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Training-Related Adaptations in Motor Unit Discharge Rate in Young and Older Adults

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Background. This study evaluated changes in motor unit (MU) firing rates in young and older adults during exercise training.

Methods. Vastus lateralis MU discharge rates were measured in 8 young and 7 older adults. Each participant performed isometric knee extension contractions at 10%, 50%, and 100% of maximal voluntary contraction or effort (MVC) on two separate occasions. Participants then completed a 6-week resistance exercise training protocol.

Results. Significant increases in maximal force were observed as early as 1 week after the first baseline testing session, and these were accompanied by increases in the MU discharge rate. Exercise training increased maximal voluntary force by 29% and 36% in the young and older adults, respectively. Motor unit discharge rates at 100% of maximal effort were significantly greater in the young (24.7 pps) than in the older adults (17.8 pps). Furthermore, the young adults also exhibited significantly greater discharge rates at 50% MVC, but there were no differences at the 10% force level. Maximal MU discharge rates increased during the 1-week period separating the two initial testing sessions. After the 6-week training period, maximal MU discharge rates were 15% higher for the young adults and 49% higher for the older adults. No changes in discharge rates were observed for either group at 10% or 50% MVC after exercise training.

Conclusions. The early increase in maximal MU discharge rate with repeated maximal force assessment may comprise an important neural mechanism mediating early, rapid gains in muscular force capability.

SIGNIFICANT losses of muscle mass and strength can occur in older adults (1). In the neuromuscular system, substantial motoneuron loss begins in about the sixth decade, resulting in fewer motor units (MU), larger MU innervation ratios, and alteration in MU territories as MUs are remodeled through collateral reinnervation (1,2). Maximal MU discharge rates also decrease with advancing age (3,4). These deleterious age-related declines in motor function have encouraged efforts to improve functional strength and increase muscle mass in older adults through various forms of exercise training. Indeed, resistance exercise training increases maximal isometric force with equal effectiveness in both older adults and younger persons (5,6).

However, a paradox exists in our understanding of the mechanisms underlying gains in maximal voluntary force achieved during a training program. The initiation of exercise training is accompanied by rapid gains in maximal force (7,8). In fact, exerting a few maximal contractions on just a few days increases muscular strength by 8% to 15% (9,10). The strength gains in this early phase are typically attributed to ''neural factors'' (8). However, the physiologic, enzymatic, morphologic, and other muscle-related changes that accompany training are only noted after about 30 days, when the rate of muscular force gains slows considerably (11). Conversely, we know little of the mechanisms underlying the early gains in force-generating capacity. Thus, our knowledge of the mechanisms governing increases in muscular force through resistance exercise training is best developed for the time period when the rate of maximal force gain is lowest (at least 30 days after training onset), but our understanding is least developed for the early training interval when maximal force is increasing at the greatest rate.

Recently, we found that the experience of performing maximal isometric contractions using the fifth finger abductor produces a marked increase in maximal MU discharge rate when remeasured 48 hours later (12). In the same investigation, resistance exercise training produced a decline in maximal MU discharge rates after 2 weeks; after 6 weeks of exercise, discharge rates were similar to those observed in the initial testing session.

The recruitment and rate coding strategies are different in small muscles than they are in larger muscles (13,14). We might reason that the adaptive response to resistance exercise training is also different in small and large muscles. We conducted an experiment to determine what changes in vastus lateralis MU discharge rate would occur while participants gained experience performing maximal isometric knee extension contractions. We then determined what changes in discharge rate would occur in young and older adults during a subsequent period of resistance exercise training. Inasmuch as the maximal discharge rate might be more important in larger muscle groups than it is in smaller muscles, we hypothesized that resistance exercise training would increase the maximal discharge rate in the knee extensors in young and older adults.

METHODS

Participant Selection

Participants consisted of 8 young adults (mean age, 21 years; age range, 18 to 29 years) and 7 older adults (mean age, 77 years; age range, 67 to 81 years). All volunteers gave informed consent. None of these persons had resistance training experience within the previous year. We excluded persons with neuromuscular or orthopedic disorders.

