Nonuniform activation of the agonist muscle does not covary with index finger acceleration in old adults

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The motor output produced by older adults is often more variable than that for young adults (2, 17, 45). The mechanisms that could contribute to this difference in motor performance include those related to motor unit properties and those involving the activation of the population of motor units. This study examined two of the potential population factors that could influence motor output variability: the distribution of activity in the agonist muscle and coactivation of the antagonist muscle.

The effect of a muscular contraction on the acceleration of a limb depends not only on the intensity of the contraction but also on the direction of the muscle force vector. Variation in the direction of the force vector will alter the moment arm relative to the joint and thereby the angular acceleration due to a given muscle force. As a consequence, the greater standard deviations of wrist acceleration during slow movements about the elbow joint exhibited by older adults can be associated with greater relative activation of the muscle (brachialis) with the longest moment arm in the group of synergist muscles (14). A similar effect could occur as a result of nonuniform activation in a single muscle that has broad attachments or multiple heads (27, 37, 41).

Motion of the index finger in its abduction-adduction plane is controlled by a single agonist muscle, first dorsal interosseus, and a single antagonist muscle, second palmar interosseus (5, 7, 10, 40). Because of this relatively simple architecture, the first dorsal interosseus muscle is often used to evaluate various neural mechanisms underlying the control of movement in humans (4, 11, 12, 21). Nonetheless, first dorsal interosseus is a bipennate muscle (24) that has been observed to exhibit nonuniform activation (48, 49). It seemed possible, therefore, that nonuniform activation of first dorsal interosseus might contribute to differences in the fluctuations of index finger acceleration between young and old adults.

Fluctuations in motor output can also be influenced by coactivation of the antagonist muscle. For example, Seidler-Dobrin et al. (30) found experimentally that older adults used greater coactivation of the antagonist muscle during rapid elbow flexion movements and demonstrated with a model that the heightened antagonist activity reduced the variability in movement accuracy. However, alternating activation of the agonist and antagonist muscles appears to enhance the fluctuations in finger acceleration during slow movements (39).

The purpose of the study was to determine the contributions of nonuniform activation of an agonist muscle and coactivation of the antagonist muscle to differences in the standard deviation of index finger acceleration during slow movements (39).
acceleration between young and old adults during position-holding and position-tracking tasks. Although the fluctuations in acceleration were usually greater for the older adults, this difference in motor output did not appear to be due to either nonuniform activation of the agonist muscle or the average level of coactivation in the antagonist muscle. Some of these results have been presented previously in abstract form (23).

METHODS

Experiments were performed on the left hand (nondominant) of 10 young [6 women, 4 men; 22.9 ± 2.7 (SE) yr, range 19–27 yr] and 10 old [6 women, 4 men; 69.3 ± 3.0 yr, range 62–72 yr] subjects with no known neuromuscular disorders. The Institutional Review Board at the University of Colorado approved the experimental procedures, and all subjects gave informed consent before participation in the study.

Experimental Setup

The experiments were conducted with each subject seated and facing a video display monitor that was positioned 1.2 m away at eye level for the subject. All subjects affirmed that they could see the video display clearly. The left arm was abducted ~30°, and the elbow was flexed to a right angle, with the hand and forearm prone and resting on a manipulandum (Fig. 1). The hand was placed so that the index finger was horizontal and the other three fingers were flexed around a semicircular grip. The thumb was braced in a horizontal position by a restraint that maintained the angle between the first and second metacarpals at ~90°. A clamp placed against the medial aspect of the wrist and the lateral aspect of the hand minimized ulnar and radial deviation of the wrist. Flexion at the phalangeal joints was prevented by an L-shaped aluminum splint during the position-holding task and by a custom-fitted, semicircular polyvinylchloride splint during the position-tracking task. These restraints were attached to the radial and palmar aspects of the left index finger.

Mechanical Recording

Subjects performed isometric contractions by pushing against a force transducer and maintained steady contractions by supporting an inertial load during the position-holding and position-tracking tasks.

Isometric contractions. With the hand positioned in the manipulandum so that the index finger was abducted to the middle of its range of motion in the abduction-adduction plane, a force transducer (model 13, Sensotec, Columbus, OH) detected the abduction force at the proximal interphalangeal joint of the index finger. The sensitivity of the force transducer was 0.053 V/N (linear range 0–220 N).

