Motor-Unit Coherence During Isometric Contractions Is Greater in a Hand Muscle of Older Adults

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INTRODUCTION

Although both motor-unit synchronization and coherence correspond to the correlated discharge of action potentials by pairs of concurrently active motor units, they are the consequence of different features of the shared input between motor neurons. Motor-unit synchronization is a time-domain measure of the strength of common input to motor neurons that is mediated through the corticospinal tract (Datta and Stephens 1990; Farmer et al. 1993a; Kirkwood and Sears 1978; Sears and Stagg 1976). In contrast, motor-unit coherence is a frequency-domain measure of the strength of common oscillatory input to motor neurons that likely originates in the cortex or brain stem (Baker and Baker 2003; Conway et al. 1995; Farmer et al. 1993b; Halliday et al. 1998). However, low-frequency oscillations in motor neuron discharge may also be produced by slow ionic conductances (Falcke et al. 2000; Szucs et al. 2001; Varona et al. 2001).

One functional consequence of this type of correlated motor-unit activity is an influence on the ability of an individual to exert a precise force during a steady contraction. For example, computer simulations have demonstrated that motor-unit synchronization can have a pronounced effect on the amplitude of force fluctuations (Taylor et al. 2002; Yao et al. 2000). However, we have recently found no difference in the strength of motor-unit synchronization between young and old adults, despite greater force fluctuations in the old subjects (Semmler et al. 2000). An alternative possibility, which has been attributed a significant role in the fluctuations experienced by young adults (Halliday et al. 1999; Kakuda et al. 1999; Wessberg and Kakuda 1999), is the common modulation of input received by the active motor units (motor-unit coherence). For this reason, we quantified the strength of motor-unit coherence in the first dorsal interosseous muscle of young and old adults using data from our previous study (Semmler et al. 2000).

METHODS

In the original investigation (Semmler et al. 2000), subjects participated in two different experiments that were performed on separate days. One experimental session consisted of steadiness measurements during constant force isometric contractions of the first dorsal interosseous muscle producing index finger abduction forces of 2.5, 5, 7.5, and 10% of maximum voluntary contraction strength (MVC). The coefficient of variation of the force fluctuations was measured for the middle 30 s of each contraction and averaged over two steadiness trials. A second experimental session involved recording the activity of single motor units during low-force isometric contractions. The data obtained from the single motor-unit experiments are the focus of the current paper. The Human Research Committee at the University of Colorado approved all experimental procedures prior to commencement of the study. Eleven young (mean age ± SD; 24.1 ± 4.1 yr) and 14 old (70.4 ± 5.9 yr) adults participated in these experiments and gave informed consent prior to commencing the study. All subjects were right-hand dominant as measured by the Edinburgh Handedness Inventory (Oldfield 1971).

The experimental arrangement used to record single motor-unit activity has been described previously (Semmler et al. 2000). Briefly, each subject was seated facing a 14-in. computer monitor that provided feedback on the force exerted by the index finger of the subject. The left arm was placed prone on a manipulandum and the elbow joint was flexed to approximately 90°. The index finger was placed in an individualized splint so that the interphalangeal joints were kept extended. The splinted index finger contacted a force transducer (Sensotec model 13, Columbus, OH) at the level of the proximal interphalangeal joint. The arm and hand were secured by restraints to minimize extraneous activity from neighboring muscles.

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Two bipolar, fine-wire intramuscular electrodes were inserted into the first dorsal interosseus muscle. Each electrode consisted of three Formvar-insulated, stainless steel wires (50 μm diameter) that were threaded through a disposable 27-gauge needle. The activity of single motor units was examined while subjects exerted a low abduction force with the index finger for 2–5 min. The subject was provided with audio feedback on the discharge of a selected unit, which was discriminated off-line using a computer-based, spike-sorting algorithm (SPS 8701; Signal Processing Systems, Malvern, South Australia). After a rest period, concurrent discharges of new pairs of motor units were recorded by manipulating at least one of the wires used to record the potentials. With this process, it was possible to record an average (±SD) of 4 ± 2 different pairs of motor units in a given experiment. Single motor-unit recordings were amplified (1000–2000 times), band-pass filtered (20–8 kHz), and stored on tape.