Measurement Schedule

Each participant came to our laboratory for four separate measurement sessions. These measurement sessions included assessment of maximal voluntary knee extensor force (MVC) and MU discharge rates during both submaximal and maximal voluntary contractions. The first two testing sessions were conducted before resistance training and separated by 7 days. Because maximal force frequently increases as a consequence of repeated assessment (7,9,10), these first two measurement sessions aimed to determine what alterations in MU discharge rate might occur during this early time interval. The third measurement session followed 2 weeks of resistance exercise training, and the fourth and final session was scheduled after the sixth and last week of the training protocol. Each testing session was scheduled at least 24 hours after a training session.

Exercise Training

After the second testing session, a 6-week resistance training protocol was initiated. Three training sessions were conducted each week using the nondominant knee extensors. The training protocol included three sets of 10 dynamic knee extension contractions using an initial load equivalent to 85% of the participant's one-repetition maximum and three 5-second maximal isometric contractions at the testing knee angle of 110°. For the dynamic contractions, the load was progressively increased as force increased so that only 10 contractions could be completed.

Force Measurements

Participants sat with both the knee and hip at 110° (180° = full extension). A force transducer, tested for linearity and hysteresis (MB-250; Interface, Scottsdale, AZ), was coupled to a stiff cuff placed around the ankle. The force signal was amplified, digitally sampled (50 samples/s), and stored on a microcomputer. Participants performed three MVCs, with the best of the three voluntary efforts recorded as the 100% MVC value. To encourage maximal effort, the participant received verbal encouragement, and force feedback was provided in real-time using a computer monitor.

Motor Unit Recordings

Muscle fiber action potentials were recorded using procedures described in previous investigations (3,15,16). The recording electrode was inserted in the vastus lateralis muscle, and the resultant signals were amplified, bandpass filtered (1 kHz to 10 kHz; –3 dB), digitally sampled (51,200 samples/s), and stored. Customized algorithms were used to identify MU discharges and group them into MU action potential trains. These procedures have been successful in recognizing MU activity at contraction intensities up to 100% MVC (3,15,16). Figure 1 shows sample MU signals obtained at maximal effort.

Testing Protocol

Each testing session began with the assessment of maximal voluntary force. The electrode was inserted into the nondominant vastus lateralis muscle and positioned into a suitable site. Several recordings were obtained while the participant performed MVCs and submaximal contractions at 10% and 50% MVC. The MU data were obtained from multiple muscle locations to minimize sampling bias.

Data Analyses

For the maximal effort contractions, maximal discharge rates were calculated using the five shortest consecutive interspike intervals at the maximal force level. Mean discharge rates during the submaximal contractions were obtained from the steady-state portion of the contraction when participants had reached either 10% or 50% MVC. In all cases, these calculations excluded trains containing doublet discharges (interspike intervals <10 ms). On each day, the discharge rates for all MUs obtained were averaged for each person and these means were used for statistical analyses.

The statistical analyses were designed to provide the answers to two questions. First, can the experience of repeating isometric contractions alter MU discharge rate? A repeated measures analysis of variance design incorporating the two groups, three force levels, and the two baseline days was conducted to aid in the interpretation of the results to this first question. Second, does a 6-week resistance exercise program alter MU discharge rates? A similar analysis of variance model was used to help interpret these results, with the three levels of the days factor comprising the second baseline day and the 2-week and 6-week testing days.

RESULTS

Muscular Force

Initial maximal isometric knee extensor force scores were 28% higher in the young adults than in the older adults, and a statistically significant difference between the two groups was maintained throughout the training regimen ($p = .02$, Figure 2). Figure 2 shows that maximal force increased as early as the second test session, averaging 10% in the older adults and 16% in the young adults. The increase in maximal force between the first two sessions was significant ($p = .006$), indicating that repeating maximal isometric contractions over as few as 2 days results in greater isometric knee extensor strength.

The resistance exercise training protocol was equally effective in both groups, resulting in an average 33% muscular force gain compared with the first baseline test ($p < .0001$, Figure 2). An analysis of variance design revealed no significant group–day interaction ($p = .25$), indicating that the muscular strength gain was achieved at the same rate in both groups of participants.