Position-holding and position-tracking tasks. A miniature piezoresistive accelerometer (model 7265A-HS, Endevco, San Juan Capistrano, CA) was attached to the radial surface of a small L-shaped aluminum angle on the finger splint. The accelerometer detected changes in movement velocity in the abduction-adduction plane during the position-holding task. The accelerometer had a mass of 5.9 g, a linear acceleration response up to ±196.2 m/s², and a linear frequency response from 0 to 125 Hz, and it was insensitive (~5%) to accelerations in other directions.

A low-friction, linear variable differential transducer (LVDT; Novotechnik, Stuttgart, Germany) was used to detect the abduction-adduction displacement of the index finger about the first metacarpophalangeal joint during the position-tracking task. The LVDT was mounted vertically and positioned perpendicular to the proximal interphalangeal joint when the index finger was abducted to the middle of its range of motion in a horizontal plane (Fig. 1). The LVDT was calibrated for each subject and session over the range of motion. The loads lifted by the subjects were suspended from the LVDT.

Electrical Recording

The surface electromyogram (EMG) of the first dorsal interosseus muscle was recorded with bipolar electrodes (4-mm diameter, silver-silver chloride; ~8 mm apart center to center) that were secured to the skin overlying the muscle. Common electrodes (4-mm diameter, silver-silver chloride) were placed on the styloid process of the ulna. The surface EMG signals were amplified (~1,000–10,000), band-pass filtered (20–800 Hz), and displayed on an oscilloscope.

Intramuscular EMG recordings were made with bipolar electrodes inserted into the first dorsal interosseus and second palmar interosseus muscles. Each electrode consisted of two Formvar-insulated stainless steel wires (100 μm diameter; California Fine Wire, Grover Beach, CA). Approximately 0.5 mm of insulation was removed from the recording end of one wire in each pair to increase the pickup area of the electrode. The two wires were threaded through a disposable 27-gauge needle that was inserted into the muscle and then removed, leaving the wires in the muscle. The signals from these electrodes were amplified (~1,000–10,000), band-pass filtered (0.02–5 kHz), and displayed on an oscilloscope.

Experimental Procedures

Each of the 20 subjects was required to perform six tasks in an experiment: 1) assessment of isometric strength with
maximum voluntary contractions (MVCs), 2) determination of the EMG-force relation with isometric contractions held at selected constant forces, 3) assessment of anisometric strength with a one-repetition maximum (1-RM) trial, 4) performance of the position-holding trials, 5) execution of the anisometric position-tracking trials, and 6) reassessment of anisometric strength.

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. The index finger force was displayed on the monitor. 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 began to plateau. Each subject performed two MVC trials, with subsequent trials performed if the difference in peak force between the first two MVCs was >5%. The trial with the highest peak force was chosen for analysis. There was a 60- to 90-s rest between consecutive trials.

EMG-force relation. Each subject was instructed to gradually increase the isometric abduction force to the target force displayed on the monitor and to hold the force steady at the target force for ~15 s. A single trial was performed at each of three submaximal target forces: 5, 35, and 65% MVC force. The sensitivity of the force display was set relative to the target force level so that the distance from the baseline to the target force was four vertical divisions on the monitor.

1-RM load. The 1-RM task was performed with the index finger moving horizontally through its passive range of motion in the abduction-adduction plane (15–25°). The mass was attached to the index finger at the proximal interphalangeal joint to provide a load in the adduction direction. The load was raised and lowered during 2 s of abduction (shortening contraction) and 2 s of adduction (lengthening contraction), respectively. A triangular template was displayed on the monitor, and each subject was given practice trials to become familiar with the timing and amplitude of the movement. The load applied in the adduction direction was increased in increments of 50–100 g until the load could no longer be raised through the complete range of motion.

Position-holding task. A load corresponding to 2.5, 10, and 35% of the 1-RM load was lifted so that the position of the index finger was abducted to the middle of its range of motion. The subject was instructed to hold this position as
steadily as possible for ~15 s (Fig. 2A) without deviation from the desired position. One of the investigators watched the index finger to ensure that this criterion was met.

**Position-tracking task.** The position-tracking trials were performed with loads of 2.5, 10, and 35% of the 1-RM load. Three trials with each load were performed with the index finger moving through the range of motion (Fig. 2B). Subjects performed two different sequences of contractions: 1) shortening-lengthening, and 2) lengthening-shortening. The duration of each contraction was 10 s. The triangular template was inverted for the lengthening-shortening (lowering-raising) sequence. The subjects were encouraged to match the desired finger displacement template (constant velocity) in the abduction-adduction plane as closely as possible. To minimize variation in the trajectory across trials (4), the displacement of the index finger was monitored by one of the investigators, and errant trials were discarded.