The single motor-unit recordings were digitized (10 kHz) and discriminated off-line using a computer-based, spike-sorting algorithm (Spike2; Cambridge Electronic Design, Cambridge, UK) that identified the action potentials belonging to a particular motor unit based on waveform amplitude and shape. Interspike intervals of identified motor units were examined for every trial, and abnormally short and long interspike intervals that were clearly the result of discrimination error were excluded from statistical analysis. For the remaining discharge times, the mean, SD, and coefficient of variation of the interspike intervals were determined using custom-designed software written in Matlab (Mathworks, Natick, MA).

The strength of motor-unit synchronization was determined by a cross-correlation analysis performed on pairs of concurrently active motor units detected with separate electrodes. All cross-correlation histograms used in the analysis had a bin width of 1 ms and spanned a period 100 ms before and 100 ms after the discharge of one of the recorded motor units. The magnitude of the central synchronous peak was quantified using the synchronization index CIS (common input strength, Nordstrom et al. 1992), which represents the frequency of extra synchronous discharges in excess of chance. For each pair of motor units contributing to the cross-correlation histogram, we calculated the geometric mean \( \sqrt{\text{mean of motor unit 1} \times \text{mean of motor unit 2}} \) of discharge rate and coefficient of variation for discharge rate.

The frequency domain characteristics of common input to the motor units was examined while subjects exerted a low abduction force with the index finger for 2–5 min. The dependent variables for the comparison between young and old adults were as follows: 1) the frequency domain characteristics of common input to the motor neurons was estimated from the coherence spectrum between pairs of motor units; 2) geometric mean CV (%) of discharge rate; 3) synchronization strength (CIS); 4) synchronization peak width; 5) strength of coherence at each frequency; 6) strength of coherence in 5-Hz bins; and 7) incidence of significant coherence at each frequency. An unpaired \( t \)-test was used to compare motor-unit discharge properties (1–4 above) between groups. Given that coherence estimates were not normally distributed at some frequencies, a nonparametric Mann-Whitney \( U \) test was used to compare the strength of coherence between young and old adults. A repeated-measures ANOVA was used to compare the strength of coherence averaged over 5-Hz bins for the young and old adults. A \( \chi^2 \) test was used to compare the incidence of significant synchronization at each frequency. Statistical significance was designated at \( P \leq 0.05 \).

**RESULTS**

From the original sample of 109 motor-unit pairs (Semmler et al. 2000), it was possible to obtain coherence data on 47/53 motor-unit pairs in young subjects and 48/56 motor-unit pairs in old subjects. The motor-unit discharge properties and synchronization data for this sample are shown in Table 1. Despite the reduced isometric force steadiness that was observed in old subjects (coefficient of variation of force at 2.5 and 5% MVC: young = 3.4 ± 1.3%, old = 6.6 ± 3.3%; Semmler et al. 2000), there was no difference in the strength of synchronization in young and old adults during low-force isometric contractions. Furthermore, the geometric mean CV of the two motor units contributing to the cross-correlation histogram was greater in young subjects.

Examples of cross-correlation and coherence analysis in one young and one old subject are shown in Fig. 1. A narrow central peak can be observed in the cross-correlation histograms for the young (Fig. 1A) and old (Fig. 1B) subject that represents synchronous motor-unit discharge in the time domain. In these motor-unit pairs, the strength of motor-unit synchronization was similar between the young (CIS = 1.11 impulses/s) and old (1.17 impulses/s) adults. In contrast, the strength of motor-unit coherence for the same motor-unit pairs was greater in the old adult, particularly at frequencies of 5–10 and 15–25 Hz (Fig. 1C). These data indicate that the size of the central synchronous peak in the cross-correlation histogram does not necessarily reflect a similar strength of motor-unit coherence in the frequency domain. Furthermore, although strong synchronization was observed in the cross-correlation histogram for the young subject, no substantial coherence was observed in this motor-unit pair above approximately 8 Hz when subjected to a coherence analysis.

