# Training-related enhancement in the control of motor output in elderly humans

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**Keen, Douglas A., Guang H. Yue, and Roger M. Enoka.** Training-related enhancement in the control of motor output in elderly humans. *J. Appl. Physiol.* 77(6): 2648–2658, 1994.—The increase in motor unit force that occurs with aging has been hypothesized to cause a decline in the ability to maintain a constant submaximal force. To test this hypothesis, young and elderly subjects performed a 12-wk strength-training program that was intended to increase motor unit force. The training program caused similar increases (%initial) in the training load (137.4 ± 17.2%), twitch force (23.1 ± 7.4%), and maximum voluntary contraction force (39.2 ± 6.8%) of the first dorsal interosseus muscle for the young and elderly subjects. The increase in strength was associated with a modest increase in muscle volume (7% of initial value) and a nonmonotonic increase in the surface-recorded electromyogram that was significant at *week 8* but not at *week 12*. The elderly subjects reduced the variability in force at the lower target forces (2.5, 5.0, and 20.0% maximum voluntary contraction force). This improvement, however, was unrelated to changes in the distribution of motor unit forces, which was not consistent with the hypothesis that the greater coefficient of variation for the force fluctuations is due to increased motor unit forces.

motor unit force; spike-triggered averaging; strength; muscle volume; electromyogram

CHANGES THAT OCCUR in the human neuromuscular system with aging include the progressive death of $\alpha$-motoneurons (2, 4, 5) and the subsequent reinnervation of some of the abandoned muscle fibers by surviving motor units (19, 25, 31). These changes appear to begin around the age of 60 yr. The consequences of this reorganization include a reduction in muscle mass, a decline in the number of surviving motor units, and an increase in the average motor unit force (8, 19, 22). Because the control of muscle force is expressed at the level of the motor unit, these changes in motor unit number and size have been implicated in the age-related decline in ability to control muscle force (12).

To test this hypothesis, we recruited elderly subjects to participate in a strength-training program that was designed to hypertrophy a hand muscle and to increase the force exerted by the single motor units of the muscle. The purpose was to determine the effect of an increase in motor unit force on the ability of the elderly subjects to control muscle force. If motor unit force is a critical factor underlying the reduced ability of elderly subjects to sustain constant submaximal isometric forces (12), then this capability should have declined further when motor unit force increased with strength training. Contrary to expectations, training resulted in a reduction in the coefficient of variation for the force fluctuations and no change in the force of low-threshold motor units. This dissociation is not consistent with the hypothesis. Rather, the reduced ability of elderly subjects to control submaximal force seems to depend on factors other than differences in motor unit force.

## METHODS

### Subjects

Experiments were performed on the left hand of 21 healthy human subjects (11 female, 10 male; 18–74 yr). These subjects were assigned to one of two age groups: an elderly group with an average age of 65 yr (6 females, 5 males; 59–74 yr) and a young group with an average age of 23 yr (5 females, 5 males; 18–27 yr). All subjects were right-hand dominant and had no known neuromuscular disorders. The experimental procedures were approved by the Human Subjects Committee at the University of Arizona, and all subjects gave their informed consent for participation in the study.

### Strength Training

Both groups of subjects participated in a 12-wk strength-training program. The purpose of the program was to hypertrophy an intrinsic hand muscle, the first dorsal interosseus. This muscle has primary responsibility for abduction of the index finger and is one of several muscles that flex the metacarpophalangeal joint of the finger. The training program comprised sequences of concentric and eccentric muscle contractions in which the index finger was moved by the first dorsal interosseus against a load that tended to adduct the finger (Fig. 1*B*). The finger was displaced through a 0.5-rad range of motion for each performance of the task.

The training was performed with a portable device that both restrained the hand and permitted the load to vary according to the needs of the subject. The hand was placed palm down on the apparatus, and a custom-fitted mold and splint were taped to the index finger. The splint was connected by a string and a pulley to the variable load. Hand position during training was maintained by a brace for the middle finger and a support for the thumb (Fig. 1*B*). Each subject was assigned an individual apparatus to take home for the duration of the training program. Because of time constraints, the 21 subjects performed the study in two groups; *group I* (5 young and 5 elderly subjects) performed the entire study before *group II* (5 young and 6 elderly subjects) began training.

The subjects were required to train for 12 wk with 3 training sessions/wk. A single session comprised 6 sets of 10 repetitions of the exercise. Initially, the training load was set at 80% of the maximum load that the index finger could lift by contraction of the first dorsal interosseus muscle. Thereafter, subjects were instructed to increase the training load so that it remained difficult to complete all 10 repetitions in the final (6th) set. Because of the substantial moment arm from the metacarpophalangeal joint of the index finger to the point of application of the load on the finger splint (Fig. 1*B*), the initial training weights were relatively low, in the range of 2–5 N. All training was done in the homes of the subjects, and additional weights were provided that could be used to increase the training load.

 

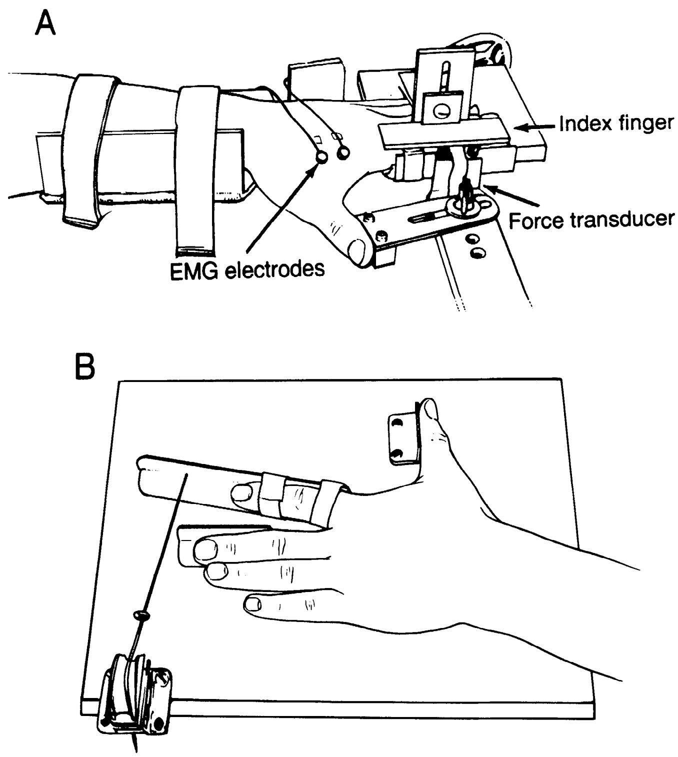


FIG. 1. Experimental (*A*) and training (*B*) apparatus used during study. All procedures were performed on left hand.

The subjects were contacted weekly to monitor their progress, and they were required to maintain a log of their training activities.

*Mechanical Recording*

For each experiment, the subjects were seated facing an oscilloscope with the left forearm comfortably supported and restrained by a manipulandum (Fig. 1*A*). The oscilloscope was used to provide feedback to the subject during the experiment. The elbow joint was flexed to a right angle, and the forearm and hand were restrained by *1*) two Velcro straps over the forearm, *2*) a strap over *fingers 3–5*, *3*) an aluminum splint that kept the index finger extended, *4*) a mechanical stop behind the elbow joint to prevent backward translation of the forearm, *5*) a metal bar between the index and middle fingers to prevent the middle finger from contributing to the abduction force exerted by the index finger, and *6*) a thumb support that maintained an angle of ~1.0 rad between metacarpals I and II. The angle between metacarpals I and II was measured carefully so that it remained consistent across all experimental sessions for each subject. The index finger was placed in a custom-fitted mold (polyvinyl silicone) and strapped inside an L-shaped aluminum splint that was positioned along the lateral and ventral surfaces of the finger.

