RESEARCH ARTICLE

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Diminished task-related adjustments of common inputs to hand muscle motor neurons in older adults

Abstract The purpose of this study was to quantify correlated motor unit activity during isometric, shortening and lengthening contractions of a hand muscle in older adults. Thirteen old subjects (69.6 ± 5.9 years, six women) lifted and lowered a light load with abduction–adduction movements of the index finger over $10°$ using 6-s shortening and lengthening contractions of the first dorsal interosseus muscle. The task was repeated 10–20 times while activity in 23 pairs of motor units was recorded with intramuscular electrodes. The data were compared with 23 motor-unit pairs in 15 young (25.9 ± 4.6 years, five women) subjects obtained using a similar protocol in a previous study. Correlated motor unit activity was quantified using time-domain (synchronization index; Common Input Strength) and frequency-domain (coherence) analyses for the same motor-unit pairs. For all contractions, there was no difference with age for the strength of motor-unit synchronization, although age-related differences were observed for synchronous peak widths (young, 17.6 ± 7.4 ms; old, 13.7 ± 4.9 ms) and motor-unit coherence at 6–9 Hz (z score for young, 3.0 ± 1.8; old, 2.2 ± 1.5). Despite increased synchrony during length-ening contractions and narrower peak widths for shortening contractions in young subjects, there was no difference in the strength of motor unit synchronization (CIS $\sim$0.8 imp/s), or the width of the synchronous peak ($\sim$14 ms) during the three tasks in old subjects. Furthermore, no significant differences in motor-unit coherence were observed between tasks at any frequency for old adults. These data suggest that the strategy used by the central nervous system to control isometric, shortening, and lengthening contractions varies in young adults, but not old adults. The diminished task-related adjustments of common inputs to motor neurons are a likely consequence of the neural adaptations that occur with advancing age.

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Introduction

Motor-unit synchronization and coherence are two commonly used measures of correlated motor-unit activity that reveal complimentary features of the common input to motor neurons. Motor-unit synchronization is a measure of the near coincident discharge of action potentials that is quantified in the time domain, and provides information on the strength of branched common input to motor neurons that appears to occur through the corticospinal pathway (Sears and Stagg 1976; Datta and Stephens 1990; Farmer et al. 1993b). In contrast, motor-unit coherence is a measure of common oscillatory input to motor neurons that is quantified in the frequency domain, and may originate in various cortical and subcortical areas, including the motor cortex (Farmer et al. 1993a; Baker and Baker 2003), although recent evidence suggests that motor-unit coherence can be induced without oscillatory drive in the central nervous system (CNS; Taylor and Enoka 2004; Moritz et al. 2005b). Nonetheless, several studies have shown a correlation between motor-unit synchronization and high-frequency ($\sim$10–30 Hz) coherence,

suggesting that both of these phenomena may share similar mechanisms (Farmer et al. 1993a; Halliday et al. 1999; Kilner et al. 2002; Semmler et al. 2002; Moritz et al. 2005b). Despite being mathematically equivalent (Rosenberg et al. 1989), motor-unit synchronization and coherence may also emphasize different features of the common input to motor neurons under some circumstances (see Semmler et al. 2003a).

Examining the strength of correlated motor-unit activity represents a powerful tool to explore activation strategies used by the CNS, and this approach has been used to provide evidence for acute plasticity in the neuromuscular system. For example, changes in motor-unit synchronization during isometric contractions have been observed for different postural and voluntary force tasks (Adams et al. 1989; Bremner et al. 1991), variation in the level of attention required for an action (Schmied et al. 2000), and changes in object compliance (Kilner et al. 2002). As with motor-unit synchronization, coherent oscillations in the motor system appear to vary with the requirements of the task, including changes in object compliance during a precision grip (Kilner et al. 2002), and the strongest coherence occurs during isometric contractions just after movement (Kilner et al. 1999). Similarly, motor-unit synchronization is enhanced during slow-lengthening contractions, and low-frequency (2–12 Hz) coherence is reduced during shortening contractions (Semmler et al. 2002), suggesting that shortening and lengthening contractions are controlled by altering the common synaptic input that is delivered to the involved motor units.

The nervous system undergoes marked changes with advancing age. These age-related changes include substantial losses of cortical (Henderson et al. 1980) and spinal motor neurons (see Doherty et al. 1993), which are accompanied by a reduced excitability of the corticospinal (Eisen et al. 1991; Sale and Semmler 2005) and spinal reflex pathways (Kido et al. 2004). Based on multiunit EMG recordings, it appears that older adults have an impaired ability to coordinate the excitatory and inhibitory activity of multiple neural oscillators during force-varying isometric contractions (Sosnoff et al. 2004), which may be a result of the neural adaptations that occur with advancing age. Although correlated motor-unit activity differs during shortening and lengthening contractions in young subjects (Semmler et al. 2002), and is greater during isometric contractions in old adults (Semmler et al. 2003a), it is not known if common input is also altered during shortening and lengthening contractions in old adults. Because correlated motor unit activity has the potential to influence force fluctuations and tremor (Yao et al. 2000), any differences in the neural control strategy between young and old adults could be responsible for the impaired motor performance during these contractions with advancing age (Enoka et al. 2003). The purpose of the study was to use measures of motor-unit synchronization and coherence to infer details of the common input to motor neurons during shortening and lengthening contractions of a hand muscle when performed by older adults. Based on a previous study (Sosnoff et al. 2004), the hypothesis was that older adults would exhibit a reduced ability to modulate common input to motor neurons during shortening and lengthening contractions. Preliminary accounts of this work have been published in abstract form (Kornatz et al. 2003; Semmler et al. 2003b).

Methods

Thirteen healthy older adults (69.6 ± 5.9, range 60–78 years, six women) volunteered to participate in the study. All subjects were moderately active, had no known neuromuscular disorders, and were not taking medication known to influence neural conduction or neuromuscular performance. The data were compared with that obtained from 15 young subjects (25.9 ± 4.6, range 22–37 years, five women) using a similar protocol in a previous study (Semmler et al. 2002). The Human Research Committee at the University of Colorado approved the experimental procedures and subjects provided written consent after receiving a written and verbal description of the protocol.