**Data Analysis**

All data collected during the experiments were recorded and stored in digital format (Sony PC 116 DAT recorder; bandwidth direct current to 5 kHz) and analyzed off-line by using the Spike2 data analysis system (Cambridge Electronic Design, Cambridge, UK) with custom-designed software. The index finger force and position signals were sampled at 208 Hz, and the acceleration and EMG data were sampled at 2,084 Hz. Power spectra were derived for the acceleration records during the position-holding and position-tracking trials. The block size for the fast-Fourier transforms was 2,048 points, which gave a bin size of ~1 Hz. To minimize data loss, a raised cosine window (Hanning) was applied to each block of data, and the power spectrum for each trial was computed as the average of overlapping (1,024 points) and contiguous data blocks. A total of 19 data blocks were used for the averages during the 15-s position-holding and the 10-s position-tracking trials.

**Dependent variables.** The dependent variables for the MVC task were the peak force and the average of the full-wave rectified EMG (AEMG) for a 0.25-s window centered at the peak force during the trial. The dependent variables for the EMG-force relation were the average force and AEMG in a 5-s window when the force was relatively constant. The EMG amplitudes were normalized to the AEMG during the MVC task for first dorsal interosseus and to the AEMG during the shortening contraction of the 1-RM task for second palmar interosseus. The dependent variables for the 1-RM task included 1) 1-RM load, 2) peak abduction position, 3) average velocity during the shortening and lengthening contractions, and 4) AEMG for a 0.5-s window centered at the middle of the range of motion in each phase.

The dependent variables for the position-holding task were the standard deviation of acceleration in the abduction-adduction plane in a 10-s window, the AEMG during the same epoch, and the frequency and power of the peak power in the acceleration spectrum. Because the AEMG for second palmar interosseus likely includes volume-conducted signals from second dorsal interosseus during a MVC, the AEMG data for second palmar interosseus are both reported as absolute values and normalized to the value for the shortening contraction of the 1-RM task. Similarly, the dependent variables for the position-tracking task were the standard deviation of acceleration in the abduction-adduction plane over the duration of the shortening or lengthening contractions, the AEMG during a 0.25-s window centered at the middle of the range of motion for each phase, and the frequency of the peak power in the acceleration spectrum.

**Statistical analysis.** A two-factor ANOVA (1 factor between and 1 within) was used to compare the dependent variables for the MVC and 1-RM tasks between groups. A two-factor ANOVA with repeated measures (1 factor between and 1 within) was used to compare the standard deviation of acceleration across loads for the position-holding task. A three-factor ANOVA with a repeated-measures design (1 factor between and 2 within) was applied to the EMG-force, EMG during position holding, and acceleration during position tracking to compare the dependent variables between groups, across forces and loads, across recording sites or contraction types, and the interaction terms. A four-factor analysis of variance with a repeated-measures design (1 factor between and 3 within) was applied to the position-tracking data to compare the dependent variables between groups, across forces and loads, across contraction types, across recording sites, and the interaction terms. An a-level of 0.05 was chosen for all initial statistical comparisons, with post hoc comparisons (Fisher’s least significant difference test) performed when necessary to determine between-group, between-contraction type, and between-load differences. Unless stated otherwise, the data are presented as means ± SD in the text and Tables 1 and 2 and as means ± SE in Figs. 1–5.

**RESULTS**

The results examine the contribution of the nonuniform activation of the agonist muscle (first dorsal interosseus) and coactivation of the antagonist muscle (second palmar interosseus) to the fluctuations in motor output exhibited by young and old subjects during the performance of position-holding and position-tracking tasks with the index finger.

**Strength Measures**

The MVC forces were not statistically different for the old and young subjects (Table 1; P = 0.24). In both groups, however, the men were stronger than the women (P < 0.05). Additionally, the absolute surface and intramuscular AEMGs of the first dorsal interosseus muscle during the MVC task were greater for the young subjects compared with the old subjects (Table 1). Nonetheless, there were no differences between the absolute surface and intramuscular AEMGs for either group of subjects. The absolute AEMG for the second palmar interosseus muscle during the MVC task was greater for the old subjects compared with the young subjects (old = 0.17 ± 0.12 mV; young = 0.04 ± 0.03 mV; P = 0.05). There was no difference between men and women in the amount of coactivation of the antagonist muscle second palmar interosseus during the MVC task.