The hand was placed in the manipulandum so that the proximal interphalangeal joint was aligned with a force transducer (model 13, Sensotec) that monitored the abduction force exerted by the index finger. A low-sensitivity force transducer (0.053 V/N, range 0–220 N) was used to record forces that were ≥50% maximum voluntary contraction (MVC) force. A more sensitive transducer (0.54 V/N, range 0–22 N) was used to measure forces <50% of MVC force. Signals from the force transducer were displayed on an oscilloscope and stored on a digital recorder [Sony PC 116 digital audio tape (DAT) recorder; bandwidth DC-2.5 kHz].

*Electrical Recording*

Surface electromyographic (EMG) signals were recorded with bipolar surface electrodes (4-mm-diam silver-silver chloride) placed ~10 mm apart over the first dorsal interosseus muscle. A common electrode was placed on the dorsal aspect of the middle finger. The signal was amplified (×1,000–10,000), band-pass filtered (0.01–10 kHz), notch filtered at 60 Hz (attenuation at −140 dB), displayed on an oscilloscope, and recorded on a DAT recorder.

Action potentials of single motor units were recorded with bipolar intramuscular electrodes inserted into the first dorsal interosseus muscle. The electrode consisted of three stainless steel wires (50 μm diam) that were insulated with Formvar, except for the cut ends of the wires. The wires were inserted into the first dorsal interosseus by a 27-gauge disposable needle under aseptic conditions. The insertion was performed before the subject was placed in the manipulandum. By varying the pairwise combinations of the wires or by displacing the wires with gentle tugs it was possible to manipulate the intramuscular electrodes to optimize the detection of action potentials belonging to several different motor units. A common electrode (8-mm-diam silver-silver chloride) was placed on the dorsal aspect of the hand. The signals were amplified (×1,000–10,000), band-pass filtered (0.3–10 kHz), displayed on an oscilloscope, and recorded on tape (Sony PC 116 DAT recorder; bandwidth DC-2.5 kHz). Discrimination based on waveform amplitude (BAK Dis-1) was used to provide audio feedback of the discharge of identified single motor units.

*Magnetic Resonance Imaging (MRI)*

The volume of the first dorsal interosseus muscle was determined with MRI before and after the 12 wk of strength training. Volume, rather than cross-sectional area, was the preferred index of muscle size because of the reduced reliability associated with identifying the maximum cross-sectional area and the overestimation of changes in muscle size by cross-sectional area (21, 26). The volume was determined by summing the data from serial image slices that were performed along the length of the muscle. For each MRI session, the subject lay prone with the left arm extended overhead and placed within a 1.5-T magnet (General Electric). The subject's hand was placed palm down on a dual 3-in. circular coil with an angle of ~1.0 rad between metacarpals I and II; this angle was the same as that used during the experiments when the hand was placed in the manipulandum. A Velcro strap was used to stabilize hand position.

The imaging protocol consisted of a volume gradient-echo pulse sequence (repetition time/echo time of 50/7 ms, 60° flip angle, 256 × 192 acquisition matrix, and 10-cm field of view). Sixty cross-sectional image slices (1.1 mm thick) were obtained in each MRI session. The slices were oriented perpendicular to the long axis of the hand with the distal end of the second metacarpal bone serving as the landmark for the first slice. The boundary of the first dorsal interosseus was identified in each slice (Fig. 2) by one investigator (*DAK*), and the cross-sectional area was determined. The volume of the first dorsal interosseus was calculated by multiplying the cross-sectional area of each slice by its thickness (1.1 mm) and summing these values. Repeat measurements of muscle volume from a given image yielded a variability of <1%.

*Experimental Procedures*

In addition to the two MRI sessions, each subject participated in four experiments (0, 4, 8, and 12 wk) that were designed to characterize the functional state of the first dorsal interosseus muscle and its motor units. In these experiments,

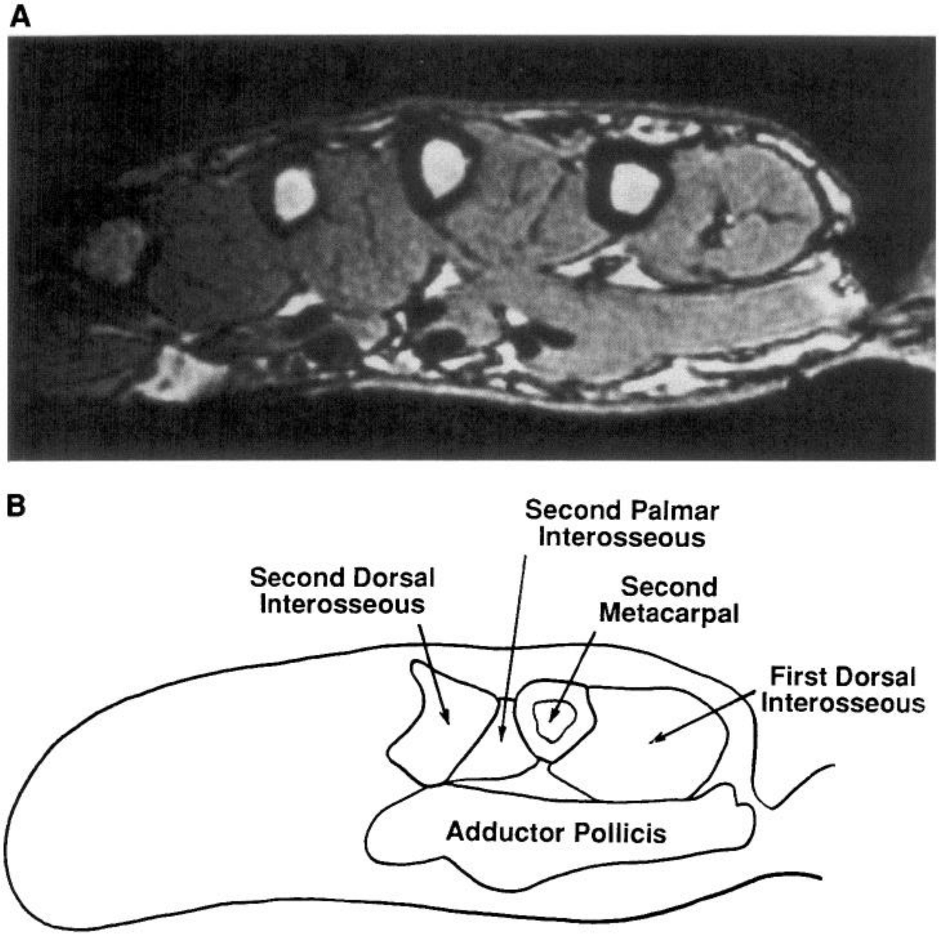


FIG. 2. Representative spin-lattice relaxation time-weighted image of intrinsic hand muscles (*A*) showing anatomic location of test muscle, first dorsal interosseus (*B*).

the subjects were required to perform the following four tasks in the order described: *1*) an isometric MVC, *2*) evoked responses, *3*) a constant-force task, and *4*) a threshold task.