Each subject participated in one to four experimental sessions that were performed on different days. A major goal of the study was to examine the discharge properties from the same pair of motor units during isometric, shortening, and lengthening contractions of the first dorsal interosseus muscle against an inertial load applied to the index finger. Care was taken by the investigators to identify the same motor units for each contraction, which included examining each motor-unit waveform for consistency and ensuring that the discharge rates were equivalent at the beginning of each task. This process was possible because the index finger position for the isometric contraction was the starting point for the shortening contraction, improving the likelihood that each motor unit was the same during the three contractions. The experiment was terminated if attempts to obtain consistent motor unit recordings remained futile. Using these stringent criteria, approximately one in three experiments were completed successfully, highlighting the difficulty in recording from the same pair of motor units during contractions that involve a change in muscle length. To facilitate comparison with the current experiments, data from the young subjects (Semmler et al. 2002) were reanalyzed by the same investigator (JGS) to maintain consistency in data analysis procedures between young and old adults.

Experimental arrangement

A detailed description of the experimental arrangement has been reported previously (Semmler et al. 2002). Briefly, each subject sat upright in an adjustable chair with the left arm and hand secured in a manipulandum.

The hand was secured in the horizontal plane by a metal restraint to keep the thumb extended, and the third to fifth digits were passively flexed and secured around a handle located on the manipulandum. A splint was positioned on the lateral surface of the index finger to keep the proximal interphalangeal joint extended. This arrangement served to isolate the abduction of the index finger at the metacarpophalangeal joint so that the horizontal movement occurred almost exclusively by contraction of the first dorsal interosseus muscle.

The abduction-adduction displacement of the index finger about the metacarpophalangeal joint was measured using a linear variable displacement transducer (LVDT; Novotechnik, Stuttgart, Germany), which produced an adduction load of 0.03 kg. The LVDT was placed in series between the finger splint and the additional load lifted by the subject. This configuration allowed the index finger to move freely throughout its range of motion while the total load opposed the abduction movement. The LVDT was calibrated over a 10° range of motion at the beginning of the experiment and checked periodically throughout each session. The subjects received feedback on index finger position via a 14-inch computer monitor that was positioned 1.5 m away at eye level. By matching the index finger position with a triangular template on the monitor, the subject performed constant velocity (1.7°/s) abduction-adduction movements of the index finger.

Electromyographic signals (EMG) of the first dorsal interosseus muscle were recorded with surface electrodes (4-mm diameter; silver-silver chloride) using a bipolar configuration that were placed 1–2 cm apart (center-to-center) on the skin overlying the belly of the muscle. A reference electrode was placed over a bony prominence on the dorsal aspect of the hand. The surface EMG signals were amplified (1000–2000×), band-pass filtered (20–800 Hz), displayed on an oscilloscope, and stored on tape (Sony PC116 DAT recorder, Sony Magnescale Inc., Montvale, NJ, USA).

Two to three fine-wire electrodes were inserted through the skin into the first dorsal interosseus muscle with a disposable 27-gauge hypodermic needle to record motor-unit discharge. Each electrode consisted of three formvar insulated, stainless-steel wires (two 50 μm and one 25 μm diameter, or three 50 μm diameter; California Fine Wire, Grover Beach, CA, USA). To facilitate stable motor-unit recordings, the ends of the wires were fixed together at the recording tip with medical-grade cyanoacrylate glue and tightly coiled around a 0.13 mm diameter wire for ∼3 mm with a custom coiling apparatus. The motor-unit recordings were obtained from two wires within each electrode, whereas the third wire was used as an alternative bipolar configuration to optimize the recorded signals when necessary. Individual motor units were detected on-line using an amplitude window discriminator (DIS-1; BAK Electronics Inc., Rockville, MD, USA) to provide audio-feedback of motor-unit discharge during the contractions. Single motor-unit recordings were amplified (1000–3000×), band-pass filtered (20 Hz–8 kHz), displayed on an oscilloscope, and stored on tape.

Experimental procedures

Prior to the experiment, the manual dexterity of the subject was tested using a Purdue pegboard (model 32020; LaFayette Instruments, Lafayette, IN, USA). This task involved placing small pegs into a vertical array of holes as quickly as possible over a 30-s period. The task was performed three times with each hand and the average score was recorded.

The subjects performed three tasks during the experiments: (1) a low-force contraction of the first dorsal interosseus muscle while supporting a light inertial load and holding the index finger in a constant position (isometric condition); (2) anisometric (shortening and lengthening) contractions of the first dorsal interosseus muscle by lifting and lowering the same light inertial load; and (3) a strength test of the first dorsal interosseus muscle to determine the maximal load that could be lifted with the index finger once (1-repetition maximum (RM) load).

Isometric contractions

A mass was attached to one end of the LVDT and provided a load in the adduction direction that was opposed by abduction of the index finger with the first dorsal interosseus muscle. The mass was adjusted to provide a resistance that was sufficient to produce tonic (repetitive) discharge at ∼10 Hz from at least one motor unit in each electrode, which is ∼2 Hz above the minimal discharge rate for low threshold motor units in this muscle (Moritz et al. 2005a). This adjustment usually required an additional 0.03–0.08 kg above the mass provided by the LVDT. Because the goal was to record the activity of the same motor units during all three tasks, motor units that were activated at very low levels were preferentially selected. The angular position of the index finger was displayed on the monitor along with a target line corresponding to 5° of abduction from the neutral position. The task involved maintaining the index finger at 5° of abduction, with the use of visual feedback, for approximately 2 min while supporting the load. This index finger position was selected because we wanted the isometric and anisometric contractions to start at the same position to facilitate motor unit identification. As the anisometric contractions were performed over 10° (see below), it was determined from previous experience that a movement from 5° to 15° represented the mid-point in the range of motion for abduction–adduction movements at the metacarpophalangeal joint for most individuals.

Anisometric contractions

The same load used for the isometric contraction was raised and lowered with anisometric contractions of the

first dorsal interosseus muscle. The angular position of the index finger was displayed on the feedback monitor along with a triangular template representing the desired trajectory. The template represented a constant-velocity (1.7°/s) contraction of 6 s over a 10° range of motion for each of the abduction (shortening) and adduction (lengthening) directions. Each subject was instructed to match the template as closely as possible for three to five contractions, after which a rest period of 60 s was provided. A total of 10–20 contractions were performed by each subject.

1-RM load

The subjects were instructed to lift and lower an inertial load slowly with the index finger throughout a range of motion of approximately 10° in a horizontal abduction–adduction plane. The load was increased after each repetition until the subject could no longer successfully complete the task. The maximal load that could be lifted over the 10° range of motion was identified as the 1-RM load. Subjects were given a 60-s rest between each attempt. Four to six trials were usually required to determine the 1-RM for each subject.