In contrast to the MVC force, the 1-RM load was greater for the young subjects compared with the old subjects (P = 0.002). Furthermore, 1-RM load was greater for the men compared with the women for both the young and old subjects (Table 1). The average displacement of the index finger during the 1-RM task was 24.3 ± 1.2° for the young subjects and 26.0 ± 1.4° for the old subjects, and the average velocity during the shortening and lengthening contractions was similar for young (9.0 ± 1.2 and 11.0 ± 1.2 mm/s, respectively) and old (10.0 ± 0.9 and 12.1 ± 1.1 mm/s, respectively) subjects.
The absolute AEMG (mV) for first dorsal interosseus during the 1-RM task for both the surface and intramuscular recordings was significantly greater for the young subjects compared with the old subjects (Table 1). There was no main effect for recording site during the 1-RM task (surface = 0.384 ± 0.249 mV; intramuscular = 0.355 ± 0.291 mV). However, there was a significant main effect for contraction type (shortening = 0.465 ± 0.300 mV; lengthening = 0.274 ± 0.195 mV) and a significant interaction between contraction type and age due to the lesser decrease in AEMG during the lengthening contractions for the old subjects (shortening = 0.356 ± 0.249 mV; lengthening = 0.253 ± 0.188 mV) compared with the young subjects (shortening = 0.605 ± 0.303 mV; lengthening = 0.347 ± 0.206 mV). There were no significant differences between the young and old subjects in the absolute (mV) AEMG of the antagonist muscle during the 1-RM task (Table 1). However, the old subjects, but not the young subjects, coactivated the second palmar interosseous more during the MVC task than the 1-RM task.

EMG-Force Relations

There were no significant differences for either group between the amount of EMG activity detected by the surface and intramuscular electrodes during the submaximal isometric contractions (Table 2). The absolute surface and intramuscular AEMG amplitudes increased linearly as a function of force for both age groups. For example, the linear relation for the surface recordings of first dorsal interosseus for the young subjects was AEMG = 0.006 × force + 0.003 (r² = 0.67) compared with AEMG = 0.004 × force + 0.009 (r² = 0.42) for the old subjects. Similarly, the linear relation for the intramuscular recordings of first dorsal interosseus was AEMG = 0.006 × force + 0.03 (r² = 0.55) for the young subjects compared with AEMG = 0.003 × force + 0.02 (r² = 0.36) for the old subjects. There were no significant differences between AEMG in the young and old subjects in the relative amplitude of the surface and intramuscular AEMGs across all forces. These results indicate that the quantity of EMG detected by the surface and intramuscular electrodes in the first dorsal interosseus muscle changed in parallel across the isometric contractions.

The absolute AEMG for the intramuscular recordings of the second palmar interosseus muscle (Table 2) also increased as a function of target force for both groups of subjects, although with more variability compared with the AEMG for first dorsal interosseus (young AEMG = 0.0004 × force − 0.001, r² = 0.42; old AEMG = 0.002 × force − 0.02, r² = 0.35). Consequently, there were no significant differences between the young and old subjects in the average absolute level of coactivation in the antagonist muscle second palmar interosseus across the three submaximal forces. However, the old subjects showed greater coactivation of the antagonist muscle than the young subjects when the AEMG was normalized to 1-RM task.

Table 2. AEMG values during constant-force contractions of the first dorsal interosseus

<table>
<thead>
<tr>
<th>MVC %</th>
<th>FDI, mV</th>
<th>FDI, mV</th>
<th>SPI, mV</th>
<th>FDI, mV</th>
<th>FDI, mV</th>
<th>SPI, mV</th>
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<td></td>
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</tr>
<tr>
<td>5</td>
<td>0.026 ± 0.011</td>
<td>0.045 ± 0.022</td>
<td>0.006 ± 0.002</td>
<td>0.026 ± 0.021</td>
<td>0.029 ± 0.024</td>
<td>0.010 ± 0.008</td>
</tr>
<tr>
<td>35</td>
<td>0.196 ± 0.092</td>
<td>0.232 ± 0.089</td>
<td>0.008 ± 0.003</td>
<td>0.153 ± 0.098</td>
<td>0.147 ± 0.116</td>
<td>0.017 ± 0.009</td>
</tr>
<tr>
<td>65</td>
<td>0.428 ± 0.183</td>
<td>0.442 ± 0.201</td>
<td>0.021 ± 0.015</td>
<td>0.289 ± 0.188</td>
<td>0.253 ± 0.197</td>
<td>0.079 ± 0.125</td>
</tr>
<tr>
<td>100</td>
<td>0.596 ± 0.236a</td>
<td>0.611 ± 0.334a</td>
<td>0.043 ± 0.033a</td>
<td>0.423 ± 0.290</td>
<td>0.352 ± 0.238</td>
<td>0.151 ± 0.127</td>
</tr>
<tr>
<td></td>
<td>Relative, %</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>5</td>
<td>4.4 ± 1.1</td>
<td>8.4 ± 3.6</td>
<td>16.2 ± 10.8</td>
<td>6.5 ± 3.9</td>
<td>8.1 ± 4.3</td>
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<td>35</td>
<td>32.4 ± 5.9</td>
<td>41.6 ± 10.8</td>
<td>21.8 ± 10.8</td>
<td>39.3 ± 14.2</td>
<td>40.2 ± 15.0</td>
<td>84.9 ± 63.4</td>
</tr>
<tr>
<td>65</td>
<td>71.4 ± 10.8</td>
<td>76.6 ± 16.5</td>
<td>40.9 ± 11.9</td>
<td>71.8 ± 22.4</td>
<td>70.2 ± 13.7</td>
<td>154.2 ± 86.3</td>
</tr>
</tbody>
</table>