*Isometric MVC.* The MVC task consisted of a gradual 3-s increase to maximum in the abduction force exerted by the index finger. The subjects were verbally encouraged to achieve maximality and to maintain a relatively constant slope for the force record during the increase in force. Subjects were able to observe their performance on an oscilloscope. The maximum force was maintained for 2–3 s before the subjects were instructed to relax. After a practice trial, each subject performed the MVC task three times and the mechanical and electrical data were recorded on tape. A fourth trial of the MVC task was performed if the peak force differed by >5% for the first three trials. Subjects rested ~60 s between trials.

*Evoked responses.* The M wave (EMG due to the synchronous activation of most muscle fibers) and twitch force were elicited in the first dorsal interosseus muscle by percutaneous electrical stimulation of the ulnar nerve at the wrist. Five responses were evoked in a relaxed muscle by supramaximal shocks (1 ms duration) that were provided by a Grass S-88 stimulator. The shocks were delivered by a bipolar electrode that was placed on the ventromedial aspect of the forearm ~10 cm from the wrist. The cathode was placed in the location that maximized the peak-to-peak amplitude of the M wave. Once this position was determined, the stimulating electrode was secured to the wrist by a Velcro strap and the stimulus intensity was increased to a supramaximal value. The responses were elicited at a rate of once every 3 s, and the force and EMG (M wave) signals were stored on digital tape for off-line analysis.

*Constant-force task.* Target forces of 2.5, 5.0, 20.0, and 50% of MVC force were calculated on the basis of the MVC force determined in the first task. In ascending order, each target force was displayed on the oscilloscope and the subject was required to exert a steady abduction force (isometric) with the index finger for 20 s to match the target force. The force exerted by the subject was also displayed on the oscilloscope. The subject performed one trial of the task at each target force and was given a rest of 30–60 s between trials.

*Threshold task.* The purpose of this task was to record the force exerted by the index finger while identified single motor units discharged at minimal rates (near the repetitive-discharge threshold). The action potentials of the single motor units in the first dorsal interosseus were recorded by the intramuscular electrode that was inserted into the muscle. The task began by the subject gradually increasing the abduction force to a level that recruited an identifiable motor unit. The units were identified on the basis of action potential shape and the force at which the unit was recruited. Once a motor unit was identified, the subject was required to sustain a minimal discharge rate for ~2 min or until the unit had discharged ~600 action potentials, as detected by an amplitude analyzer. The subject received audio and visual feedback on the discharge of the motor unit. To minimize the effects of fatigue, the duration of the threshold task was reduced if the identified unit was recruited at a force of >20% MVC force. Successive motor units were tested for as long as the subject was willing to comply or until the electrode was extracted from the muscle in the search for additional motor units. Subjects rested for 1–2 min between tests on successive motor units. We recorded an average of 8.4 ± 0.2 (SE) motor units in a single experiment.

### *Data Analysis*

All data recorded during the experiments were stored in digital format (Sony PC 116 DAT recorder) and analyzed off-line using the Spike2 data analysis system (Cambridge Electronics Design) and custom-designed software. For the MVC task, the dependent variables were peak force and the average of the full-wave rectified EMG; the latter is referred to as the average EMG (AEMG). To facilitate comparison of the AEMG across experiments and across subjects, the maximum AEMG achieved during the MVC task was expressed relative to the peak-to-peak amplitude of the M wave. This ratio minimized differences due to electrode placement and changes in impedance. For the evoked responses, the dependent variables were *1*) peak-to-peak amplitude of the M wave, *2*) peak twitch force, *3*) time to peak twitch force, and *4*) one-half relaxation time. For the constant-force task, the dependent variable was the coefficient of variation (SD of force fluctuations/mean force × 100) of the force fluctuations about the target force. For the threshold task, the dependent variable was the force contributed by the motor unit to the sustained index finger force.

Motor unit discrimination was accomplished with the use of a computer-based template-matching algorithm (model SPS 8701, Signal Processing Systems). The action potentials of single motor units were distinguished by waveform shape. Interimpulse intervals of the identified motor units were measured (125 $\mu$s resolution) with a built-in function of the discriminator (SPS 8701). The mean, SD, and coefficient of variation of the interimpulse interval were determined with custom-designed software. With the identified action potential as the trigger event, spike-triggered averaging of the force exerted during the threshold task was performed to determine the contribution of the motor unit to the force exerted by the index finger. This was accomplished with the Spike2 data analysis system. The duration of the spike-triggered average was 200 ms with a pretrigger average of 50 ms. The average only included interimpulse intervals ≥100 ms so that the average was limited to discharge rates ≤10 Hz, which provided an estimate of the unfused force contributed by the motor unit to the net force. This restriction was necessary because the hypothesis claims an association between the force fluctuations during the constant-force task and the force contributed by the most recently recruited motor units.

### *Statistical Analysis*

Two-factor analysis of variance (ANOVA) with a repeated-measures design (1 factor within and 1 between) was applied to compare the following values between groups and within groups (across time) and the group-by-time interaction: *1*) muscle volume; *2*) MVC AEMG; *3*) MVC peak force; *4*) training weight; *5*) M-wave amplitude; *6*) peak twitch force, time to peak force, and one-half relaxation time; and *7*) spike-triggered average motor unit force. Subsequently, tests of multiple contrasts were used to locate the differences in these variables within each group. A three-factor ANOVA with two repeated measures (2 factors within and 2 between) was applied to determine the effects of age, force level (%MVC), and time on the coefficient of variation of the force fluctuations during the constant-force task. Unless stated otherwise, the data are reported as means ± SE and a significance level of $P < 0.05$ was used for statistical comparisons.

## RESULTS

The effects of the 12-wk strength-training program were determined after 4, 8, and 12 wk of training and were compared with data obtained before the beginning of training. The training program caused an increase in the volume and strength of the hand muscle and an improvement in the ability of elderly subjects to sustain constant submaximal forces by decreasing the normalized variability in force. However, changes in the ability to control index finger force were not associated with changes in the distribution of motor unit forces.

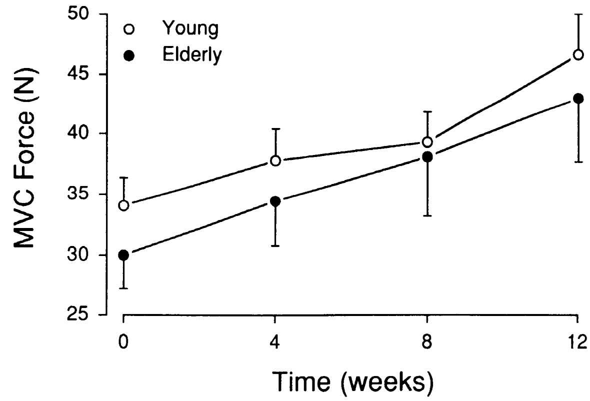


FIG. 3. Increase in maximum voluntary contraction (MVC) force exerted by index finger during isometric contraction in abduction direction. MVC force increased significantly for both young and elderly subjects.