Data analysis

All electrophysiological data were stored on tape and digitized (CED 1401, Cambridge Electronic Design, Cambridge, UK) for subsequent analysis. The sampling rate was 200 samples/s for index finger position, 2 k samples/s for the surface EMG, and 20 k samples/s for the single motor unit recordings.

Single motor-unit discharges were discriminated using a spike-sorting algorithm, which identified the action potentials belonging to a particular motor unit based on waveform shape (Spike2, Version 5.02; CED, Cambridge, UK). Individual motor units were identified between contractions by matching waveform shape and discharge rate during the isometric contraction and the start of the shortening contraction, as the index finger position and external load was the same for each of these tasks. Furthermore, we were able to track any small deviations in waveform shape during changes in muscle length by continual adjustments in the waveform-matching template. If discrimination accuracy was low (< 5%) the discharges were manually edited based on waveform shape and expected discharge times on a spike-by-spike basis. The mean, standard deviation, and coefficient of variation of the interspike intervals were determined using custom-designed software written in MATLAB (Mathworks Inc., Natick, MA, USA). Because there was usually a change in discharge rate during the anisometric contractions, the slope of a linear regression line was subtracted from the data, and the standard deviation and coefficient of variation were calculated from the detrended data. Motor units

detected with separate electrodes during the same trial were paired for analysis to assess the strength of motor-unit synchronization and coherence for each of the three contractions.

Motor-unit synchronization was measured by constructing a cross-correlation histogram, which involved correlating the discharge time of one motor unit (termed the reference unit) with respect to the other motor unit. Each cross-correlation histogram had 1-ms bin widths spanning a period 100 ms before and 100 ms after the reference motor unit. The cumulative sum (CUSUM; Ellaway 1978) technique was used to estimate the location and width of the central synchronous peak. When no significant peak was detected with the CUSUM, a standard analysis window of 11 ms centered at time 0 ms was used to measure synchronization, as this represents the mean peak width obtained from a large population of motor units recorded in this muscle (Nordstrom et al. 1992). The magnitude of the central synchronous peak in the cross-correlation histogram was quantified using the synchrony index CIS (Common Input Strength), which indicates the number of synchronous discharges above that due to chance divided by the duration of the trial when both motor units were tonically active. This index is mathematically independent of the discharge rate of the motor units contributing to the cross-correlation histogram (Nordstrom et al. 1992) and is not correlated with the small changes in discharge rate that are usually observed with these types of contractions (Semmler et al. 2002).

Motor-unit coherence was quantified from the frequency spectrum produced with the discharge times of the pair of motor units. The coherence indicates the degree of linear correlation in the frequency domain between the two motor-unit discharge times on a scale from zero to one. The method used was similar to that developed by Rosenberg et al. (1989) and was implemented using MATLAB. The discriminated motor-unit data were divided into contiguous, non-overlapping epochs of 1.28 s that comprised 256 bins. Each 5-ms bin was assigned a value of one when it contained a discharge and a value of 0, when it did not. The time-series data from each disjoint section were transformed to the frequency domain, resulting in a frequency resolution of 0.78 Hz. Auto-and cross-spectra were estimated by averaging over the disjoint sections, and coherence estimates for two concurrently recorded motor-unit discharges were computed. Values of coherence exceeding the 95% confidence level (Rosenberg et al. 1989) for the frequencies of interest (0–50 Hz) were regarded as significant. Differences in the magnitude of coherence for each contraction were determined by pooling all trials for each subject using the pooled coherence procedure (Amjad et al. 1997) and then pooling data within each subject group. The coherence estimates between groups and tasks were compared by normalizing the coherence data into z scores according to the formula $z = \sqrt{(2 N)} \tanh^{-1} R$, where N is the number of disjoint segments, and R is coherence (Rosenberg et al. 1989). If

no coherence exists between the two signals, the z score will be normally distributed with a standard deviation of one and a mean that is dependent on the number of segments.

Statistical analysis

Subject characteristics were compared using the dependent variables of 1-RM load and Purdue Pegboard score. Individual motor-unit discharge properties were quantified by the number of discharges, mean discharge rate, standard deviation and coefficient of variation of discharge rate, and the slope (trend) in motor-unit discharge rate. Motor-unit synchronization was quantified using the synchrony index CIS and the width of the central synchronous peak, whereas motor-unit coherence was quantified using mean coherence z scores in 3-Hz bins up to 30 Hz. For strength and manual dexterity, statistical differences were assessed using a one-way ANOVA with age group (young, old) as the main factor. For the motor-unit analysis, the dependent variables were analyzed using a two-way, repeated-measures ANOVA with age and contraction type (isometric, shortening, lengthening) as factors. Statistical significance was designated at $P < 0.05$. Data are shown as mean $\pm$ SD in the text and tables, and mean $\pm$ SEM in the figures.

Results

The strength of the left first dorsal interosseus muscle was quantified using a 1-RM load test and was different for the young group (2.59 ± 0.69 kg) compared with the old group (1.87 ± 0.87 kg, $P < 0.05$). Manual dexterity, as assessed with the Purdue Pegboard, was significantly lower in the right hand of the old adults (13.7 ± 0.9 pegs) compared with the young subjects (17.3 ± 0.8 pegs, $P < 0.01$), but there was no difference for the left hand (12.7 ± 0.9 vs. 14.8 ± 0.8 pegs, respectively).

Discharge properties of individual motor units

Figure 1 shows an example of experimental data from one 78-year-old man. The data show recordings from a pair of motor units obtained from the first dorsal interosseus muscle while index finger position was held constant (isometric) and while the index finger tracked a triangular template to lift (muscle shortening) and lower (muscle lengthening) a 0.08-kg load (10% of 1-RM load). The bottom traces show the superimposed motor unit waveforms obtained from each contraction, with a consistent waveform indicating that the same motor unit was recorded during each contraction. Although the amplitude of the single motor unit potential increased during the shortening contraction, likely due to move-

ment of the electrode relative to the active muscle fibers, the waveform maintained its characteristic shape. These data represent a portion of the total recorded data for this pair of motor units. For the whole duration of the contraction, the geometric mean discharge rate was 7.8 Hz for the isometric contraction, 9.6 Hz for the shortening contraction, and 8.3 Hz for the lengthening contraction. The variability of motor-unit discharge, as measured by the geometric mean coefficient of variation for the pair of motor units, was 24.3% for the isometric contraction, 26.2% for the shortening contraction, and 28.7% for the lengthening contraction.