Values are group means ± SD. Relative AEMG values for FDI and FDIi are with respect to the AEMG during the MVC task. Relative AEMG values for SPI are with respect to the shortening contraction during the 1-RM task. *P < 0.05 compared with old.

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(P = 0.01). This effect was consistent across loads for men and women.

Postural Steadiness During Position Holding

A representative record for an older subject performing the position-holding task with the index finger is shown in Fig. 2A. The steadiness of the contractions during these trials was assessed by the standard deviation of acceleration in the abduction-adduction plane. The standard deviations of acceleration (Fig. 3A) were greater for the old subjects at the 2.5% load (old = 0.072 ± 0.052 m/s²; young = 0.030 ± 0.010 m/s²), 10% load (old = 0.065 ± 0.035 m/s²; young = 0.033 ± 0.015 m/s²), and 35% load (old = 0.068 ± 0.031 m/s²; young = 0.050 ± 0.017 m/s²). Although it appeared that the standard deviation of acceleration increased linearly as a function of load for the young subjects but not the old subjects (Fig. 3A), there was no interaction between load and age (P = 0.1).

The AEMG (%EMG during the MVC) for the surface and intramuscular recordings of the first dorsal interosseus muscle increased linearly (P < 0.05) as a function of load during the position-holding task for both groups of subjects (Fig. 3B). There were no differences in AEMG between the two age groups (P = 0.18) or between the two recording sites at each load (P = 0.11).

Despite the differences in the standard deviation of acceleration, the superficial and deep parts of the agonist muscle were activated to the same relative levels by the young and old subjects when supporting submaximal loads (2.5, 10, and 35%) during postural contractions.

The absolute (mV) AEMGs for the second palmar interosseus muscle were not different for the two groups of subjects during the position-holding task. Furthermore, there was no difference in second palmar interosseus AEMG at the 35% force during the contraction for the EMG-force relation (0.0132 ± 0.0083 mV) and the 35% load during the position-holding task (0.0193 ± 0.0172 mV). However, the normalized AEMG for second palmar interosseus during the position-holding task did not change with load for the old subjects (2.5% = 62.5 ± 55.8%; 10% = 66.3 ± 54.1%; 35% = 66.8 ± 62.4%), and the old subjects had greater normalized AEMGs across all loads (89.3 ± 56.5%) compared with the young subjects (23.9 ± 11.5%; P = 0.02). There was no association across all loads between the amount of second dorsal interosseus AEMG and the standard deviation of acceleration for either group of subjects during the position-holding task (Fig. 4, A and D).

The frequency at which the peak power occurred in the acceleration spectrum did not differ with load or age. These frequencies were 19.2 ± 6.4, 26.7 ± 20.4, and 16.0 ± 20.7 Hz at the three loads (2.5, 10, and 35%, respectively) for the young subjects and 18.2 ± 15.4, 16.8 ± 15.7, and 25.5 ± 22.5 Hz, respectively, for the old subjects. Because the acceleration spectra for the position-holding task usually had two prominent peaks, the large standard deviations in the frequency were due to the peak power occurring in either the <10-Hz band (24/60 spectra) or the 15- to 30-Hz band (25/60 spectra). The number of spectra in which the peak occurred in the <10-Hz band increased with load, whereas the number declined in the 15- to 30-Hz band.

