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RESEARCH ARTICLE

Motor unit firing variability and synchronization during short-term light-load training in older adults

L. Griffin · P. E. Painter · A. Wadhwa · W. W. Spirduso

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Abstract We compared motor unit synchronization and firing rate variability within and across synergistic hand muscles during a pinching task following short-term light-load training to improve force steadiness in older adults. A total of 183 motor unit pairs before training and 158 motor unit pairs after training were recorded with intramuscular fine-wire electrodes within and across the first dorsal interosseous (FDI) and adductor pollicis (AdP) muscles during a pinch task performed by ten older adults before and after a 4-week short-term light-load training program. Nine younger adults performed the same experimental sessions 4 weeks apart with no training intervention. Two-minute sustained contractions of 2, 4, 8, and 12% maximal voluntary contraction (MVC) were performed with the non-dominant hand. The coefficient of variation (CV) of force was greater in older than in younger adults and was lower at the 2 and 4% MVC levels in both the finger (0.12 ± 0.01 vs. 0.08 ± 0.01, and 0.08 ± 0.01 vs. 0.05 ± 0.01, respectively) and thumb (0.11 ± 0.01 vs. 0.08 ± 0.01, and 0.09 ± 0.01 vs. 0.05 ± 0.01, respectively) compared to higher force levels following training in the older adults. There were no changes in CIS or k'-1 values following training. Motor unit firing rate variability significantly decreased at low force levels in the FDI muscle and also tended to decrease with training in the AdP muscle ($p = 0.06$). No changes occurred in the younger control group. These findings are the first to show that motor unit synchronization does not change during light-load training. Thus, it is likely that force steadiness in older adults improves by reducing motor unit firing variability rather than by changing motor unit synchronization.

Keywords Force steadiness · Short-term light-load training · Motor unit · Synchronization

Introduction

Many degenerative effects accompany aging, including a decline in hand and finger strength, reduced speed, decreased sensitivity, and reduced ability to control submaximal pinch force and posture (Ranganathan et al. 2001). Force steadiness is lower in older than in younger adults, particularly at low force levels (Galganski et al. 1993; Keen et al. 1994; Laidlaw et al. 2000). However, the mechanisms underlying the decline in force steadiness during functional hand tasks are not well understood.

Higher motor unit firing rate variability in older adults may account for the lower force steadiness in single digit contractions (Laidlaw et al. 2000; Tracy et al. 2005). High motor unit firing rate variability contributes to greater force fluctuations in high- versus low-force contractions in both experimental and simulated hand studies of young adults (Moritz et al. 2005). Furthermore, light-load training to improve single-digit force steadiness reduces motor unit firing rate variability in older adults (Kornatz et al. 2005).

Many studies have also suggested a relationship between motor unit synchronization and force steadiness, but these

L. Griffin (✉) · P. E. Painter · W. W. Spirduso
Department of Kinesiology and Health Education,
University of Texas at Austin, Bellmont 222,
1 University Station, D3700, Austin, TX 78712, USA
e-mail: l.griffin@mail.utexas.edu

A. Wadhwa
Department of Electrical and Computer Engineering,
University of Texas at Austin, Austin, TX, USA

studies show mixed results. Some studies found that motor unit synchronization increased with force tremor amplitude in young adults (Dietz et al. 1976; Logigian et al. 1988; Erimaki and Christakos 1999). Whereas others found no correlation between tremor amplitude and motor unit synchronization in young adults (Semmler and Nordstrom 1995).

Motor unit synchronization occurs to a greater degree at low force levels (Huesler et al. 2000). Force steadiness is also reduced at low force levels (Galganski et al. 1993), yet no differences in motor unit synchronization have been observed between younger and older adults in single digit tasks (Semmler et al. 2000, 2004). Motor unit synchronization has been found to be the same (Hockensmith et al. 2005) or higher (Huesler et al. 2000) within compared to across muscles during precision grip in young adults. In the present study, we chose to investigate differences in motor unit firing rate synchronization within and across intrinsic muscles of the index finger and thumb during a pinching task because this task is close to what would occur in a functional setting. Moreover, it is possible that training could affect motor unit synchronization differently within versus across synergistic muscle groups.

How motor unit synchronization changes with training is also unclear. Motor unit synchronization has been found to be higher (Kamen et al. 1992; Schmied et al. 1994; Hockensmith et al. 2005) or lower (Semmler and Nordstrom 1995, 1998) in the dominant compared to the non-dominant hands of untrained younger adults. It is higher in strength trained individuals (Semmler and Nordstrom 1998), but short-term resistance training did not increase synchronization (Kidgell et al. 2006). Motor unit synchronization (Semmler and Nordstrom 1998) and coherence (Semmler et al. 2004) are lower in skill-trained compared to untrained individuals. Thus, it is possible the skill training with light loads could reduce motor unit synchronization in older adults.