### *MVC*

Before training, there was no difference in strength between the young (MVC force of 34.0 ± 2.3 N) and elderly (30.0 ± 2.6 N) subjects or between the young (34.1 ± 2.7 N) and elderly (37.7 ± 3.3 N) male subjects. However, the young female subjects (33.9 ± 4.6 N) were significantly stronger than the elderly female subjects (23.5 ± 1.4 N). All subjects experienced a significant increase in MVC force with the training program (Fig. 3). After 12 wk of training, MVC force had increased by 36.9 ± 11.9% for the young subjects and by 41.2 ± 8.2% for the elderly subjects. There was no statistical difference due to age between the two groups of subjects in the size of the increase in MVC force ($P = 0.5$) or in its time course ($P = 0.8$). There was, however, an age-gender interaction in that the elderly male subjects had a much bigger increase in strength (53.9 ± 15.3%) than the elderly female subjects (30.7 ± 7.6%). Similarly, the training load increased significantly for the young (127.3 ± 18.9%) and elderly subjects (148.5 ± 30.8%) with the 12-wk program. The initial training load was 3.6 ± 0.3 N for the young subjects and 3.4 ± 0.5 N for the elderly subjects. As with the MVC force, there was no difference between the two groups of subjects in the size of the increase in training load ($P = 0.9$) or in the time course of the increase ($P = 0.7$).

Although there were no differences in the initial and final MVC forces between the two groups of subjects, there was a difference in AEMG associated with MVC (Fig. 4*A*). Before training, AEMG during MVC for the young subjects (0.83 ± 0.09 mV) was significantly greater than that for the elderly subjects (0.58 ± 0.06 mV). In contrast to the changes in MVC force and training load, however, AEMG (mV) did not increase with strength training for either group. After 12 wk of training, AEMG

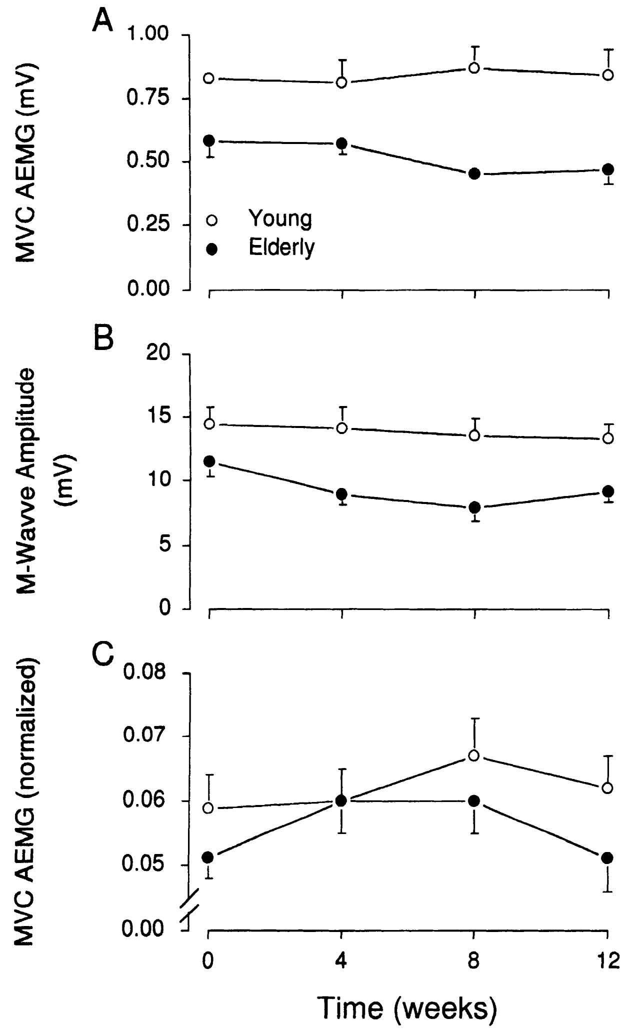


FIG. 4. Change in EMG over course of training program. *A*: absolute rectified average EMG (AEMG) associated with isometric MVC. *B*: change in peak-to-peak amplitude of M wave. *C*: AEMG normalized to peak-to-peak amplitude of M wave. Only significant change in AEMG was increase in normalized AEMG at *week 8* compared with initial value.

increased by 2.5 ± 10.0% for the young subjects and decreased by 20.2 ± 5.6% for the elderly subjects. ANOVA indicated a significant difference between groups, with AEMG greater for the younger subjects.

*Muscle Volume*

As expected with the similar MVC forces, there was no significant difference between the two groups of subjects in the volume of the first dorsal interosseus muscle either before or after the 12-wk strength-training program. The initial volume of the muscle was 8.4 ± 0.6 $cm^3$ for the young subjects and 7.4 ± 0.8 $cm^3$ for the elderly subjects. On the basis of an average muscle fiber length of 3.17 cm and angle of pennation of 9.2° (17), these muscle volumes correspond to average physiological cross-sectional areas of 262 $mm^2$ for the young subjects and 230 $mm^2$ for the elderly subjects. The training program resulted in a significant increase in muscle volume for both the young (9.1 ± 2.2%) and elderly (4.3 ± 0.8%) subjects. The increase was significantly greater for the young subjects. Measurements of the maximum cross-sectional area were less than the change in muscle volume. The initial values for the maximum cross-sectional area were 239 ± 15 and 233 ± 22 $mm^2$ for the young and elderly subjects, respectively. The training program elicited an increase in the maximum cross-sectional area of 7.8 ± 2.9% for the young subjects ($P = 0.018$) and 2.8 ± 1.2% for the elderly subjects ($P = 0.07$).

Although the increase in MVC force was associated with an increase in muscle size (volume and cross-sectional area), the relationship was not consistent across subjects. There was considerable variability in the relationship between MVC force and muscle size both before (Fig. 5, *A* and *B*) and after training (Fig. 5, *C* and *D*). For the young subjects (Fig. 5*D*), there was a negative relationship between the relative increase in muscle size (%initial) after training and the relative increase in MVC force. More of the posttraining variability in muscle size among all subjects was explained by muscle volume ($r^2 = 0.194$) than by cross-sectional area ($r^2 = 0.083$).

*Evoked Responses*

There were no differences between the two groups of subjects, either before or after strength training, in the magnitude and time course of the evoked twitch force. Before training, the peak twitch force evoked by percutaneous electrical stimulation of the ulnar nerve at the wrist was 2.74 ± 0.72 N for the young subjects; this increased by 23.4 ± 13.2% with training. For the elderly subjects, the initial peak twitch force was 2.56 ± 0.27 N; this increased by 22.9 ± 9.2%. The increase in peak twitch force was significant ($P = 0.01$) after 12 wk of training but not after 4 or 8 wk of training and was not different for the two groups ($P = 0.5$).

The time course of the twitch response was not different for the two groups of subjects and did not change with training. Twitch contraction time was 64.9 ± 3.7 and 65.9 ± 3.6 ms before and after training, respectively, for the young subjects. For the elderly subjects, twitch contraction time was 64.4 ± 3.1 and 68.6 ± 2.3 ms before and after training, respectively. Similarly, one-half relaxation time was 64.5 ± 7.7 and 64.3 ± 4.7 ms before and after training, respectively, for the young subjects and was 69.6 ± 2.1 and 68.8 ± 2.9 ms before and after training, respectively, for the elderly subjects.

The amplitude of the compound muscle action potential (M wave) associated with the evoked response was consistently larger for the young subjects. Before training, the amplitude was 14.4 ± 1.4 and 11.5 ± 1.2 mV for the young and elderly subjects, respectively. The amplitude of the M wave did not change for the young subjects over the course of the training study (Fig. 4*B*). In contrast, M-wave amplitude declined significantly during the 12-wk strength-training program for the elderly subjects. It was significantly less at 4, 8, and 12 wk compared with the initial value (Fig. 4*B*). After 12 wk of training, M-wave amplitude (%change) had declined by 2.9 ± 9.6 and 16.5 ± 7.2% for the young and elderly subjects, respectively.