Movement Steadiness During Position Tracking

A representative record for an older subject performing the shortening-lengthening sequence of the position-tracking task is shown in Fig. 2B. There were no differences between groups and across loads for any of the kinematic variables during the shortening and lengthening contractions. The average velocities across loads were similar for the young subjects (shortening = 2.25 ± 0.67°/s; lengthening = 2.27 ± 0.65°/s) and old subjects (shortening = 2.56 ± 0.60°/s; lengthening = 2.72 ± 1.02°/s). However, the standard deviations of acceleration were greater for the old subjects compared with the young subjects for both the shortening and lengthening contractions at all loads (Fig. 5A). For example, the standard deviation for the shortening contractions with the 2.5% load was 0.20 ± 0.10 m/s² for the old subjects compared with 0.10 ± 0.04 m/s² for the young subjects. Similarly, the standard deviation for the lengthening contractions with the 2.5% load was 0.26 ± 0.14 m/s² for the old subjects compared...
with 0.12 ± 0.03 m/s² for the young subjects. For both age groups, the standard deviation of acceleration at each load was similar for the shortening and lengthening contractions. Furthermore, there was a main effect of load (P < 0.04), although an interaction of load and age (P < 0.01) indicated that this was specific to the old adults. Post hoc comparisons (Fisher’s paired least significant difference test) indicated that the standard deviation of acceleration was significantly less at the 35% load compared with the 10% load for the old subjects (P < 0.02). There were no differences in the standard deviation of acceleration across loads for the young subjects. These relations were independent of the order in which the shortening and lengthening contractions were performed.

The normalized AEMG (%EMG during MVC) for first dorsal interosseus increased with load for both the shortening and lengthening contractions performed by the young and old subjects (P < 0.05; Fig. 5, B and C). The AEMG for the surface and intramuscular recordings from first dorsal interosseus were less during the lengthening contractions (14.5 ± 12.0%) compared with the shortening contractions (22.3 ± 20.8%) for the young and old subjects at all loads. However, the difference in AEMG between the shortening and lengthening contractions was less with the lighter loads for both young and old subjects, as indicated by an interaction between load and contraction type (P < 0.05).

There was a significant difference in AEMG between the two recording sites because of greater values for the intramuscular recording compared with the surface recording for both the shortening and lengthening contractions and both groups of subjects (Fig. 5, B and C; P < 0.05). Although there was no main effect of age for AEMG, an interaction between age and load (P < 0.05) indicated that the old subjects had significantly less AEMG (%MVC) than the young subjects at both recording sites with the 35% load for both the shortening (old = 31.4 ± 15.1%; young = 46.2 ± 31.3%) and lengthening (old = 19.6 ± 9.4%; young = 27.0 ± 18.0%) contractions. Furthermore, a significant interaction between contraction type and load was due to a lesser increase in AEMG with load for the lengthening contractions compared with the shortening contractions (Fig. 5, B and C).

The absolute AEMG (mV) for second palmar interosseus was greater for both groups of subjects during the lengthening contractions (0.030 ± 0.014 mV) compared with the shortening contractions (0.017 ± 0.010 mV) during the position-tracking task. Furthermore, the old subjects (shortening = 0.024 ± 0.015 mV; lengthening = 0.040 ± 0.009 mV) coactivated the antagonist muscle more than the young subjects (shortening = 0.010 ± 0.007 mV; lengthening = 0.025 ± 0.012 mV) when lifting the 2.5% load. When normalized to the AEMG of the shortening contraction during

Fig. 4. Association between the absolute (A–C) and normalized (D–F) average levels of coactivation in the antagonist muscle SPI and the SD of acceleration during the position-holding task (A, D), shortening contraction of the position-tracking task (B, E), and the lengthening contraction of the position-tracking task (C, F). Normalized data are expressed relative to the values during the shortening contraction of the 1-RM task. Each data point corresponds to a single trial, and each scattergram includes the data for all three loads (2.5, 10, and 35%).
The acceleration spectra for the position-tracking task usually comprised a single peak in the 5- to 12-Hz band. The frequency at which the peak power occurred did not differ for age, load, or contraction type. The frequencies for the young and old subjects combined were $6.8 \pm 0.4$, $6.1 \pm 0.4$, and $5.8 \pm 0.3$ Hz for the shortening contractions with the three loads (2.5, 10, and 35%, respectively) and $7.5 \pm 0.4$, $7.4 \pm 0.4$, and $6.2 \pm 0.4$ Hz, respectively, for the lengthening contractions.

**DISCUSSION**

The main finding was that differences in the amount of EMG recorded in superficial and deep regions of the first dorsal interosseus muscle were not associated with differences between young and old subjects in the fluctuations in acceleration of the index finger during the position-holding and position-tracking tasks. The two groups of subjects activated the deep and superficial regions of the muscle to similar levels during the position-holding task, whereas the deep region was activated more intensely during the shortening and lengthening contractions of the position-tracking task by both groups of subjects. Despite these differences, the standard deviation of acceleration was usually greater for the old subjects compared with young subjects for both tasks, but especially during the position-tracking task.