The first aim of this study was to compare force steadiness, motor unit firing rate, motor unit firing rate variability, and motor unit synchronization within and across the first dorsal interosseous (FDI) and adductor pollicis (AdP) muscles during low-force pinching tasks between younger and older adults. The second aim was to measure changes in these variables after versus before short-term light-load training to improve force steadiness in older adults. We hypothesized that force steadiness during a pinching task, motor unit firing rate variability, and motor unit synchronization would be greater at low compared to high force levels and would be greater in older compared to younger adults. We further hypothesized that light-load skill training in older adults would improve force steadiness and reduce motor unit firing rate variability and synchronization.

Methods

Participants

Ten healthy older (66.1 ± 1.27 years; five male, five female) and nine healthy younger (28.2 ± 9.5 years; five male, four female) adults participated in this study. All were right-hand dominant with no history of extensive hand-use training. All were free of neurological disorders and none had history of injury to the hands. Each volunteer was fully informed of the experimental procedures prior to the study and signed a consent form before participation. All procedures were approved by our Institutional Review Board. The older group did not train but participated in two testing sessions as well as eight short-term light-load training sessions over 4 weeks. The younger group participated in two testing sessions that were 4 weeks apart.

Pre-/post-testing

Each participant was seated with his/her left forearm immobilized in a custom made splint to reduce postural movement of the hand and forearm. The hand was fastened with the palm face down and the thumb and index fingers placed on the outer sides of two different force transducers with the respective digit in full contact with a metal bar such that the proximal joint extended 9.6 cm from the respective strain gauge. Force was measured independently from the index finger and the thumb. The remaining digits of the left hand were secured with a Velcro strap to eliminate movement. A schematic of the experimental arrangement is shown in Fig. 1. A computer screen was placed in front of the participant for visual feedback of the force.

Participants were instructed to match a target that moved from the bottom left part of the screen to a point located up and to the right of the starting point. To do this, they applied a force with their thumb, which would move a cursor along a horizontal line to the right. They also applied force with their index finger, causing the same cursor to move vertically. The resultant of both of these forces was a diagonal displacement. The experimenter could view the thumb and finger forces separately on another monitor as shown in Fig. 1.

Participants first performed three maximal voluntary contractions (MVCs) of the thumb and index finger. Each person was instructed to pinch by applying force maximally through the proximal joint of the two digits for 3 s. Each pinch was separated by a 10-s rest. The highest force attained for each digit was used for scaling to different force levels in order to standardize across subjects.

After the MVCs for the thumb and index finger were determined, participants performed a practice very similar to the experimental procedure in order to acquaint themselves