Table 1 shows the discharge characteristics of the individual motor units that were successfully followed throughout the isometric and anisometric tasks. Discharge times were recorded from 35 single motor units in 13 old subjects (range 2–5 motor units/subject), and this was compared with 37 single motor units in 15 young subjects (range 2–4 motor units/subject) from our previous study (Semmler et al. 2002). No significant differences were observed between age groups for all motor-unit discharge properties with the exception of the number of discharges, which were significantly greater for the young adults than the old adults during the isometric contractions. The external load that was applied to the index finger (relative to the 1-RM load) to activate the motor units was significantly (unpaired t-test, $P < 0.001$) greater in old ($9.3 \pm 5.7\%$; range, 2.8–23.5%) compared with young ($3.5 \pm 1.8\%$; range, 1.7–8.5%) subjects. This difference is consistent with the increased contraction intensities observed previously for older adults to activate motor units during isometric contractions (Semmler et al. 2000). Despite these differences, these data suggest that the activity of low threshold motor units were recorded in both subject groups.

Representative cross-correlation histograms and coherence spectra during isometric, shortening, and lengthening contractions are shown in Fig. 2. These data were obtained from the same pair of motor units shown in Fig. 1. Cross-correlation analysis revealed a significant central peak in each histogram, which is indicative of motor-unit synchronization. The synchrony index CIS indicated that the strength of motor-unit synchronization was 0.66 imp/s for the isometric contraction, 0.69 imp/s for the shortening contraction, and 0.67 imp/s for the lengthening contraction. The width of the central synchronous peak was 12 ms for the isometric contraction, and 11 ms for both the shortening and lengthening contractions. These data show that motor-unit synchronization was similar for isometric, shortening, and lengthening contractions in this pair of motor units. In contrast, there were small differences in the coherence spectra for motor-unit discharge between tasks. Maximum low- (0–10 Hz) and high- (10–30 Hz) frequency coherence was 0.061 at 0 Hz and 0.066 at 14 Hz for the isometric contraction, 0.084 at 4 Hz and 0.088 at 20 Hz for the shortening contraction, and 0.132
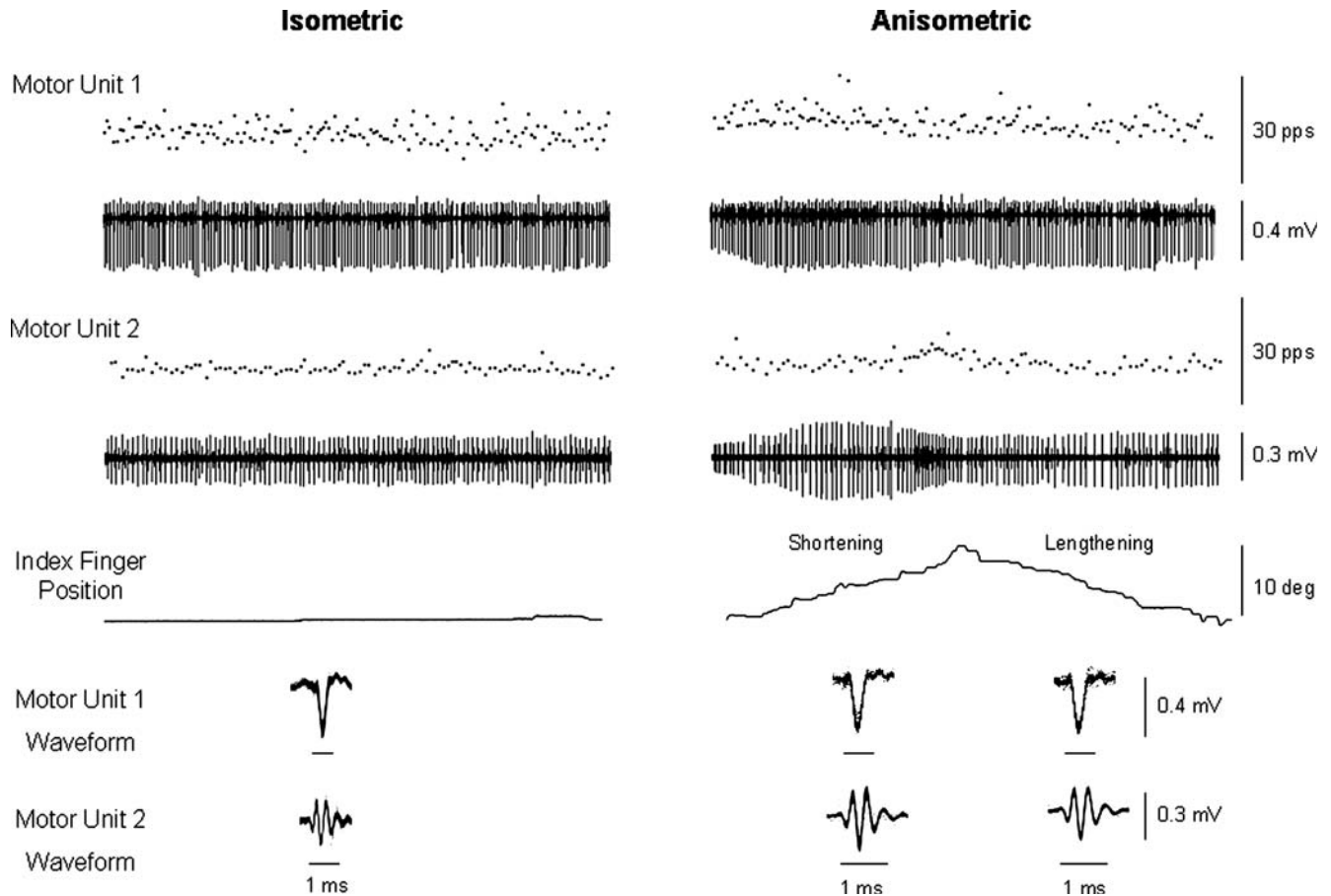
Fig. 1 Original experimental recordings from a 78-year-old man during the performance of an isometric (*left panel*) and a shortening and lengthening (anisometric; *right panel*) contraction performed with the first dorsal interosseus muscle. Shown are single motor-unit recordings and the motor unit discharge rate from two different motor units in the first dorsal interosseus muscle along with index finger position. The superimposed motor-unit action potential waveforms (*bottom*) show that the same motor units were recorded during the isometric and anisometric contractions

Table 1 Motor unit discharge properties during isometric, shortening, and lengthening contractions in young and old adults