**Nonuniform Activation of First Dorsal Interosseus**

Motor units are arranged topographically within some muscles (44), which enables discrete regions to be activated in various tasks and for the direction of the force exerted by the muscle to be altered (28). This feature, which has been termed “functional compartmentalization” (20), has been demonstrated in human muscles such as biceps brachii (37), masseter (27), and triceps brachii (41). For example, ter Haar Romeny et al. (37) found three classes of motor units within anatomically defined regions of the long head of biceps brachii: 1) motor units in the lateral portion that were active only during flexion; 2) motor units in the medial portion that were active only during supination; and 3) motor units in the middle portion, overlapping the boundaries of flexion and supination motor units, that were active during combinations of flexion and supination.

The first dorsal interosseus muscle is located between the thumb and index finger and is innervated by the ulnar nerve to control abduction of the index finger away from the longitudinal axis of the hand (5, 7, 16, 47). It is a flat, triangular muscle with two heads, superficial and deep, that are separated by a fibrous arch. The superficial head arises from the dorsal surface of the ulnar border of the first metacarpal, and the deep head arises from the proximal three-fourths of the radial border of the second metacarpal (24). The surface EMG recordings in the present study were probably dominated by signals emanating from the superficial head, whereas the recordings made with the
intramuscular electrode likely included signals from the deep head. The variability in EMG for the intramuscular recordings was probably influenced by variation in the placement of the electrode across subjects. Both heads insert into a common tendon that attaches to the radial side of the proximal phalanx of the index finger (10).

When subjects performed isometric contractions at 5, 35, 65, and 100% MVC force, we found that the absolute EMG (mV) was similar and increased linearly for both the surface and intramuscular recordings (Table 2). Similarly, the normalized EMG (%MVC) recorded at the two sites increased with load during the position-holding task for the young and old subjects (Figs. 3 and 5). In contrast, there was greater activity recorded at the intramuscular site compared with the surface site for both groups of subjects during the position-tracking task. There are at least two precedents in the literature that report nonuniform activity in the first dorsal interosseus muscle during isometric contractions. Zijdewind et al. (48) found that the change in EMG activity of first dorsal interosseus during a fatiguing contraction sustained at 50% MVC force differed for surface recordings from the same muscle, where one site could exhibit an increase in EMG during the contraction and another site could show a decrease in the EMG. Subsequently, they found a similar dissociation between the EMG recorded with surface and intramuscular electrodes during the same fatigue task with first dorsal interosseus (49). Our results are consistent with those of Zijdewind et al. and demonstrate that the neural drive to the motoneuron pool of first dorsal interosseus is not always distributed uniformly. Nonetheless, the nonuniform activation of first dorsal interosseus was not associated with differences in the standard deviation of index finger acceleration between young and old adults.

**Fluctuations in Acceleration**

When subjects perform submaximal contractions with first dorsal interosseus, the fluctuations in motor output are usually greater for old adults compared with young adults, especially when exerting low forces and lifting light loads (2, 12, 22). This difference in motor output could be attributable to either the properties of individual motor units (1, 6) or the size and behavior of the population of motor units (9, 11, 35, 36, 39).

**Motor unit properties.** The two motor unit properties that could influence the variability in motor output are motor unit force and discharge rate variability. Apoptosis of spinal motoneurons results in a decline in the number of motor units in the muscles of older adults but an increase in the innervation number of surviving motor units (3, 8, 13, 25, 38). Accordingly, the force contributed by recently recruited motor units to the net force exerted by first dorsal interosseus is greater in old adults (12). However, several weeks of performing strengthening exercises with first dorsal interosseus reduced the fluctuations in force but did not change the distribution of motor unit forces (19). Furthermore, computer simulations indicated that a 40% increase in the range of motor unit forces had only a minor effect on the fluctuations in force (35). Hence the larger motor units in the first dorsal interosseus of old adults do not appear to contribute significantly to the differences in the force fluctuations between young and old adults.

Similarly, the effect of variability in discharge rate on the differences in fluctuations appears to be uncertain. Computer simulations indicate that the coefficient of variation for discharge rate can have a substantial effect on the fluctuations in force during an isometric contraction (35, 36, 46). Accordingly, Laidlaw et al. (22) reported greater coefficients of variation for discharge rate and larger fluctuations in motor output of first dorsal interosseus for old adults compared with young adults. However, Semmler et al. (32, 33) found no differences in the coefficient of variation for the discharge rate of motor units in first dorsal interosseus between young and old adults, despite significant differences in the fluctuations in motor output. Thus, although discharge rate variability can influence the fluctuations in force, there is sometimes an association between the two variables, and other times there is not.