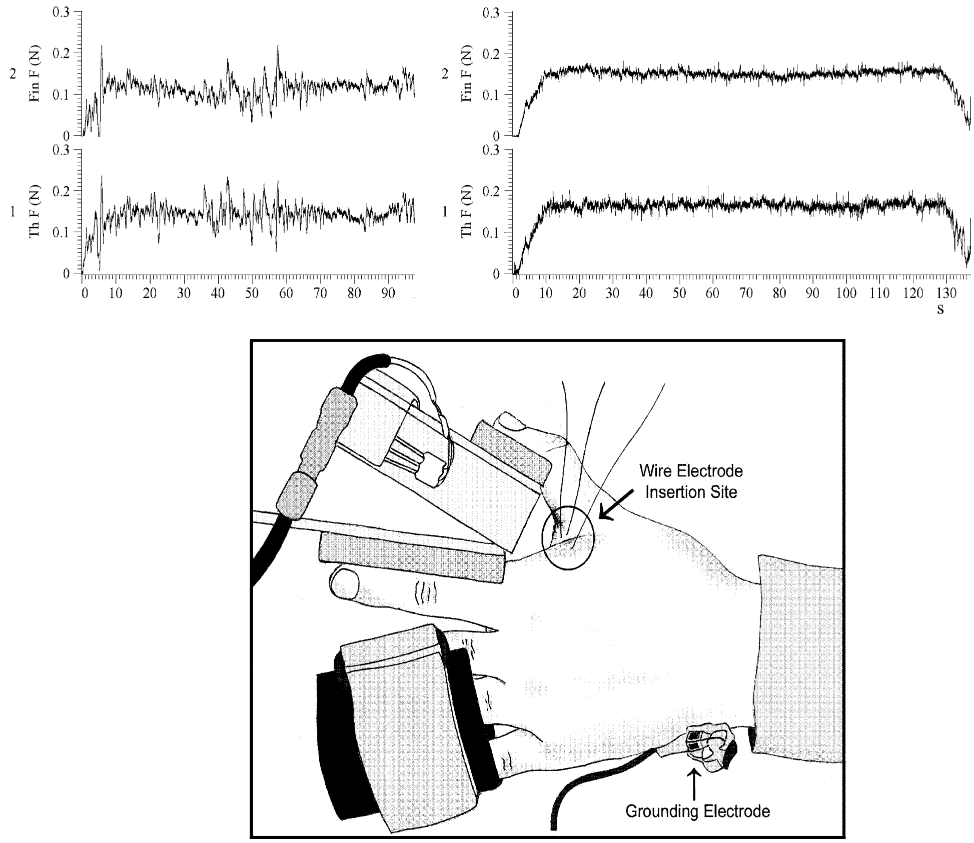


Fig. 1 Experimental arrangement. An example of thumb and finger force during a 4% MVC before and after training in older adults is also shown

with the equipment and task. This practice consisted of a series of 60 s contractions. The hold contractions were set to 2, 4, 8, and 12% MVC. Two contractions at each force level were performed during the pre-test practice and one contraction was performed in the practice of the post-test. To prevent fatigue, rest periods of 15 s between the 2 and 4% levels, 30 s between the 8% levels, and 60 s rest between the 12% levels separated each contraction. The visual gain was not adjusted between the force levels or before and after training. Thus, any changes with training were not due to greater resolution at the lower force levels.

Following the practice protocol, 70% isopropyl alcohol was used to clean the area of skin overlying the FDI and AdP muscles. Subsequently, fine-wire electrodes made of three stainless steel fine wires (0.002″ in diameter; California Fine Wire Company, Grover Beach, CA, USA) were inserted in the AdP and FDI muscles (two in the AdP and one in the FDI) with 25 gauge disposable hypodermic needles. For each insertion site, one of the three wires was used as the active electrode while another served as the reference. The third wire was used as a spare. An Ag/AgCl surface electrode of 5 mm diameter (Danlee Medical Products, Syracuse, NY, USA) was placed at the lateral styloid process and was used as a ground. Dual monitors provided displays of the target and actual forces as well as the intramuscular EMG recordings throughout data collection. Locations of the electrodes were confirmed by asking the participant to press only with the index finger to confirm the placement into the FDI and the AdP channel was monitored to ensure that no motor unit activity occurred on that channel. Likewise, the participant pressed with only the thumb to verify AdP placement with no visible activity on the FDI channel

The testing protocol was the same as the practice protocol except for the lengths of the holding contractions. Each force level (2, 4, 8, and 12% MVC) was held for 2 min followed by rests of 60, 90, 120, and 120 s for the 2, 4, 8, and 12% MVC levels, respectively. Each volunteer was randomly assigned to perform the ramps in an ascending order from 2 to 12% MVC or in descending order from 12 to 2% MVC to control for an order effect. Motor unit data was analyzed during the central steady portion of the holding phase for approximately 110 s during each trail. The number of motor unit pairs recorded during each force level for younger and older adults is shown in Table 1.

Motor units were discriminated by insuring that there was a difference in inter-spike intervals for different motor units. During some trials, there was more than one motor unit present on one electrode, while in others there was one or none. All channels were continuously monitored to ensure that motor units recorded by individual electrodes were different from each other.

Table 1 Motor unit pairs

Young day 1				Young day 2		
f-level (%)	FDI	AdP	Across	FDI	AdP	Across
2	14	4	23	13	4	25
4	12	32	51	29	19	54
8	18	8	32	8	16	35
12	12	8	29	14	18	29
Old pre test				**Old post test**		
f-level (%)	FDI	AdP	Across	FDI	AdP	Across
2	7	6	18	4	6	13
4	8	6	29	4	7	21
8	6	15	35	9	12	30
12	4	16	23	7	8	30

Training protocol

For the short-term light-load training in the older group, the participant was seated with his/her left forearm immobilized in a custom made apparatus with his/her hand placed palm down. This apparatus was designed to match the pinching arrangement for performance during the motor unit collection. The training apparatus consisted of strain gauges mounted on a magnetic block. Participants could pinch on two opposing buttons to measure force in the thumb and index finger. There was a set of buttons that allowed up to 10 lbs of force and another that allows up to 20 lbs. The block was movable on the board so that the buttons could be aligned in such a way that each individual could pinch with the proximal joint of the thumb and index finger. The buttons were also vertically adjustable. Participants flexed their remaining three fingers into their palm. On the first training day, when the MVC was recorded, the subject pinched on the 20 lb buttons. Every other day, training was performed on the 10 lb buttons. A computer screen was placed in front of the participant for visual feedback of the force steadiness and accuracy during training. MVCs were only performed on the first training day so that strength training effects were minimized.