	Young ($n=37$)			Old ($n=35$)		
	Isometric	Shortening	Lengthening	Isometric	Shortening	Lengthening
Number of discharges*	1426 ± 690**	859 ± 268	711 ± 237	958 ± 323	829 ± 318	709 ± 309
Discharge rate (pps)	10.7 ± 1.3	12.3 ± 2.8	10.4 ± 1.5	11.2 ± 2.1	13.1 ± 1.9	11.0 ± 1.7
SD Discharge rate (pps)	2.2 ± 0.6	2.8 ± 0.8	2.6 ± 0.7	2.1 ± 0.6	2.7 ± 1.0	2.7 ± 0.5
CV Discharge rate (pps)	20.3 ± 4.1	22.9 ± 6.1	24.7 ± 6.0	18.9 ± 4.7	20.5 ± 3.7	24.7 ± 4.2
Discharge rate trend (pps/s)	-0.01 ± 0.01	0.55 ± 0.47	-0.33 ± 0.37	-0.02 ± 0.03	0.70 ± 0.60	-0.43 ± 0.39

Values are means ± SD. *SD* standard deviation, *CV* coefficient of variation
*Significant age ($P < 0.05$) and age × task ($P < 0.001$) effects in the ANOVA
**$P < 0.001$ compared with isometric contractions in old adults

at 5 Hz and 0.076 at 22 Hz for the lengthening contraction.

Motor-unit synchronization

The mean strength of motor-unit synchronization and width of the central synchronous peak are shown in Fig. 3 for the young and old subjects. These data represent the mean of 23 motor unit pairs in young subjects (range; 1–4 motor unit pairs/subject) and 23 motor unit pairs in old adults (range; 1–5 motor unit pairs/subject). No significant main effects were observed for age ($F=2.7$, $P=0.11$) and the age × task interaction just failed to reach statistical significance ($F=3.0$, $P=0.06$). For both subject groups combined, a two-way, repeated-measures ANOVA revealed a significant main effect for task ($F=5.1$, $P=0.008$) for the synchrony index CIS,
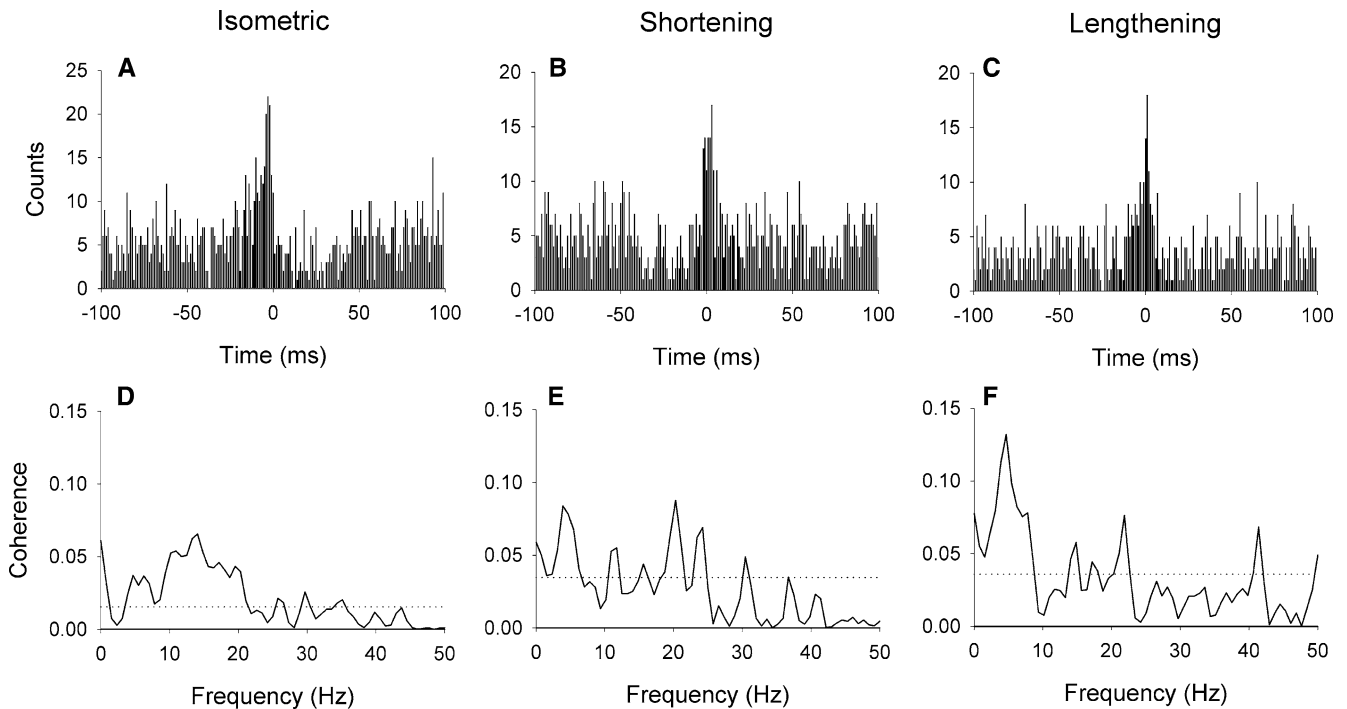
Fig. 2 Cross-correlation histograms (**a–c**) and coherence spectra (**d–f**) from one motor unit pair during the three tasks in an old subject. The data are for the two motor units in Fig. 1. The peak in the center of each *cross-correlation histogram* represents significant synchronization for all three contractions, whereas the *dotted horizontal line* represents the 95% confidence interval for the coherence spectra. For this pair of motor units, the strength of synchronization was similar for all three tasks (CIS ∼0.7 pps), whereas the greatest coherence was observed at 5 Hz during the lengthening contraction

and post-hoc analysis revealed significantly greater ($P=0.01$) synchronization during the lengthening contraction compared with the isometric contraction (data not shown).

A two-way, repeated-measures ANOVA revealed significant main effects for age ($F=7.7$, $P=0.008$), task ($F=10.8$, $P<0.001$), and the age × task interaction ($F=3.4$, $P=0.04$) for the width of the synchronous peak (Fig. 3b). Post hoc analysis showed a broader peak width in young adults (17.6 ± 7.4 ms) compared with old adults (13.7 ± 4.9 ms, $P=0.005$), and there was a narrower peak width for shortening contractions compared with isometric ($P=0.006$) and lengthening ($P<0.001$) contractions for all subjects combined. Furthermore, the peak width for shortening contractions were 5 ms narrower compared with the isometric contractions ($P=0.004$) and 7 ms narrower compared with lengthening contractions ($P<0.001$) in young subjects. No significant differences in peak width were observed between any of the tasks in old adults (Fig. 3b).