**Population characteristics.** In contrast to the absence of a consistent effect due to motor unit properties, there does appear to be an association between some activation characteristics of the motor unit population and the fluctuations in motor output. Some of the population factors include nonuniform activation of the agonist muscle, alternating activity with the antagonist muscle, and oscillatory input to the motoneuron pool. In the present study, we considered the potential contributions of a nonuniform activation of first dorsal interosseus and the level of coactivation to differences in the fluctuations of acceleration. Because of the different origins of the superficial and deep heads of first dorsal interosseus, nonuniform activation of the muscle would alter the direction of the net force vector acting on the first phalanx of the index finger and thereby differentially influence the angular acceleration of the finger. Although both young and old adults exhibited episodes when the AEMG activity differed at the two recording sites, this nonuniform activation of first dorsal interosseus was not associated with the differences in the standard deviation of acceleration. Furthermore, the EMG activity recorded at the superficial and deep sites did not involve alternating bursts of activity during either the position-holding task or the position-tracking task (Fig. 2, A and B, 2nd and 3rd traces). Thus the greater standard deviations of acceleration observed in the old subjects were not associated with the nonuniform activation of first dorsal interosseus.

Another possibility is that the fluctuations in acceleration could be caused by coactivation of the antagonist muscle, involving either differences in the average level of coactivation or alternating activation of the agonist and antagonist muscles (30, 39). Although old adults tend to coactivate the antagonist muscle (second palmar interosseus) more often than young adults dur-
ing abduction of the index finger, this activity was not associated with differences in fluctuations between young and old adults (2, 34). Figure 4 underscores the absence of an association between the average level of coactivation and the fluctuations in acceleration for either group of subjects across the various tasks. Furthermore, although some subjects exhibited alternating activity in the agonist and antagonist muscles, this was infrequent (Fig. 2) and was not associated with the amplitude of the fluctuations in acceleration produced by young and old adults during isometric and anisometric contractions (2). Nonetheless, the discharge rate of many motor units in antagonist muscles is modulated at a common frequency (6–12 Hz) with acceleration during slow wrist movements (42), which could contribute to the fluctuations in acceleration (43).

Some of the uncertainty over the mechanism responsible for variability in motor output seems to be related to differences between tasks (15, 18, 26). The standard deviations of acceleration in the present study, for example, were much greater during the slow movement (Fig. 5) compared with the postural task (Fig. 3), which is consistent with the findings of Kakuda et al. (18) for similar tasks performed by muscles that cross the wrist. Furthermore, the power spectra for acceleration were different for the two tasks. There was a prominent single peak at a frequency of ~6–7 Hz during the shortening and lengthening contractions, whereas the acceleration spectra for the position-holding task usually comprised two peaks: one at <10 Hz and the other in the 15- to 30-Hz band. Halliday et al. (15) reported similar peaks in the spectrum (12, 20, and 30 Hz) for acceleration of the middle finger during a position-holding task. In contrast, Kakuda et al. (18) found a broad peak between 2 and 10 Hz in the acceleration spectrum when the wrist was held at a constant position. These task-related differences may underlie the absence of a difference in MVC force between young and old adults but the presence of difference in 1-RM load (Table 1).

The rhythmicities appear to be influenced by common modulation of motor unit discharge rate. When the discharge of motoneurons is correlated due to the delivery of common synaptic input (29, 31), discharge rate exhibits coherent modulation in the 1- to 12- and the 15- to 30-Hz bands (15, 18). The contribution of this modulation in discharge rate to the fluctuations in acceleration, however, appears to differ across tasks. The discharge of a single motor unit can account for ~30% of the fluctuations in acceleration during slow movements but only ~4% during position holding (15, 18). The activity of multiple motor units, as indicated by the rectified EMG, can account for up to 20% of the fluctuations in acceleration during position holding (15). These findings indicate that common input to the motoneuron pool can contribute significantly to fluctuations in acceleration during the position-holding and position-tracking tasks. The relative contribution of this mechanism to the difference in the standard deviation of acceleration between young and old adults, however, remains to be determined.

In summary, the results confirm previous findings that older adults typically exhibit greater fluctuations in acceleration than young adults when supporting light loads and performing slow movements. The mechanisms responsible for this difference in motor output do not appear to include either nonuniform activation of the agonist muscle (first dorsal interosseus) or the average level of coactivation by the antagonist muscle (second palmar interosseus).

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