During the training, the participants performed 10 trials of a tracing task, 10 of a tracking task, and 10 of a matching task. For each task, the protocol was five trials set at a level of 2% MVC and five trials set at 4% MVC. During the tracing task, the individual manipulated a cursor to trace a line set at 45° up to the specified target value (either 2 or 4% MVC). The cursor movement was a resultant movement of a horizontal displacement caused by the thumb and a vertical displacement by the index finger (Spirduso et al. 2005). Next, the participant completed the tracking trials. During these tests, the individual matched a moving target that traversed the same 45° line that appeared in the tracing task. The target moved up and down the line at a rate of 0.5% MVC/s. Finally, the matching trials were performed. In this task, the cursor was moved vertically, due to the sum of the forces made by the thumb and index finger, until the cursor reached a horizontal line that represented the target force. Once the target line was contacted, the cursor began a computer-controlled horizontal movement across the screen until the cursor reached the end. This concluded the trial. Each of these trials lasted for 20 s. Each training session was performed exactly the same way for every participant on all 8 training days. A depiction of the training protocol is provided in Fig. 2. All tasks were performed only at the 2 and 4% MVC levels to avoid muscle hypertrophy.

During the short-term light-load training, a manual force quantification system equipped with four strain gauges (0.00–4.45 N, non-linearity of each less than 1%) mounted to a data-acquisition board was used. A 500-MHz Pentium II personal computer with a NIM1016 data acquisition card (National Instruments, Austin, TX, USA) and LabVIEW graphical language Version 5.11 software was used for data collection during the training sessions.

Data collection and analysis during experimental testing

A personal computer (Sony, Pentium IV with Windows XP OS) was used to collect all pre/post training data. Data collected during the pre- and post-training experiments were analyzed off-line using Spike2 for Windows (v 5) software package (Cambridge Electronic Design, Cambridge, UK).

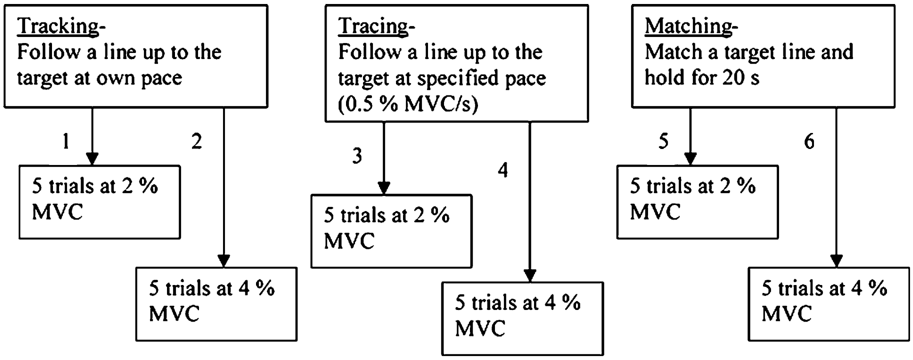


Fig. 2 Schematic of short-term light-load training protocol for older adults

The force was amplified through a bridge amplifier at a gain of 100 and low-pass filtered at 1 kHz (World Precision Instruments, Sarasota, FL, USA) and sampled at 1,000 Hz (Micro 1401, Cambridge Electronics Design, Cambridge, UK). Mean and standard deviation (SD) values of force were computed during the steady-state portion of the contraction. Any force values occurring outside the 99% bounds (±2.58 SD) were removed, and mean and SD values were re-calculated. Force steadiness was reported as a coefficient of variation (CV) about the mean force that was maintained.

The intramuscular EMG signal was transferred to a pre-amplifier (Motion Lab Systems, Baton Rouge, LA, USA, gain: 20, bandwidth: 15 Hz–3.5 kHz or B & L Engineering, Tustin, CA, USA gain: 330, bandwidth: 10 Hz–3.12 kHz) and then sampled at 25 kHz. Matlab® version 7.1 with the Signal Processing toolbox was used for the synchronization calculations.

To measure the amount of synchronization during constant force contractions within and across the FDI and AdP muscles, a cross-correlation analysis was performed (Sears and Stagg 1976) to identify the amount of time lag between the firing times of motor unit pairs. The cross-correlation analysis was executed using a time-window of ±100 ms and a bin width of 1.0 ms. The cumulative sum technique was used for the identification of peaks in the cross-correlation histogram (Ellaway 1978; Weigner and Wierzbick 1987; Nordstrom et al. 1992) and to calculate the synchronization indexes, common input strength (CIS) and k’-1 (Nordstrom et al. 1992).