To reduce some of the variability in AEMG measurements due to changes in skin impedance and electrode placement, we normalized AEMG values associated with

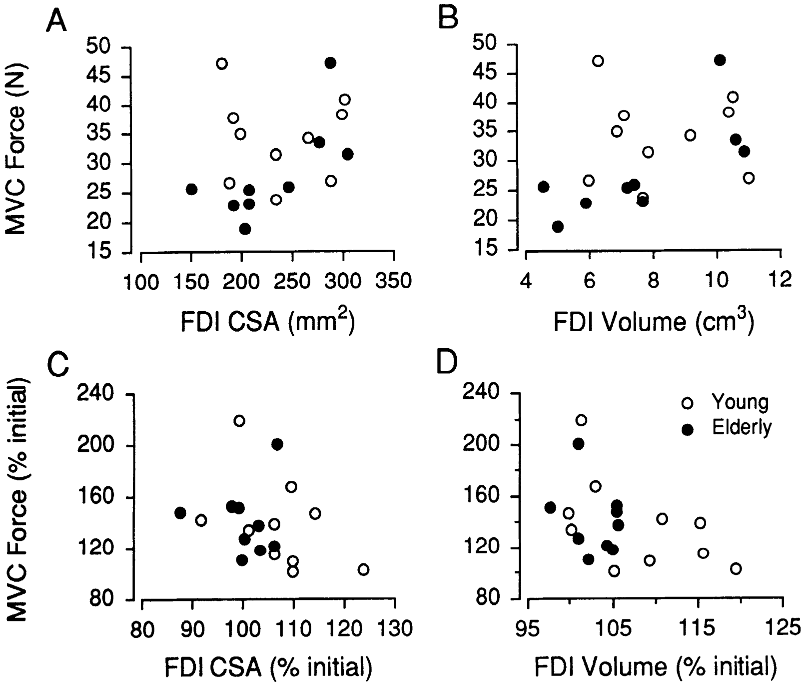


FIG. 5. Relationship between muscle size and MVC force before (*A–B*) and after (*C–D*) 12 wk of strength training. FDI, first dorsal interosseus; CSA, cross-sectional area. For 1st 2 subjects measured (1st 2 data points in *C*), hand was not aligned correctly in magnetic resonance imaging machine, which resulted in change in CSA of <100% of initial. Linear regression analysis for all subjects indicated that <20% of variability in MVC force was explained by differences in muscle size for each data set (*A–D*). *A*: $r^2$ = 0.115. *B*: $r^2$ = 0.181. *C*: $r^2$ = 0.083. *D*: $r^2$ = 0.194.

MVC for each experiment relative to the amplitude of the M wave recorded in that experiment. In contrast to the absolute AEMG (mV), the normalized AEMG before training was not different for the young (5.9 ± 0.5%) and elderly (5.1 ± 0.3%) subjects. Furthermore, the change in normalized AEMG over the course of the training program was similar for the two groups of subjects (Fig. 4*C*); there was no significant interaction. After 8 wk of training, there was a significant increase in normalized AEMG for both the young (10.8 ± 13.8% change) and elderly (10.1 ± 15.9% change) subjects. By *week 12*, however, the normalized AEMGs declined for both groups of subjects and were not different from the initial values.

### *Constant-Force Task*

As Galganski et al. (12) have reported, the elderly subjects had greater normalized force fluctuations than the young subjects when sustaining a submaximal isometric force at a constant value for 20 s (Fig. 6). This difference, however, was only evident (Table 1) at the low target forces (2.5, 5.0, and 20.0% MVC) and not at the greatest force (50% MVC). Additionally, the coefficient of variation declined, especially for the elderly subjects, as the target force increased. The training program had a minimal effect on the ability of the young subjects to sustain a constant force, but the elderly subjects improved significantly at the lowest three target forces. For example, after 12 wk of training the coefficient of variation for the 20% target force declined by 0.38 ± 10.7% for the young subjects and by 11.7 ± 14.0% for the elderly subjects (Fig. 7*A*; Table 1). This effect was not present for the 50% target condition (Fig. 7*B*).

In contrast, there was no difference statistically in the size of the absolute force fluctuations (SD) either due to age or across the 12-wk training program at each of the target forces. For example, for the 2.5% MVC target force the mean (±SE) of the SD of the force fluctuations was 0.055 ± 0.005 N for the young subjects across the 12 wk and 0.069 ± 0.004 N for the elderly subjects. Similarly, for the 50% MVC target force the values were 0.607 ± 0.040 N for the young subjects and 0.720 ± 0.057 N for the elderly subjects. There was, as indicated by these examples, a substantial increase ($P < 0.0001$) in SD of the

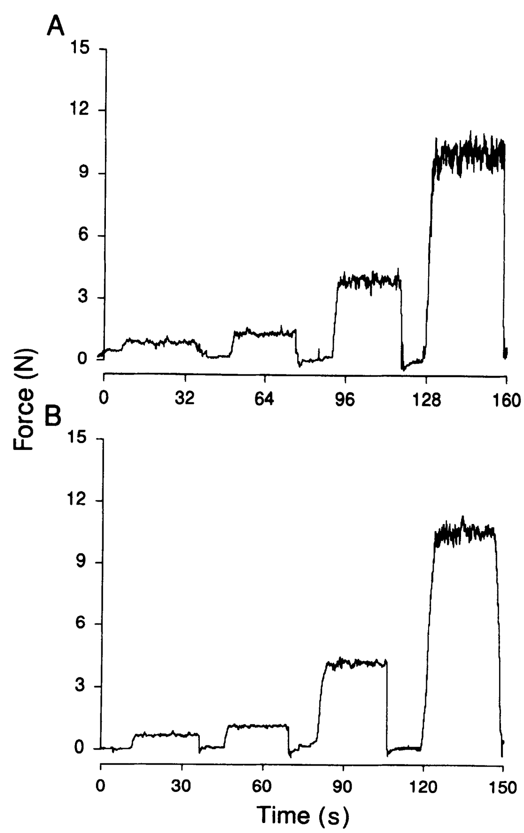


FIG. 6. Representative performances by elderly subjects during constant-force task before (*A*) and after (*B*) 12 wk of strength training. Target forces were set at 2.5, 5.0, 20.0, and 50% of MVC force. Records show reduction in force fluctuations at conclusion of training program.

TABLE 1. *Coefficient of variation of force fluctuations for constant-force task performed at submaximal target forces by young and elderly subjects before and after 12 wk of strength training*

| | Young | | | Elderly | | |
|---|---|---|---|---|---|---|
| | Before | After | %Change | Before | After | %Change |
| 2.5% MVC | 5.6±1.0 | 4.8±0.7 | 4.4±22.0 | 9.5±1.5 | 5.8±0.7 | −29.3±10.2 |
| 5% MVC | 3.9±0.7 | 3.7±0.5 | 7.7±17.8 | 5.4±0.7 | 4.2±0.8 | −20.6±10.3 |
| 20% MVC | 2.0±0.4 | 2.0±0.2 | −0.4±10.7 | 3.8±0.8 | 2.7±0.3 | −11.7±14.0 |
| 50% MVC | 3.5±0.4 | 3.1±0.3 | −3.1±11.8 | 3.7±0.4 | 3.9±0.5 | 6.1±6.4 |

Values are means ± SE; $n$ = 10 young and 11 elderly subjects. Coefficients of variation are expressed in percentages. MVC, maximum voluntary contraction.

force fluctuations for both the young and elderly subjects with an increase in target force.