Motor Unit Discharge Rates

Across the 4 testing days, a total sample of 1145 MU action potential trains were identified in the young and older adults. The sample included 439 trains at 100% MVC, 406 trains at 50% MVC, and 149 MU trains at 10% MVC. As expected, MU discharge rates in the vastus lateralis increased with muscular force ($p < .0001$). Average

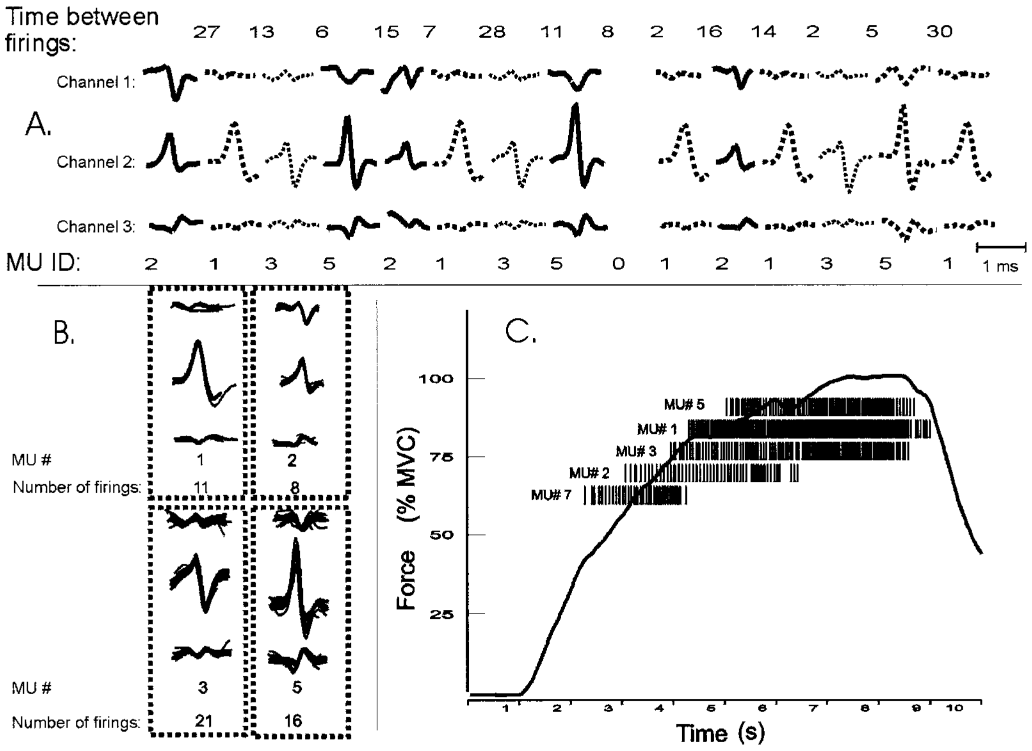

Figure 1. Sample motor unit (MU) signals were recorded from 1 participant at maximal effort. **A,** Four different MUs were followed in this portion of the contraction; MU 0 was not included in the analysis. Successive occurrences of these MU firings are plotted; the time between epochs is shown at the top. The multichannel recording enhances the ability to track these MUs at high force levels. **B,** Superimposed consecutive firings display the ensemble template of these 4 MUs. **C,** The overall time course of the MU firings and muscular force produced during this contraction is shown. The spikes plotted in A and B were obtained at approximately 5.3 seconds from the start of the contraction. Because MUs 2, 3, and 7 were not tracked at maximal effort, they were not included in the statistical analysis. MVC, maximal voluntary contraction or effort.

pretraining discharge rates were 9.3 impulses/second (imp/s) at 10% MVC, 15 imp/s at 50% MVC, and 21.6 imp/s at maximal effort (100% MVC).

Vastus lateralis MU discharge rates were significantly lower in the older adults than in the college-age participants (Figure 3). These between-group discharge rate differences were significant at 50% MVC ($p = .02$) and 100% MVC ($p = .005$); little difference between the two groups was evident at 10% MVC ($p = .56$). At 50% MVC, for example, the mean MU discharge rate was 17.8 imp/s for the young adults and 14.0 imp/s for the older adults.