Statistical analysis

A standard Type I error ($p \leq 0.05$) of rejecting a null hypothesis was used for all statistical analysis. A two-way repeated measures ANOVA with Bonferroni post hoc analysis was used to compare the differences in MVC before and after short-term light-load training. Separate three-way repeated measures mixed model ANOVAs with Bonferroni post hoc analysis were used to compare force CV, motor unit firing rate, firing rate CV and motor unit synchronization values across force levels, digits, time, and age group. Linear regression analysis was performed to determine correlations between force CV and motor unit firing rate, firing rate CV and synchronization values. All results are reported as mean ± standard error.

Results

Force steadiness

In the older group, the mean MVCs for the index finger and thumb did not change significantly following training (6.8 ± 0.9 Nm (pre) and 7.1 ± 0.8 Nm (post) for the finger; 7.6 ± 1.0 Nm (pre) and 7.5 ± 0.7 Nm (post) for the thumb).

Plots of force CV across force levels are shown in Fig. 3 for the index finger and thumb for the younger and older adults before and after the 4 weeks. There were main effects for force CV across groups, session and force level. Before and after training force CV was higher at 2 and 4% MVC than at 8 and 12% MVC in the older adults for both the index finger and the thumb ($p < 0.05$). In the younger adults, the force CV at 2% was significantly higher than at the other three force levels for both the finger and the thumb ($p < 0.05$). Older individuals had significantly higher values of force CV compared to the younger group for both the index finger and the thumb at 2% ($p = 0.038$ for the finger, $p = 0.022$ for the thumb) and 4% MVC with no difference at 8 and 12% MVC.

In the older group, there was a significant effect due to training for force CV in both the index finger ($p < 0.001$) and the thumb ($p < 0.001$). Significant reductions in force CV occurred for both the index finger and the thumb at 2% ($p = 0.001$ for the finger, $p < 0.001$ for the thumb) and 4% MVC ($p < 0.001$ for the finger, $p < 0.001$ for the thumb) with no significant changes at the 8 and 12% MVC after training. There was no significant difference in force CV between Day 1 and Day 2 at any force level in the younger group who did not train.

Motor unit firing rate

Figure 4 shows the mean motor unit firing rate and firing rate CV measured at each force level for the index finger and thumb before and after training in the older group. There was no main effect for firing rate or firing rate CV between younger and older adults and no main effect for training in the older group.

There was a main effect for firing rate CV with training in the older adults ($p < 0.001$). In the FDI muscle, motor unit firing rate CV was significantly lower at the 2% ($p = 0.001$), 4% ($p = 0.047$), and 8% ($p < 0.001$) MVC levels after versus before training with no change occurring at 12% MVC. In the AdP muscle, there was also a trend for the firing rate CV to decrease with training (main effect of $p = 0.06$). There was no main effect for firing rate CV after versus before the 4 weeks in the younger group.

There were no significant correlations between firing rate CV and force CV in either the FDI or AdP muscle in either the older training group or the younger control group. However, the change in motor unit firing rate CV was significantly correlated to the change in force CV ($r^2 = 0.96$, $p = 0.004$) for the 2% MVC force level in the finger in the older adults. There were no significant correlations at other force levels or in the thumb.