Motor-unit coherence

Coherence analysis was performed on the discharges of the same 46 motor unit pairs used for cross-correlation analysis during isometric, shortening, and lengthening contractions in young and old adults. The pooled coherence values are shown for each task in young and

old adults in Fig. 4a,b, whereas the mean z scores are shown in Fig. 4c,d. For the young subjects, significant coherence was observed from 3.9 to 7.0 Hz for isometric contractions and from 3.9 to 8.6 Hz for the lengthening contractions. In contrast, significant coherence was only observed from 0 to 5.5 Hz for the isometric contractions in older adults. When the coherence data were normalized using z scores, no qualitative difference in coherence was observed between the three tasks in older adults.

For statistical purposes, the mean coherence z scores in Fig. 4c,d were averaged over 3-Hz bins, and a summary of the statistical analysis of these data is shown in Table 2. These data show no differences in coherence between young and old adults, except at 6–9 Hz where the mean coherence z score was significantly larger in young (3.0 ± 1.8) compared with old (2.2 ± 1.5) subjects. In contrast, there were significant differences in the mean coherence z scores between tasks, but largely for the young subjects. The mean coherence z scores were greater in isometric contractions than shortening contractions at 0–9 Hz and 12–27 Hz for all subjects, and this difference was observed in young subjects at 0–9 Hz and 21–27 Hz. The coherence z scores were also significantly larger in isometric contractions than lengthening contractions at 0–6 Hz and 18–24 Hz in all subjects, with significant differences in young subjects between these two tasks at 0–3 Hz and 21–27 Hz. Furthermore, coherence was significantly lower in shortening contractions than lengthening contractions at 6–9 Hz in the
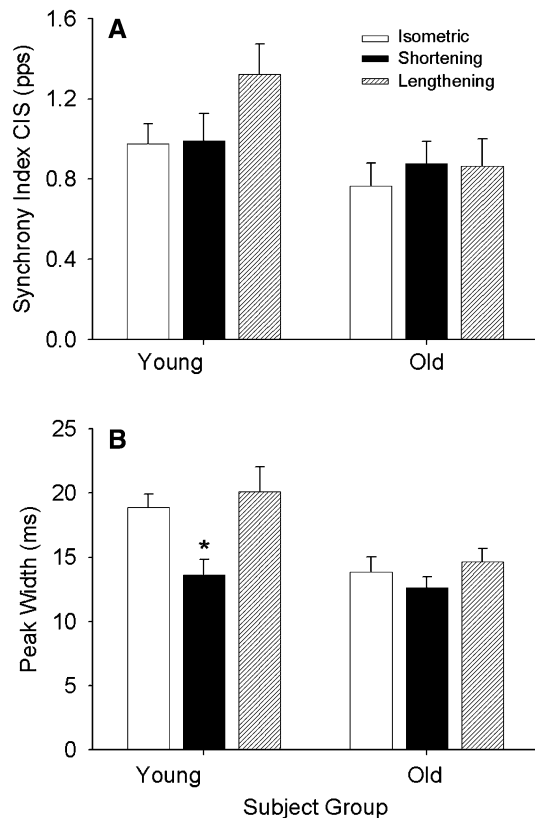
Fig. 3 Motor-unit synchronization during isometric, shortening, and lengthening contractions in young and old adults. Data show the mean ($\pm$SEM) strength of motor-unit synchronization measured with the synchrony index Common Input Strength (**a**) and the width of the central synchronous peak (**b**) in 23 motor-unit pairs in young and 23 motor-unit pairs in old adults during different contractions. * $P < 0.01$ compared with isometric contractions and $P < 0.001$ compared with lengthening contractions

young subjects only. No significant differences in motor-unit coherence were observed between tasks in the old subjects.

Discussion

The current study quantified the timing of motor-unit discharges during isometric, shortening, and lengthening contractions of the first dorsal interosseus muscle in old adults to infer details about the common input received by pairs of motor neurons. A previous study on young subjects found that the strength of motor-unit synchronization was greatest during slow-lengthening contractions, and low-frequency motor-unit coherence was reduced during shortening contractions, indicating that the strength of common input received by the motor neurons varied during contractions that involved slow changes in muscle length (Semmler et al. 2002). In contrast, there was no difference in motor-unit synchronization and coherence during the three contractions in older adults, suggesting an age-related decline in the modulation of common input to motor neurons across these types of contractions.

Examining the same pair of motor units during each task represents a powerful approach to explore alterations in the CNS strategy used to control different types of contractions in humans. Using this protocol, it was not possible to obtain a large number of motor units, so the sample of motor units obtained from each subject was relatively low. One advantage of this approach is that we can be relatively certain that each motor unit was unique, and not simply a recording from different muscle fibers of the same motor unit, which can occur when manipulating the recording electrode to sample from as many motor units in the muscle as possible. However, this low yield does introduce a potential bias, as the behavior of the selected motor unit may not be representative of the entire motor unit population. Clearly, task-related differences in motor unit behavior exist within a single motor neuron pool, and it is not known why the CNS may adopt a different input strategy to some motor neurons and not others during variations in task demands. Nonetheless, from the population of first dorsal interosseous motor units obtained under the conditions of the current study, the data suggest that the alterations in correlated motor unit activity during movements are greater in young compared with old adults.