A 19% increase in maximal (100% MVC) discharge rate occurred during the 1-week interval between the two preexercise testing sessions ($p = .08$). The increase in maximal discharge rate corresponded approximately to the increase in maximal force during this period. Once exercise training began, further increases in the MU discharge rate were modest, with no significant increase noted between the second baseline session and the last testing session ($p = .31$). Consequently, when pooled over all four testing sessions, the MU discharge rate increased significantly at 100% MVC ($p = .04$, Figure 3). The rate of discharge rate increase over the exercise training interval was similar between the two groups, as demonstrated by the nonsignificant group–day statistical interaction ($p = .43$). Figure 3 shows that the MU discharge rate changed very little at 50% MVC during the 4 days for either group. Similar changes were noted for the 10% MVC condition, with no change in discharge rate during the four testing sessions and no difference between the two participant groups.

Discharge Rate–MVC Relationships

The Pearson correlation coefficient between the mean discharge rate and maximal force was computed on each day

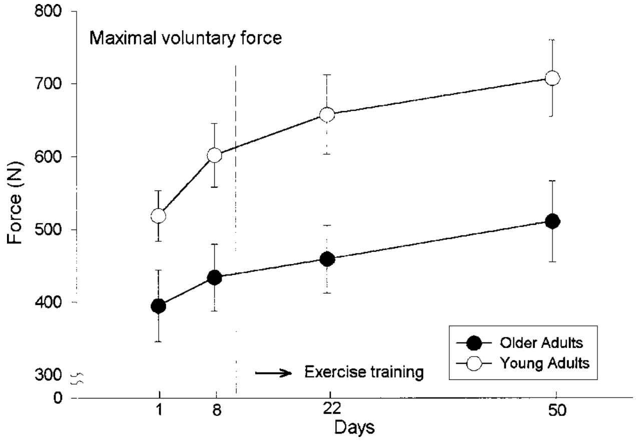

Figure 2. Maximal voluntary isometric knee extensor force is shown in young and older adults during the experiment. Resistance exercise training was initiated on the eighth day and continued for 6 weeks.

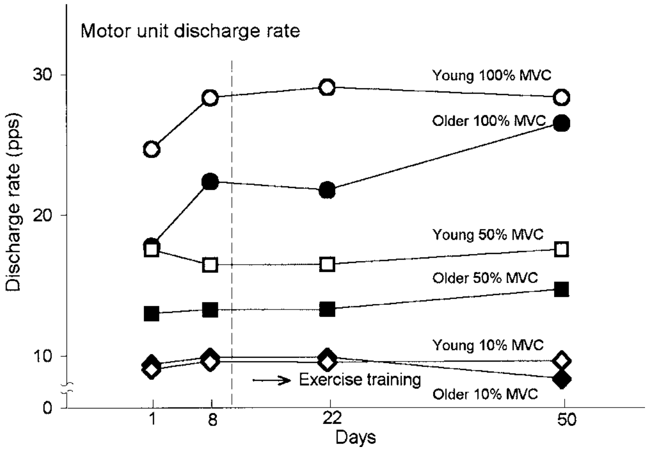

Figure 3. Motor unit discharge rates are shown for young and older adults after two baseline tests (1 week apart) and 6 weeks of resistance exercise training. ○, Young adults 100% maximal voluntary contraction (MVC); ●, older adults 100% MVC; □, young adults 50% MVC; ■, older adults 50% MVC; <diao>, young adults 10% MVC; and <diaf>, older adults 10% MVC.

to identify the source of the rapid change in maximal force. Figure 4 shows that these correlation coefficients increased considerably between the first and second testing sessions (from $r = 0.62$ to $r = 0.88$ in young adults, and from $r = 0.25$ to $r = 0.83$ in the older adults). During the exercise training period, the relationship between these two variables declined to nearly initial values: slightly higher for older adults and slightly lower for young adults.

Discussion

The current data correspond with previous observations that MU discharge rates are higher in young adults than in older adults. The firing rate difference between the two groups is greatest at the higher force levels. In the current study, no between-groups difference was observed at 10% MVC. Kamen and colleagues (3) also found no difference in first dorsal interosseous (FDI) firing rates at 50% MVC, although a 40% difference existed between the young and older groups at 100% MVC. An earlier study from our laboratory revealed no difference in discharge rate between young and older adults in the tibialis anterior at submaximal force levels (15). Other investigators have reported either no difference or a trend toward lower firing rates in older adults at lower force levels (4,17,18).