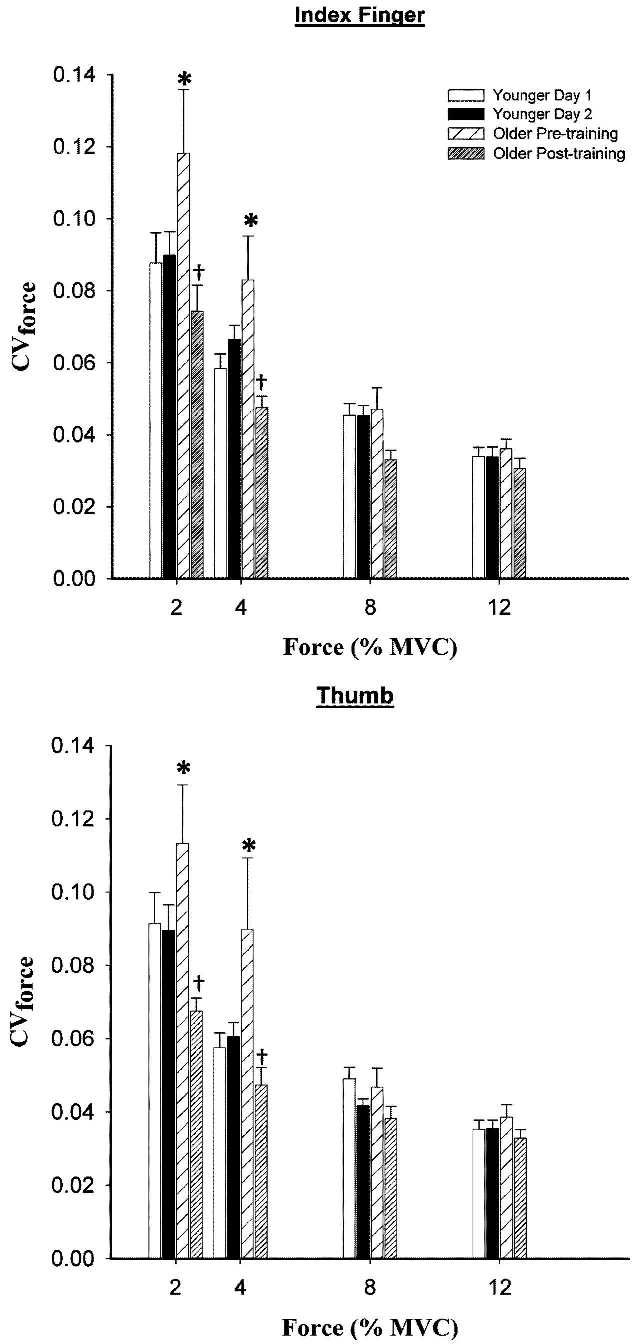


Fig. 3 Force coefficient of variations (CV) for the index finger (*top*) and thumb (*bottom*) for younger and older groups before and after 4 weeks. Significant differences occurred at the 2 and 4% MVC levels after training for both the index finger and thumb in the older adults. *Asterisks* indicate significant differences between the younger and older group and the crosses indicate significant differences with training in the older group

Motor unit synchronization

Figure 5 shows motor unit synchronization Day 1 values for both groups There were no differences in CIS or k’-1 values after versus before the 4 weeks in either group. CIS values were not different between younger and older adults. There was also no main effect for k’-1 values in either the AdP muscle or the across muscle data but there was for FDI muscle ($p < 0.001$). k’-1 values were significantly higher in the older adults at the 2% ($p < 0.001$), 8% ($p = 0.024$) and 12% ($p < 0.001$) MVC levels in the FDI muscle. There were also main effects for CIS and k’-1 for force level in the AdP and FDI muscles with 12% MVC showing higher motor unit synchronization than the lower force levels.

There were no overall main effects in the CIS or k’-1 indices due to time in either group. There were no significant correlations between force CV and synchronization measured as either CIS or k’-1 for either the FDI or AdP muscles before versus after the 4 weeks. Figure 6 shows pre- versus post-training motor unit synchronization values for the older group.

Discussion

The main findings of the present study were that improvements in force steadiness in older adults were accompanied by significant reductions in motor unit firing rate CV with no changes in motor unit synchronization.

Several studies have demonstrated that a decrease in force steadiness occurs with age and that the decrease in steadiness occurs predominantly at low force levels (Galganski et al. 1993; Keen et al. 1994; Laidlaw et al. 2000). In the present study, the force CV was also higher at low force levels and significantly decreased with short-term light-load training.

Motor unit synchronization

Synchrony of motor units is believed to originate from common inputs from the branching of last order neurons (Sears and Stagg 1976; Kirkwood and Sears 1978). Motor unit synchronization has also been proposed to be a cause of the reductions in force steadiness with age in both experimental and simulation studies (Christakos 1982; Yao et al. 2000). In the present study, we found that motor unit synchronization as measured by k^{-1} but not CIS values was higher in the FDI muscle of older compared to younger adults. Theoretically, the higher motor unit synchronization in older adults could contribute to the higher force fluctuations. However, it was highest at the 12% MVC level compared to the lower levels before and after training, and it did not change with training to improve force steadiness. Thus, it is unlikely that motor unit synchronization plays a major role in unsteadiness in older adults during isometric pinching tasks as performed in the present study. CIS values may be a more accurate measure of synchronization than k’-1 (Nordstrom et al. 1992). Moreover, Semmler et al. (2000)