### Motor Unit Force

Because each subject was tested on four occasions (*weeks 0, 4, 8,* and *12*) and an average of 8.4 motor units were examined in each experiment, the force and discharge characteristics of 668 motor units were recorded in this study. Each motor unit was characterized by the index finger force at which the unit could sustain a minimal continuous discharge and the spike-triggered average force at that discharge rate. The average discharge rates during this task were 8.50 ± 0.07 Hz for the young subjects and 9.00 ± 0.09 Hz for the elderly subjects. The measurement of spike-triggered average force did not represent motor unit twitch force but rather was an estimate of the unfused force contributed by the motor unit when it discharged at the rates that occur at the time of recruitment. The average (±SE) number of events included in the spike-triggered average was 568 (±11) with a range of 24–2,088. The distribution of motor unit forces indicated that for both the young and elderly subjects there was a linear relationship between the sustained force and the spike-triggered average force (Fig. 8). Accordingly, the spike-triggered average force was greater for those units that required a greater force to sustain a minimal discharge rate.

Because the distributions (mN and %MVC) of motor unit force were not normal for the two groups of subjects, the data were transformed with logarithms (base 10). The mean values of the transformed forces for the young subjects were significantly less (1-way ANOVA) than those for the elderly subjects. Motor unit force ($n$ = 668) for the young subjects was 10.5 ± 0.8 mN and 0.038 ± 0.002% MVC compared with 11.9 ± 0.8 mN and 0.036 ±

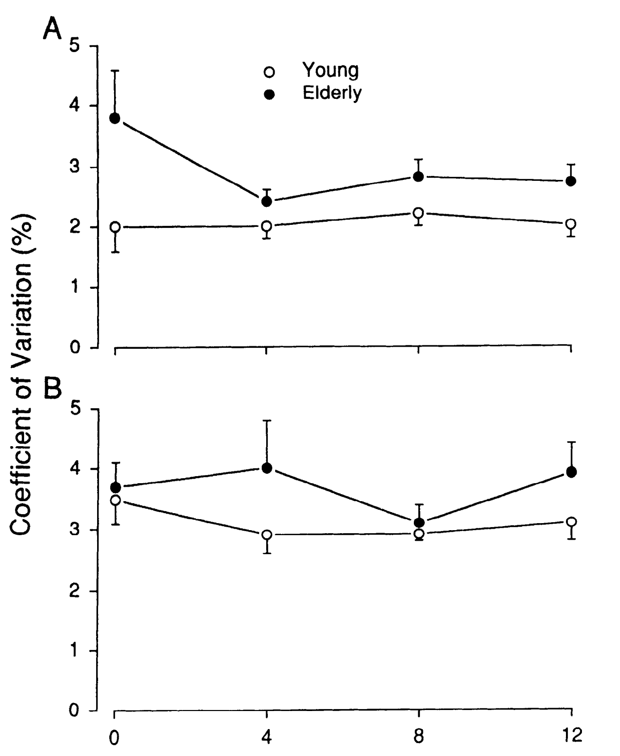


FIG. 7. Coefficient of variation in force about each mean target force for young and elderly subjects over course of training program. Data are means ± SE for 20% (*A*) and 50% target force (*B*). Reduction in coefficient of variation over 1st 4 wk, which was significant for elderly subjects, was similar to those for 2.5, 5.0, and 20.0% target forces.

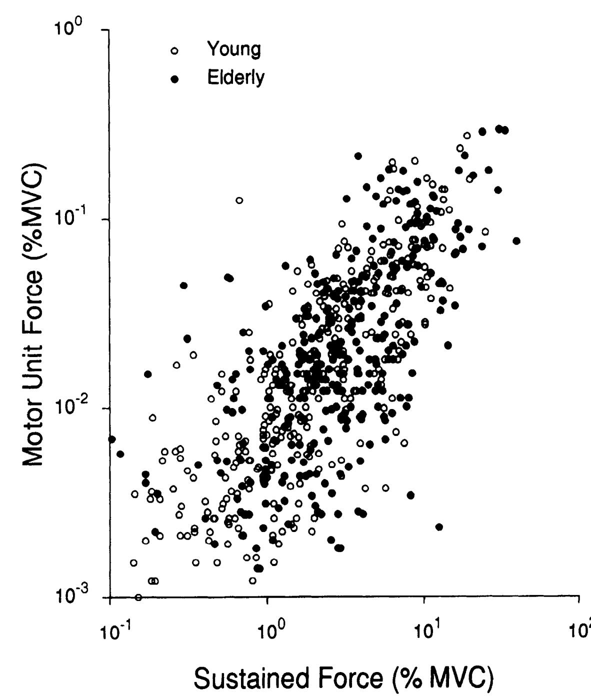


FIG. 8. Log-log plot of spike-triggered average motor unit force as function of index finger force that was sustained during threshold task. Sustained force corresponds to force required for isolated motor unit to discharge at minimal rate. Forces are normalized to MVC force. Data are for all experiments (*weeks 0, 4, 8,* and *12*) for young and elderly subjects. Distributions indicate that fewer low-threshold motor units were observed for elderly subjects.

TABLE 2. *Threshold force and absolute, normalized, and logarithm of motor unit force as determined by spike-triggered average for young and elderly subjects at different times during 12-wk strength-training program*

| | Young | | | | | Elderly | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $n$ | Threshold, N | Absolute, mN | Normalized, %MVC | Transformed, log mN | $n$ | Threshold, N | Absolute, mN | Normalized, %MVC | Transformed, log mN |
| *Week 0* | 91 | 1.686±0.170* | 13.0±2.7 | 0.040±0.0083 | 0.933±0.047 | 76 | 1.995±0.238† | 12.9±3.2 | 0.045±0.0101 | 0.898±0.047 |
| *Week 4* | 83 | 0.989±0.112 | 7.3±2.3 | 0.021±0.0072 | 0.650±0.053 | 82 | 1.433±0.181 | 9.4±1.9 | 0.030±0.0067 | 0.743±0.052 |
| *Week 8* | 85 | 1.213±0.128 | 11.3±2.4 | 0.029±0.0053 | 0.600±0.054 | 88 | 1.329±0.157 | 12.2±1.9 | 0.035±0.0083 | 0.773±0.058 |
| *Week 12* | 87 | 1.007±0.129 | 9.5±3.1 | 0.021±0.0084 | 0.772±0.061 | 76 | 1.720±0.219 | 13.1±2.5 | 0.030±0.0097 | 0.826±0.059 |

Values are means ± SE; $n$, no. of motor units (MUs). * Significantly different compared with *weeks 4, 8,* and *12*, $P < 0.05$. † Significantly different compared with *weeks 4* and *8*.

0.002% MVC for the elderly subjects. This difference is apparent in Fig. 8 by a lesser number of low-threshold motor units for the elderly subjects.

In contrast to the difference in motor unit force between the young and elderly subjects, the strength-training program did not increase the spike-triggered average force of the motor units for either group of subjects (Table 2). The statistical analysis of the effect of training was performed on the logarithmically (base 10) transformed motor unit forces for the two groups of subjects separately. Before training, the average force was 13.0 ± 2.7 mN (log 0.933 ± 0.047) for the young subjects and 12.9 ± 3.2 mN (log 0.898 ± 0.047) for the elderly subjects. The final average forces were 9.5 ± 3.1 mN (log 0.772 ± 0.061) and 13.1 ± 2.5 mN (log 0.826 ± 0.059) for the young and elderly subjects, respectively. On the basis of a comparison of the log data, this change with training was not significant. When the motor unit forces were averaged for each subject and the percent change was determined across sessions, there were nonsignificant changes of −22.1 ± 25.2 and 13.2 ± 26.8% between the initial and final values for the young and elderly subjects, respectively.