Interpretation of the correlated motor-unit discharge

It is a commonly held view that motor-unit synchronization arises from the shared input from branched corticospinal neurons. Evidence from spike-triggered averaging indicates that single corticospinal cells in primates branch to facilitate most motor units in an intrinsic hand muscle (Mantel and Lemon 1987), suggesting that these inputs can contribute to motor-unit synchronization, even within a single motor neuron pool. Several less-direct observations in humans have supported the view that these branched inputs are mediated via the corticospinal pathway, at least for low-force isometric contractions. For example, motor-unit synchronization is altered in stroke patients following a lesion in the internal capsule (Datta et al. 1991; Farmer et al. 1993b), absent in patients with primary lateral sclerosis or amyotrophic lateral sclerosis (Schmied et al. 1999), and present in homologous hand muscles (one motor unit in each hand) of a Klippel–Feil patient known to have abnormal branching of corticospinal fibers that project to both sides of the spinal cord (Farmer et al. 1990). Although the inputs responsible for motor-unit coherence are less well established, experimental and computational studies have shown an association between motor-unit synchronization and high-frequency ($\sim$12–32 Hz) coherence (Davey et al. 1993; Farmer et al. 1993a; Moritz et al. 2005b), which suggests that the corticospinal pathway influences both of these features of correlated motor-unit activity (Farmer et al. 1993a; Halliday et al. 1999; Kilner et al. 2002; Semmler et al. 2002; 2004).
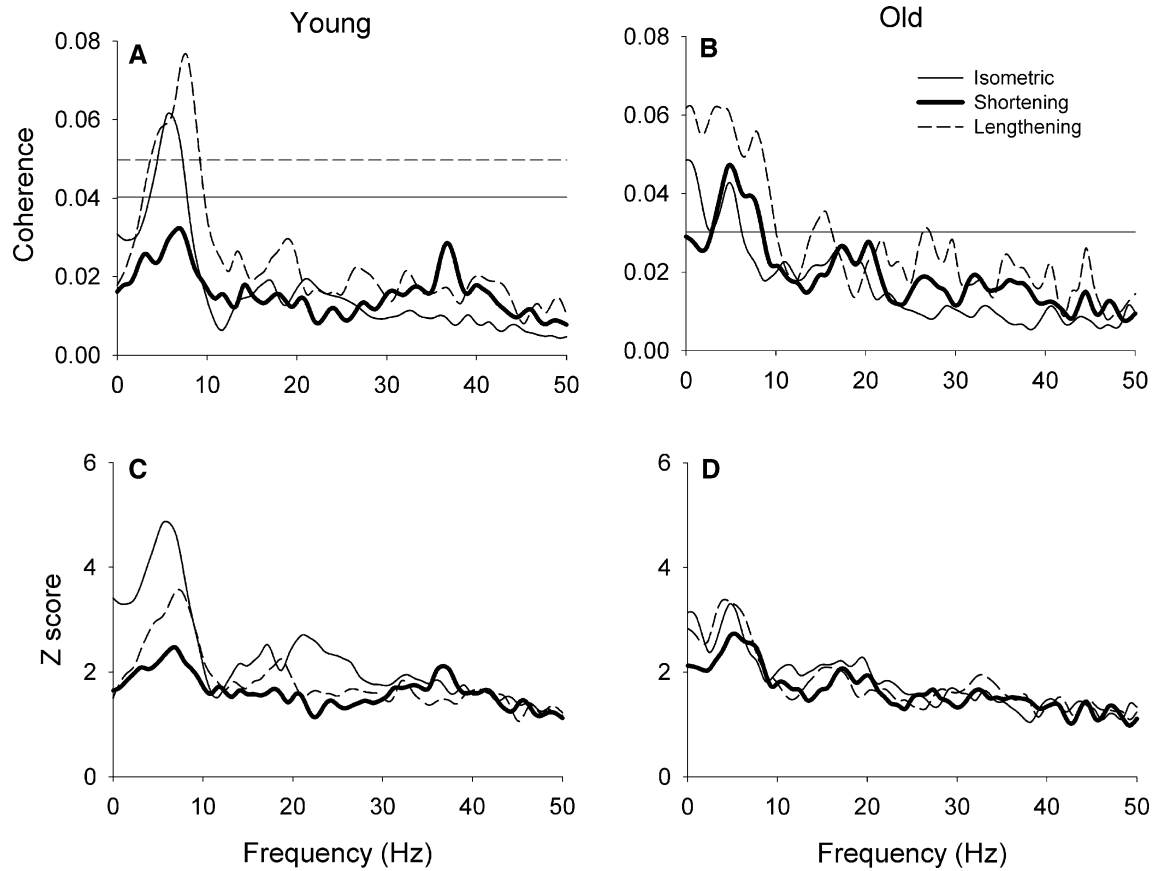
Fig. 4 The mean strength of motor-unit coherence during isometric, shortening and lengthening contractions in young and old adults. Data show the pooled coherence (**a**, **b**) and the mean coherence z scores (**c**, **d**) for 23 motor-unit pairs in each group of young and old adults. The *horizontal lines* represent the 95% confidence interval where significant coherence was observed for the isometric and lengthening contractions in young subjects and the isometric contractions in old subjects. The 95% confidence intervals for the remaining tasks were 0.045 for the shortening contractions in young subjects, 0.074 and 0.071 for the shortening and lengthening contractions in old subjects. The z score data show differences in coherence between isometric, shortening and lengthening contractions in young but not old adults (see also Table 2)

Along with the strength of common input, the width of the central synchronous peak is often used to infer details about how the common input is delivered to the motor neurons. A narrow central peak reflects common input to motor neurons that occurs directly, whereas a broad peak represents common input that is delivered through one or more interneurons (Kirkwood and Sears 1978; Sears and Stagg 1976). Under this scheme, any

Table 2 Summary of two-way, repeated-measures ANOVA comparisons between age group, task, and the age × task interaction for coherence z-scores averaged over 3-Hz bins

Frequency (Hz)	Age group df = 1,88	Task df = 2,88	Interaction df = 2,88
0–3	$F = 0.1$, n.s.	$F = 10.8$, $P < 0.001$[a,b]	$F = 4.3$, $P = 0.02$[a,b]
3–6	$F = 0.4$, n.s.	$F = 12.7$, $P < 0.001$[a,b]	$F = 7.7$, $P < 0.001$[a]
6–9	$F = 4.2$, $P < 0.05$	$F = 4.6$, $P = 0.01$[a]	$F = 5.7$, $P = 0.005$[a,c]
9–12	$F = 0.02$, n.s.	$F = 0.6$, n.s.	$F = 1.4$, n.s.
12–15	$F = 0.02$, n.s.	$F = 4.4$, $P = 0.02$[a]	$F = 0.3$, n.s.
15–18	$F = 0.07$, n.s.	$F = 3.9$, $P = 0.03$[a]	$F = 1.0$, n.s.
18–21	$F = 0.3$, n.s.	$F = 7.3$, $P = 0.001$[a,b]	$F = 2.4$, n.s.
21–24	$F = 1.5$, n.s.	$F = 14.2$, $P < 0.001$[a,b]	$F = 4.8$, $P = 0.01$[a,b]
24–27	$F = 1.6$, n.s.	$F = 4.7$, $P = 0.01$[a]	$F = 6.0$, $P = 0.004$[a,b]
27–30	$F = 0.1$, n.s.	$F = 2.0$, n.s.	$F = 0.7$, n.s.

df degrees of freedom for the main independent variable and the residual, n.s. not significant
[a] Isometric contractions greater than shortening contractions
[b] Isometric contractions greater than lengthening contractions
[c] Shortening contractions less than lengthening contractions. The interactions reflect differences in young subjects only

change in the width of the peak between tasks is interpreted as an alteration in the relative contribution of direct and indirect common input to motor neurons. For young subjects, the duration of the central peak was 14 ms for shortening contractions, which were 5 ms narrower than isometric contractions and 7 ms narrower than lengthening contractions. These data suggest that shortening contractions in young subjects are controlled with relatively more direct common input to motor neurons compared with isometric and lengthening contractions. In contrast, peak width was similar during all tasks in older adults (~14 ms), and was of an equivalent width as the shortening contractions in young subjects. These data indicate that shortening and lengthening contractions are performed without altering the pathways by which common input is delivered to hand muscle motor neurons in older adults.