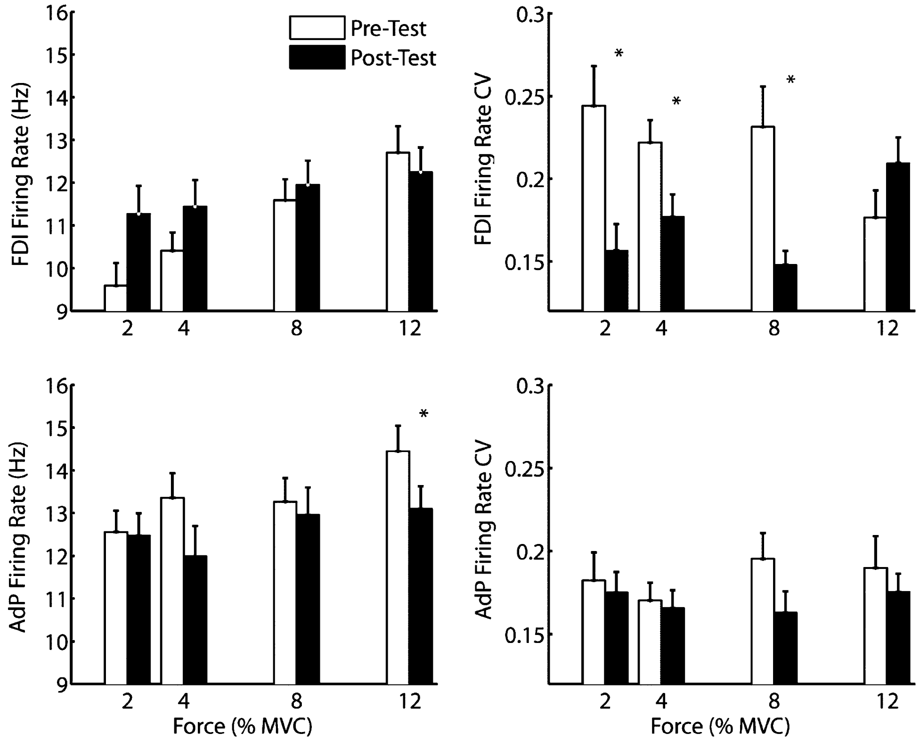


Fig. 4 Motor unit firing rate (*left*) and firing rate coefficient of variation (*right*) at each force level before and after training in the FDI (*top*) and AdP (*bottom*) muscles. *Asterisks* indicate significant changes with training at $p < 0.05$

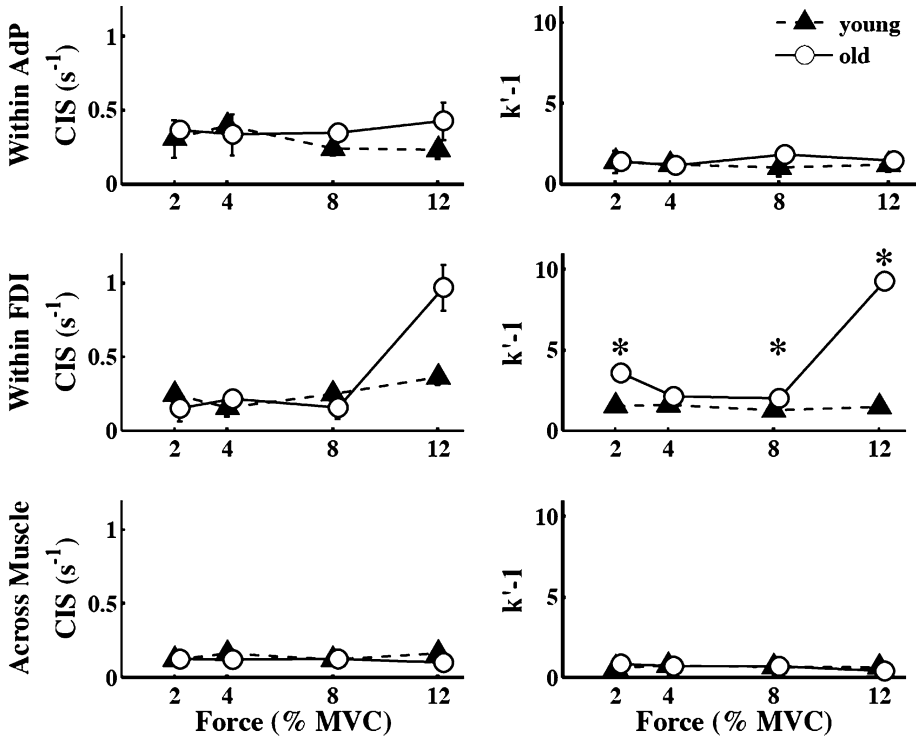
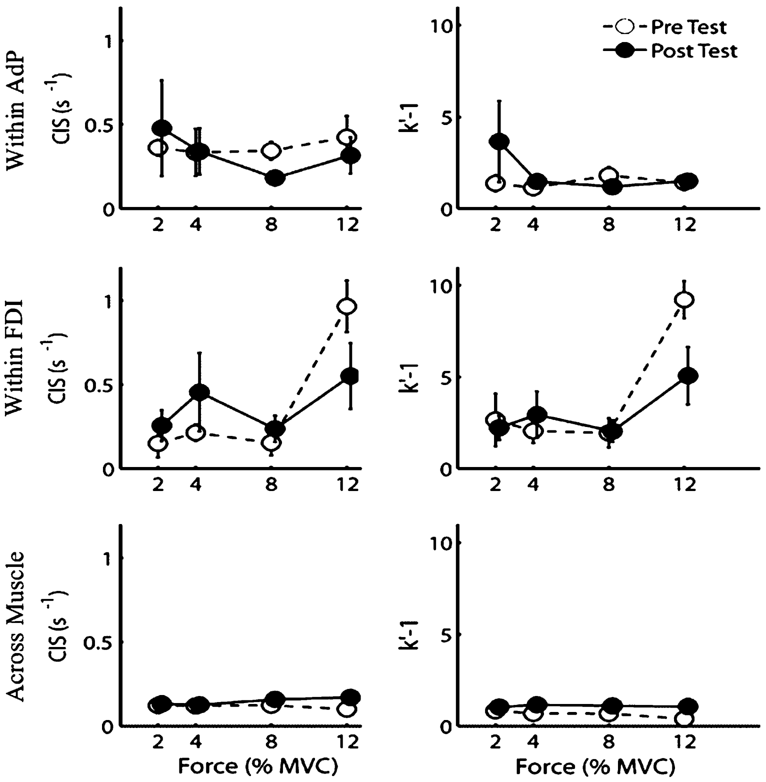


