover, the old adults had greater difficulty with the lengthening contractions, when the discharge rate was most variable and the surface EMG activity was proportionally greater compared with the young adults.

**Variability of Motor Unit Discharge Rate.** There are at least four features of the motor output from the spinal cord that could contribute to the observed differences in steadiness among young and old adults. These include the average force produced by motor units,\(^{1,5,15}\) the pattern of coactivation by the agonist and antagonist muscles,\(^{40,41}\) the amount of motor unit synchronization,\(^{7,37}\) and the discharge behavior of motor units.\(^{10}\) The results of the present study suggest a probable role for the variability of motor unit discharge in the steadiness of muscle contractions, at least for low-force and light-load contractions.

In previous studies, we have found that old adults...
recruit motor units in the first dorsal interosseous muscle at similar forces and at similar discharge rates compared with young adults. The current study is our first attempt to measure the discharge rate of motor units when subjects attempted to exert a steady force with the first dorsal interosseous muscle. The subjects were instructed to match a target force level for the isometric contractions and a position template for the anisometric contractions, so that measures of motor unit behavior could be related directly to the performance. The direct comparison of motor unit discharge behavior between young and old subjects was possible because the recruitment thresholds and the average discharge rates were similar (Table 3 and Fig. 7). The two tasks were used because of differences in the modulation of discharge rate. Within this context, it appears that steadiness (variability in force or position) is influenced by the variability with which motor units discharge action potentials.

We evaluated the variability of motor unit discharge in absolute and normalized quantities as the SD and CV, respectively. The novel finding of this study was that although the CV of motor unit discharge was similar for the young subjects when performing the two tasks (15 to 20%), the old subjects had greater discharge rate variability for the lengthening contractions (>40%) and lower but similar variability for the isometric and shortening contractions (28 to 34%). Additionally, the spike-by-spike discrimination of trains of motor unit action potentials made it possible to identify consecutive discharges with brief interspike intervals (<20 ms). The old adults had a significantly greater incidence of double discharges compared with young adults. Most of the double discharges occurred during isometric contractions (in 51% of these trials), whereas only 24% of the double discharges contained double discharges (equally distributed between shortening and lengthening contractions).

The mechanisms that could affect discharge rate variability include changes in transmission efficacy over corticospinal and reflex pathways (the contributors to the synaptic input to motor neurons) and the biophysical properties of motor neurons. There is ample evidence that both of these mechanisms are affected by age. For example, anatomical studies show that after 60 years of age, approximately 40% of cortical neurons are lost or nonfunctioning. Additionally, there is a concurrent but more modest loss of about 25% of spinal motor neurons in old age. Moreover, there are increases in the absolute latencies of sensory and motor evoked potentials, primarily affecting the large-diameter, fast-conducting motor fibers in the pyramidal tract. The consequence of these changes is that the efficacy of signal transmission along the corticospinal pathway is altered, with reductions in the amplitudes of motor evoked potentials and compound excitatory postsynaptic potentials. These changes probably have significant consequences for tasks requiring manual dexterity because of the larger area of representation of hand muscles in the motor cortex. Furthermore, Corden and Lippold found that the short-latency, but not the long-latency, reflex response of first dorsal interosseous muscle was impaired in old adults and that the decrease was not due to changes in the mechanical properties of the muscle. Together, these findings suggest that there are age-related changes in the efficacy of signal transmission to the motor neurons.

![Figure 7](image-url)

**FIGURE 7.** Motor unit discharge behavior for young (○, □) and old (●, ■) subjects performing slow shortening (○, ●) and lengthening (□, ■) contractions with the 2.5% (left panels) and 5% (right panels) loads. Data shown represent mean ± SEM. Although there were no differences due to age in the average discharge rate of motor units during the shortening and lengthening contractions with either load, for both groups the discharge rate was lower during the lengthening contraction compared with the shortening contraction (A). Moreover, both the SD (B) and the CV (C) were greater for the old subjects performing the shortening and lengthening contractions. The CV was greater during the lengthening contractions compared with the shortening contractions for the old subjects, whereas for the young subjects the variability was the same.
Similarly, age alters the propagation of electrical potentials along peripheral nerve pathways. Declines in conduction velocity and the amplitude of action potentials, especially after the fifth decade, have been attributed primarily to the loss of large-diameter sensory and motor neurons and changes in the biophysical properties of motor neurons. For example, aging is associated with an increase in input resistance and a decrease in rheobase current of cat motor neurons. The changes in the biophysical properties of motor neurons are known to parallel morphological changes, such as a reduced size of the soma. Furthermore, there is evidence that group Ia synaptic transmission is affected by age and that there is considerable reorganization occurring in the spinal cord, including dendritic arborization and neosynaptogenesis, which would affect the net synaptic input to motor neurons. Together, these findings indicate that the nature of the synaptic drive to motor neurons and the properties of motor neurons change with age, either of which would influence the ability to modulate the discharge rate of motor units.

The Difficulty with Lengthening Contractions. There is accumulating evidence that unique activation strategies are used by the nervous system to control anisometric, especially lengthening, contractions. The relatively few studies on motor unit behavior during anisometric contractions have shown that there are significant differences compared with isometric contractions. For example, in a sequence of studies on the control of the elbow flexor muscles, Tax and colleagues found that although recruitment order is similar, both recruitment threshold and discharge rate are different for movement tasks compared with isometric tasks at equivalent load torques and that these differences even vary among synergists. Under low-velocity trials, the recruitment threshold of motor units in biceps brachii was lower during voluntary flexion and extension movements than for isometric contractions. However, the recruitment thresholds of motor units in brachialis and brachioradialis were higher during voluntary movements compared with isometric contractions. The initial discharge rate for all three elbow flexors was higher during voluntary flexion movements than isometric contractions, whereas during voluntary extension movements, the initial discharge rate was lower than the other two conditions. These findings suggest that the relative contribution of the two force-grading mechanisms (recruitment and modulation of discharge rate) is dependent on the task performed.

Another unique characteristic of lengthening contractions is the changes that occur in the distribution of activity among synergist muscles. For example, Nardone and Schieppati found that the EMG was greatest for soleus during a shortening contraction, whereas lateral gastrocnemius was more active during the lengthening contraction. Similar effects have been observed with the elbow flexor muscles. For the calf muscles, the redistribution of activity between shortening and lengthening contractions appeared to involve a change in the motor units that contribute to the task. With the first dorsal interosseous muscle, we did not find a change in the motor units that were activated during the slow lengthening contractions when lowering light loads. However, we have observed an increase in the coactivation of the antagonist muscle, especially for the old adults, when the first dorsal interosseous muscle performs a lengthening contraction.

Taken together, these findings indicate that the strategy used by the nervous system varies across contraction type. The variations can include changes in the recruitment threshold and initial discharge rate of motor units, the timing of the activation of a particular set of motor units, and the distribution of the activity among motor units within a group of synergist muscles. It appears that the aging central nervous system has greater difficulty in organizing the inputs to a motor neuron pool to produce a steady lengthening contraction.

In summary, we have found that the age-related decline in the steadiness of low-force isometric and anisometric muscle contractions appears to be at least partially due to an increased variability in the discharge rates of motor units. The greater relative amplitude of the surface EMG suggests an altered recruitment strategy for the old subjects performing low-force contractions probably combined with greater coactivation of the antagonist muscle.

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