Alternatively, it has recently been shown that common inhibitory inputs to motor neurons have a tendency to broaden the central synchronous peak (Türker and Powers 2001) and promote greater motor-unit coherence in simulated contractions (Taylor and Enoka 2004). This mechanism is supported by the recent finding that broad-peak synchronization is strongly correlated with high-frequency (10–30 Hz) motor-unit coherence, particularly in strength-trained subjects who have stronger synchrony and wider peaks than untrained subjects (Semmler et al. 2004). Although peak width is likely to be influenced by a combination of these factors, the current data suggests that the CNS strategy used to activate the motor units is altered during isometric, shortening, and lengthening contractions in young adults, but not old adults.

Implications for aging

Healthy aging is associated with a marked reorganization of the neuromuscular system. The most frequently studied neuromuscular adaptation is the loss of muscle mass (sarcopenia), which is largely due to a decrease in the number of muscle fibers and a decline in the number of motor neurons, resulting in an increased innervation ratio of the surviving motor units (see Doherty et al. 1993). Along with the changes in the peripheral nervous system, neurons in the motor cortex appear to be modified with advancing age. For example, approximately 50% of large diameter (≥19 μm) motor cortex neurons are lost or become non-functional throughout full adult life (Henderson et al. 1980). Furthermore, electrophysiological studies using transcranial magnetic stimulation (TMS) suggest an impairment of the corticospinal system in older adults (Eisen et al. 1991, 1996; Pitcher et al. 2003; Sale and Semmler 2005), which could indicate either a reduction in the number of corticospinal neurons or an impaired ability to activate the corticospinal system with advancing age.

These changes in the neuromuscular system do not seem to have a substantial influence on the common input to motor neurons during isometric contractions, as indicated by the absence of an age-related difference in motor-unit synchronization (Semmler et al. 2000). However, old adults did exhibit an increase in motor-unit coherence at 5–9 and 12–13 Hz compared with young subjects (Semmler et al. 2003a). When performing shortening and lengthening contractions, the current study again found no age-related difference in the strength of motor-unit synchronization, although the width of the peak in the cross-correlation histogram was broader (Fig. 3b) and motor-unit coherence at 6–9 Hz was greater in young subjects (Table 2). However, there was a substantial change in motor-unit synchronization and coherence between tasks in young subjects that was not evident in old adults. This finding suggests that the CNS alterations that occur with advancing age may influence the mechanisms and pathways that induce task-related adjustments in the control of the motor neuron pool. There is some evidence that older adults have more difficulty in modulating the descending (excitatory and inhibitory) inputs to motor neurons during force-varying isometric contractions (Sosnoff et al. 2004), which is consistent with the present findings. In contrast, it has recently been shown that the ability to modulate corticospinal responses during functional isometric contractions is intact in older adults (Sale and Semmler 2005), although it is not yet known if this extends to more difficult contractions involving changes in muscle length that are known to engage the corticospinal pathway when activated by TMS (Abbruzzese et al. 1994).

Muscle spindle afferents do not appear to contribute significantly to motor-unit synchronization during isometric contractions. Vigorous vibration of a hand muscle did not alter the size of the central peak in the cross-correlation histogram (see Fig. 6 of Farmer et al. 1997) and synchronization was not significantly different in a patient who had lost sensory feedback (Farmer et al. 1993a). However, there is increased reliance on sensory feedback during changes in muscle length (Burke et al. 1978; Schieber and Thach 1985), suggesting that muscle spindles are a potential source of common input, especially during lengthening contractions (Ljubisavljević et al. 1998). Furthermore, EMG–EMG coherence at 15–30 Hz is reduced in a deafferented subject (Kilner et al. 2004), which suggests that afferent input may be important for coherent oscillations in the motor system.

There is a substantial decline in the number of muscle spindles and an alteration in muscle spindle morphology with advancing age (Kararizou et al. 2005), which includes a reduction in the number of intrafusal fibers per spindle (Swash and Fox, 1972) due to a decline in the number of nuclear chain fibers (Liu et al. 2005). These changes in the muscle spindle are likely to be involved in the impaired position sense and movement detection thresholds (Skinner et al. 1984; Verschueren et al. 2002) as well as the reduced amplitude of the monosynaptic stretch reflex (Corden and Lippold 1996) in older adults. The reduced modulation of common input observed in

older adults is supported by the recent finding of a less pronounced task-dependent modulation of spinal reflexes during locomotion in older adults (Kido et al. 2004). Based on this evidence, it seems reasonable to suggest that reduced muscle spindle sensitivity may play a role in the reduced task-dependent adjustments of common input to motor neurons in older adults, particularly during lengthening contractions.

It is recognized that the shortening and lengthening contractions performed in the current study were relatively slow movements, which facilitated the identification of single motor units during changes in muscle length. Using similar contraction velocities, it has previously been shown that old adults are less accurate at matching index finger position during slow shortening and lengthening contractions of the first dorsal interosseous muscle, and that this was associated with altered motor unit activity in older adults (Laidlaw et al. 2000). As contraction velocity increases, the age-related difference in motor performance is accentuated (Sosnoff et al. 2004), which may be related to motor unit factors that influence the frequency-domain characteristics of the EMG (Christou et al. 2003). It is possible that differences in the ability to adjust the common inputs to motor neurons depending on the details of the task may contribute to these performance differences in young and old adults during rapid contractions, where *inter alia* motor-unit synchronization is likely to be more functionally relevant (see Semmler 2002).

In conclusion, a previous report indicated that motor-unit synchronization and coherence was influenced by the type of contraction performed by young subjects (Semmler et al. 2002), which suggests that the timing of common inputs to motor neurons was altered during slow shortening and lengthening contractions compared with isometric contractions. In the present study, the strength of motor-unit synchronization did not vary with task for older adults, and there were minor changes in motor-unit coherence with task in the old subjects. The reduced modulation of common inputs to motor neurons across the three types of contractions were likely caused by changes in the corticospinal system and muscle spindle afferents that occur with advancing age.

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