Fig. 5 Motor unit synchronization results reported as common input strength (CIS) and k'-1 values on Day 1 testing days for young and older adults for AdP, FDI, and across muscles at all force levels

also found no difference in motor unit CIS values between young and older adults. Yet, it must be taken into consideration that it is not possible to sample from all motor units that are active at a given time and that computer simulation studies have clearly shown that motor unit synchronization can influence force steadiness.

It should also be noted that in the present study, force variability was reduced only at the force levels that were trained (2 and 4% MVC) and not for the higher force levels (8 and 12% MVC). Motor unit firing rate variability in the FDI muscle also decreased predominantly at the lower force levels and did not change for the 12% MVC level.

Fig. 6 Motor unit synchronization results reported as common input strength (CIS) and k'-1 values before and after training in the older group for AdP, FDI, and across muscles at all force levels



Motor unit firing rate variability

In the present study, motor unit firing rate variability significantly reduced with training in the older adults. However, differences between younger and older adults failed to reach statistical significance. Some studies have also found no difference in motor unit firing rate variability between younger and older adults (Galganski et al. 1993; Semmler et al. 2000; Vaillancourt et al. 2003). Whereas others have reported greater firing rate variability in older compared to younger adults (Laidlaw et al. 2000; Moritz et al. 2005; Tracy et al. 2005). Higher motor unit firing rate variability in older versus younger adults is proposed to be caused by changes in the central nervous system that occur during aging. For example, there are reductions in cortical (Henderson et al. 1990) and spinal motoneurons (Gardner 1940), reductions motor evoked potential and compound excitatory postsynaptic potential amplitudes (Eisen et al. 1991), and increases in the latencies of sensory and motor evoked potentials (Evans and Starr 1994).

As in the present study, Kornatz et al. (2005) found that reductions in motor unit firing rate variability occurred in conjunction with a reduction in force CV following training to reduce force steadiness in older adults. The decrease in force steadiness with higher levels of motor unit firing rate variability is likely to reflect an increase in synaptic noise, presumably due to increased excitatory and inhibitory inputs to the motor neuron pool (Mathews 1996, 1999). An increase in the number of doublets (Laidlaw et al. 2000), or short-interspike intervals, which can increase the twitch forces significantly (c.f. Garland and Griffin 1999) may also contribute to motor unit firing rate variability. Doublets also increase during fatigue (Griffin et al. 1998) which may also increase physiological tremor. Some studies have found weak correlations between motor unit firing rate CV and force CV(Tracy et al. 2005; Kornatz et al. 2005), but they were not significant in the present study. Although there was a significant correlation between the change in force CV and the change in motor unit firing rate CV with training in the finger at the 2% MVC level in the older adults.

In the present study, there were no changes in synchronization that accompanied improvements in force steadiness with short-term light-load training. However, there was a robust decrease motor unit firing rate variability that occurred in the FDI muscle and a trend for the same in the AdP muscle. Thus, reductions in motor unit firing rate variability likely plays a key role in improving muscle force steadiness following short-term light-load training in older adults, whereas motor unit synchronization did not influence force steadiness.

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