Although training did not increase motor unit force for either group of subjects, there were some differences between sessions. For example, for the young subjects the logarithmically transformed forces were less after 4 and 8 wk of training compared with values before training. This effect was due to a sampling bias in the motor units studied at the different time points (*weeks 0–12*). For the young subjects, the average threshold of the motor unit sample was 1.686 N at *week 0*, which was significantly greater than 0.989 N at *week 4*, 1.213 N at *week 8*, and 1.007 N at *week 12* (Table 2). A similar trend was observed with the elderly subjects in which the threshold force at *week 0* (1.995 N) was significantly greater than those at *week 4* (1.433 N) and *week 8* (1.329 N). For the elderly subjects, however, there were no significant differences in the logarithmically transformed motor unit forces across time.

To underscore that these differences were due to a change in the motor unit samples and not a training effect, Table 3 presents the repetitive-discharge threshold data based on the chronological sequence (*groups I* and *II*) in which the data were obtained. For the young subjects in *group I*, the mean threshold at *week 12* was significantly less than the means at *weeks 0, 4,* and *8*. For the young subjects in *group II*, the mean threshold at *week 0* was significantly greater than those at *weeks 4, 8,* and *12*. For the elderly subjects in *group I* there was no difference across time, whereas in *group II* the mean threshold at *week 0* was greater than those at *weeks 4* and *8*. These comparisons suggest that there were small but significant shifts in the motor units sampled at each time point (*weeks 0–12*) for the young and elderly subjects. Consequently, the apparent association between the decline in motor unit force (Table 2) and the coefficient of variation for the force fluctuations (Table 1) was not due to covarying physiological phenomena. Taken together, the data indicate that motor unit force did not change across the 12-wk training program.

## DISCUSSION

The main findings of this study were that a 12-wk strength-training program increased the strength of a hand muscle and was associated with an improvement in the ability of elderly subjects to maintain a constant submaximal force. Contrary to expectations, these observations indicated that the reduced ability of elderly subjects to maintain a constant submaximal force was not dependent on motor unit size (spike-triggered average force).

TABLE 3. *Number of MUs tested and repetitive-discharge threshold for young and elderly subjects tested in groups I and II for 12-wk strength-training program*

| | *Group I* | | | | *Group II* | | | |
|---|---|---|---|---|---|---|---|---|
| | $n$ | Young, N | $n$ | Elderly, N | $n$ | Young, N | $n$ | Elderly, N |
| *Week 0* | 41 | 1.532±0.213 | 34 | 2.257±0.449 | 50 | 1.813±0.256† | 42 | 1.785±0.238‡ |
| *Week 4* | 40 | 1.336±0.195 | 33 | 2.064±0.336 | 43 | 0.668±0.096 | 49 | 1.010±0.179 |
| *Week 8* | 43 | 1.493±0.204 | 38 | 1.503±0.259 | 42 | 0.927±0.142 | 50 | 1.197±0.201 |
| *Week 12* | 44 | 0.862±0.117* | 32 | 2.063±0.384 | 43 | 1.156±0.231 | 44 | 1.472±0.250 |

Values are means ± SE where indicated, $n$, no. of MUs. * Significantly different compared with *weeks 0, 4,* and *8*, $P < 0.05$. † Significantly different compared with *weeks 4, 8,* and *12*. ‡ Significantly different compared with *weeks 4* and *8*.

Furthermore, the increase in strength could not be explained completely by increases in muscle volume or activation (EMG).

*Constant-Force Task*

Galganski et al. (12) reported that elderly subjects produced greater force fluctuations during a constant-force task and that this effect was associated with greater motor unit forces, as determined by spike-triggered averaging. This association led to the hypothesis that the inability of elderly subjects to sustain a constant submaximal force was due to their larger motor units. The purpose of this study was to determine the effect of a strength training-induced increase in motor unit force on the ability of elderly subjects to control submaximal isometric force.

The ability of elderly subjects to sustain a constant force improved over the course of the training program. For two reasons, however, this adaptation was unrelated to the distribution of low-threshold motor unit forces within a muscle. First, the reduction in the coefficient of variation for the force fluctuations was greatest in the 1st 4 wk of training (Fig. 7), before the time at which significant muscle hypertrophy occurs (7, 23). Furthermore, the improvement in performance may have been evident even before *week 4*, but we did not test our subjects before that time point. Second, there was no change in the distribution of spike-triggered average forces for the low-threshold motor units with training (Table 2), despite significant reductions in the coefficient of variation (Table 1). Because the motor units isolated in the threshold task typically had recruitment thresholds of <10% MVC force (Fig. 8), these motor units would have been responsible for the force exerted during the 2.5 and 5% constant-force tasks. The dissociation between the coefficient of variation for these tasks and spike-triggered average force suggests that motor unit force is not the primary determinant of the force fluctuations.

This conclusion, however, assumes that the increase in the absolute target force with training was not responsible for the decline in the coefficient of variation. Because MVC force increased with training and there was an inverse relationship between the coefficient of variation and target force, it is possible that the increase in the absolute target force might explain the reduction in the coefficient of variation. If we assume that the increase in MVC force was linear (Fig. 3), the average increase in MVC force would be ~14% of the pretraining MVC for each 4-wk period. Consequently, after 4 wk of training (when most of the reduction occurred) the target force for the constant-force task would have been 2.9% of the pretraining MVC for the 2.5% task, 5.7% for the 5.0% task, 22.8% for the 20.0% task, and 57% for the 50.0% task. The increases in target force for the two lowest targets were well below those forces associated with a pronounced decline in the coefficient of variation (12). It seems, therefore, that the decrease in the coefficient of variation of the force fluctuations cannot be explained by the absolute increase in the target forces.

It is not surprising that the training program elicited an increase in muscle cross-sectional area but no change in spike-triggered average force for the low-threshold motor units. An animal model of compensatory hypertrophy, for example, has been shown to produce marked whole muscle hypertrophy but minimal changes in the cross-sectional area of muscle fibers belonging to type S and type FR motor units (33). Although some training programs can produce an increase in the size of type I muscle fibers, most human studies have indicated that type II muscle fibers typically experience the greatest increases in cross-sectional area (11, 14, 29). Although the motor unit forces reported in Table 2 appear to decline with training, these changes were only statistically significant for the young subjects at *weeks 4* and *8* compared with *week 0*, and this effect appeared to be due to small but significant shifts in the motor units sampled at each time point as indicated by the variation in the repetitive-discharge threshold (Table 3).

These results are not consistent with the hypothesis that the greater coefficient of variation is due to increased motor unit forces in elderly subjects. Instead, we are left with the observation that the coefficient of variation for the force fluctuations is initially greater in the elderly subjects but that this declines with practice. One possible explanation for the change in force fluctuations with practice may be related to conditioning (9, 34) of the pulsatile control strategy of agonist and antagonist muscles adopted by the nervous system in the performance of stationary and slow finger movements (32). However, this possibility awaits further evaluation.