Previous studies have shown that maximal muscular force can increase rapidly when a person merely exerts several high-force isometric contractions for 1 or more days (7,10,19). The current data extend these observations to the larger knee extensor muscles and to older adults. In an earlier study, we reported that MU discharge rates in the abductor digiti minimi increase as early as 48 hours after the initial experience performing maximal effort contractions (12). In the current study, a 19% increase in the vastus lateralis discharge rate occurred between the first two testing sessions. Although the effect size was somewhat small (<.3), it seems possible that increases in discharge rate may account for some of these earliest increases in force.

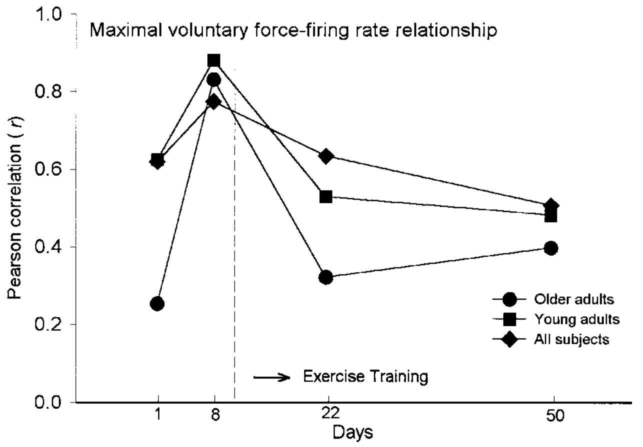

Figure 4. The relationship between MVC force and maximal motor unit discharge rate on each of the 4 testing days is summarized. The correlation was greatest on the second baseline testing day.

When all four testing sessions were incorporated in the experimental design, the MU discharge rate increased significantly during the 100% MVCs. However, there was no significant difference in maximal MU discharge rate when it was measured between the start of exercise training and the end of the study. Thus, the discharge rate can be altered with combined repeated testing and exercise training, and the role of the MU discharge rate as an important contributor to muscular force gains lessens as formal exercise training ensues. In a previous study involving fifth finger abduction, we reported that the sharp increase in MU discharge rate 48 hours after initial MVC assessment was actually followed by a decrease in discharge rate, so that by the end of 6 weeks of resistance exercise training, the maximal discharge rate was similar to that on the first testing day (12). Apparently, the MU discharge rate spikes rapidly and sharply and then decreases when muscle contractile characteristics begin to be modified by the training stimulus. Rich and Cafarelli (20) also noted no change in 50% MVC firing rate after 8 weeks of training, but they provided no data regarding firing rate changes at any other interval after the onset of training.

What is the source of the early and rapid increase in MU discharge rate? One possibility lies in the role of antagonist muscles during forceful contractions. Repeated activation of the agonists during assessments of MVC may result in less antagonist activity (21). That antagonist activity decreases during motor learning provides further evidence that reduced antagonist activity might be one source of the greater MU discharge rate (22).

The enhanced agonist MU discharge rate could then occur as a result of either a diminution of spinal reciprocal inhibition or changes in descending pathways involving antagonist muscle groups. Spinal reflexes are affected by training (23), learning (24), and by detraining (25). Recent studies using transcranial magnetic stimulation provide further evidence that some spinal sites may be responsible for the discharge rate changes observed here (26). However, the role of the supraspinal centers cannot be ruled out, and the enhancement of long-latency reflexes in weight lifters could be considered further evidence of the existence of some adaptation in the higher centers affecting MU discharge rate (27).

Conclusion

Repeated force assessment using the knee extensors is accompanied by rapid increases in MU discharge rate. It seems certain that these discharge rate adaptations explain part of the rapid increase in muscular force capability obtained by the mere expression of maximal force (10,19). These discharge rate increases seem to comprise part of the ''neural factors'' previously thought to accompany the initial phase of strength training, when increases in muscular force occur at rates far greater than can be explained by improvements in contractile processes.

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