*Mechanisms Mediating Increase in Strength*

Although many studies have indicated a decline in muscle mass and strength with age (8), we have found only minor changes in these variables for the first dorsal interosseus muscle of healthy elderly subjects (60–75 yr). Sometimes the decline in MVC force has been statistically significant (29.4 vs. 24.1 N, $P = 0.05$; Ref. 12), but at other times it has not (34.0 vs. 30.0 N; present study). Gender can affect this comparison; however, as in the present study, we found no difference in MVC force due to age for the male subjects but a significant decline for the elderly female subjects compared with the young female subjects. Nonetheless, the training program produced marked increases in the strength of the hand muscle, as indicated by significant increases in MVC force, training load, and twitch force. Importantly, the magnitude of the increase in strength was similar for the young and elderly subjects. The observation that a hand muscle of elderly subjects is capable of hypertrophy has considerable functional significance and is consistent with previous reports for such muscles as the elbow flexors (3) and the knee extensors and flexors (10, 11). These findings clearly indicate that many skeletal muscles of elderly individuals are responsive to stress associated with exercise.

Another noteworthy feature of the training program was the type and amount of exercise that was used to produce significant increases in strength. For 12 wk, each subject performed 3 training sessions/wk, with each training session involving 6 sets of 10 repetitions. Each repetition involved abduction and adduction of the index finger while lifting a load that acted in the adduction direction. For the first dorsal interosseus muscle, a single repetition required a concentric and an eccentric contraction. Although the training program involved only a moderate amount of unsupervised exercise, the subjects experienced an average increase of 140% in the load that could be lifted over the 12-wk period. Furthermore, this activity produced a smaller (39%) but highly significant increase in the maximum isometric force that the index finger could exert in the abduction direction. Rutherford and Jones (27) reported similar increases in training load and isometric MVC for the knee extensor muscles after 12 wk of strength training.

In general, the observed increase in strength could be mediated by an enhancement of the neural activation (EMG) or an adaptation related to muscle factors (i.e., size, specific force, and angle of pennation). As others have reported for cross-sectional area (18, 23), we found that a moderate strength-training program elicited a modest increase in muscle volume in both the young and elderly subjects. After 12 wk of strength training, the average increase in muscle volume for all subjects was 7.1 ± 1.4% compared with an increase in MVC force of 39.2 ± 6.8%. Because the specific force of muscle ($N/cm^2$) does not increase with hypertrophy (1, 18, 20), only a minor component of the increased MVC force (strength) can be explained by an increase in muscle size. Furthermore, there was significant variability across subjects in the training-related increases in muscle size (volume and cross-sectional area) and MVC force (Fig. 5).

Although many studies have reported an increased EMG with strength training (23, 28), others have found no such effect (13, 30). Our subjects exhibited a nonmonotonic increase in the normalized EMG that involved a significant increase after *week 8* but a subsequent decline by *week 12* (Fig. 4). Because of the large intra- and intersubject variability with multiple EMG measurements, we found no significant changes in the absolute (mV) EMG. To minimize the variability with these measurements, we normalized AEMG relative to the peak-to-peak amplitude of the M wave, which resulted in a significant increase in EMG at *week 8*. This normalization procedure minimized the variation in EMG across sessions and subjects due to differences in electrode placement and skin impedance.

The changes in the normalized EMG were influenced by an age-related decline in the M-wave amplitude (Fig. 4*B*). The peak-to-peak amplitude of the M wave is influenced by *1*) the excitability of the muscle fibers (due to changes in the resting membrane potential), *2*) the proportion of the muscle fibers within the recording area of the electrodes, and *3*) skin impedance. In contrast to our observation of a training-induced decline in M-wave amplitude for the elderly, Hicks et al. (15) reported an increase in M-wave amplitude for two of three muscles (brachioradialis and thenar but not tibialis anterior) in elderly subjects after participation in a 12-wk whole body conditioning program. They attributed this effect to a hyperpolarization of the resting membrane potential due to enhanced activity of the $Na^+$-$K^+$ pumps as a consequence of training (16). Although the two studies used different recording techniques (monopolar for Hicks et al. and bipolar in the present study), this difference was probably not important because our M-wave amplitudes were greater than those for the elderly subjects of Hicks et al. Interestingly, the two muscles reported by Hicks et al. to exhibit an increase in M-wave amplitude with training (brachioradialis and thenar muscles) had the smallest pretraining average amplitudes (4.8 and 5.2 mV, respectively). In contrast, the average pretraining M-wave amplitude for the tibialis anterior muscle, which did not change with training, was 8.8 mV (15). Similarly, we found an average pretraining M-wave amplitude for the first dorsal interosseus of 11.5 mV. Perhaps the direction of the change in M-wave amplitude with training depends on its pretraining amplitude.

In addition to an increase in MVC force, the training program produced an increase in twitch force. Although the twitch is influenced by the quantity of contractile protein in a muscle, it is equally sensitive to changes in the processes involved in excitation-contraction coupling and to changes in series elasticity. The twitch was evoked by ulnar nerve stimulation, which activates the antagonist muscle (second palmar interosseus) as well as the first dorsal interosseus. This may explain why we did not observe an increase in twitch contraction time for our elderly subjects, as has been reported previously when the stimulation was applied directly over the muscle (24). Nonetheless, twitch force increased over the 12-wk training program. The mechanisms underlying the increase in twitch force, however, were not identical to those associated with the increase in MVC force because the changes in the two variables did not occur in parallel. The increase in MVC force was essentially linear (Fig. 3), whereas twitch force for both groups of subjects was not different from initial values at *weeks 4* and *8* but was greater only at *week 12*. This dissociation suggests that twitch force is not a valid index of muscle strength.

Perhaps our most puzzling result was the consistent increase in MVC force for the duration of the study but the decline in normalized EMG by the end of the training program. This suggests that the increase in MVC force at 12 wk was not due to greater motor unit activity (recruitment and discharge rate). Furthermore, because the average increase (%initial) in muscle volume was only 7%, some other mechanism, often referred to as "neural factors," must have been responsible for the increase in MVC force. Some candidates include a reduction in the coactivation of antagonist muscles, enhanced distribution of activity among synergist muscles, and qualitative changes in the pattern of motor unit discharge (e.g., double discharges, reflex potentiation, and synchronization).

Some studies have found a reduction in the coactivation of antagonist muscles (6), differences in the distribution of activity among synergist muscles (23), and an improvement in the coordination among the muscles involved in the task (27) as a consequence of strength training. One of the advantages of our experimental paradigm was that it involved a relatively simple task (abduction of the index finger) for which there is a single agonist muscle (first dorsal interosseus) with an EMG we could measure. Because EMG declined from *weeks 8–12*, we cannot attribute the increase in MVC force to a consistent improvement in the ability to maximally activate the first dorsal interosseus muscle. Rather, we suspect a significant role for changes in the distribution of neural activation to the involved muscles (antagonists and synergists). For example, in other experiments we have found that the level of coactivation of the antagonist muscle (second palmar interosseus) can be substantial during an MVC task involving abduction of the index finger as performed by both young and elderly subjects (unpublished observations of D. Glendinning and R. M. Enoka). If the subjects can learn to decrease the amount of coactivation during the training program, this will result in a net increase in the index finger force for the same EMG input to the first dorsal interosseus muscle. This possibility is being examined with magnetic resonance imaging techniques (35).

In conclusion, a 12-wk strength-training program involving a dynamic finger exercise resulted in a significant increase in the isometric strength of a hand muscle. This increase in strength, however, could not be explained completely by the increase in muscle volume or the changes in the surface-recorded EMG. Furthermore, the elderly subjects exhibited an improved ability to maintain a constant submaximal force that was unrelated to the measured training-induced adaptations. These results were not consistent with the hypothesis that the greater coefficient of variation for the force fluctuations in elderly subjects is due to increased forces for single motor units.

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