The mean strength of motor-unit coherence for young and old adults is shown in Fig. 2. The typical pattern of coherence observed in young and old subjects comprised an increased strength of coherence at low (5–10 Hz) and high (15–30 Hz) frequencies (Fig. 2A). However, the old subjects exhibited significantly greater (Mann-Whitney \( U \) test) motor-unit coherence at 4.7 Hz (\( P = 0.03 \)), 8.5 Hz (\( P = 0.01 \)), 12.4 Hz (\( P = 0.04 \)), 13.2 Hz (\( P = 0.01 \)), 35.7 Hz (\( P = 0.05 \)), and 44.2 Hz (\( P = 0.05 \)) compared with Old.

**TABLE 1. Discharge characteristics of the motor unit pairs that contributed to the cross-correlation histograms**

<table>
<thead>
<tr>
<th></th>
<th>Young</th>
<th>Old</th>
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<tr>
<td>Synchrony index CIS (impulses/s)</td>
<td>0.68 ± 0.42 (0.13–1.169)</td>
<td>0.76 ± 0.52 (0.10–2.47)</td>
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<tr>
<td>Peak width (ms)</td>
<td>15.8 ± 5.0 (7.0–29.0)</td>
<td>15.3 ± 6.6 (3.0–39.0)</td>
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<tr>
<td>Geometric mean rate (Hz)</td>
<td>10.8 ± 1.4 (7.9–14.2)</td>
<td>11.0 ± 1.8 (7.4–15.3)</td>
</tr>
<tr>
<td>Geometric mean CV (%)</td>
<td>18.4 ± 3.6 (11.4–26.5)</td>
<td>17.0 ± 2.7 (11.4–23.2)</td>
</tr>
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</table>

Values are means ± SD with ranges in parentheses. CIS, common input strength; CV, coefficient of variation. * \( P < 0.05 \) compared with Old.
0.01), and 48.8 Hz ($P = 0.05$) compared with young subjects. When the data were averaged over 5-Hz bins (Fig. 2B), a significant group $\times$ frequency interaction ($P = 0.02$, repeated-measures ANOVA) was detected for young and old adults. The largest difference between young and old adults was observed at the lowest frequencies of 5–10 Hz, although post-hoc analysis within this frequency range just failed to reach statistical significance ($P = 0.058$). For the incidence of significant coherence (data not shown), no consistent differences were observed between young and old subjects. The older adults exhibited significantly greater ($\chi^2$ test) incidence of coherence at 20.9 Hz (56 vs. 36%). In contrast, the young subjects displayed significantly greater incidence of coherence at 27.1 Hz (45 vs. 25%), 29.5 Hz (38 vs. 19%), 38.0 Hz (32 vs. 15%), and 41.9 Hz (32 vs. 10%).

**DISCUSSION**

The purpose of the study was to quantify the strength of motor-unit coherence in young and old adults using data obtained in a previous study (Semmler et al. 2000). In the prior study, we found no differences in motor-unit synchronization between young and old adults, which suggested that the strength of common input to motor neurons was not altered with advancing age. In contrast, the current analysis indicates that the amplitude of common oscillatory inputs (motor-unit coherence) was greater in old adults, particularly at low frequencies. Furthermore, although motor-unit synchronization and coherence are both measures of common input to motor neurons, these data clearly demonstrate that each method highlights unique features of the same common input.

Motor-unit coherence is a measure of the amplitude of common oscillatory input to motor neurons measured in the frequency domain. When hand muscles perform low-force isometric contractions, motor neurons typically receive common input in both low (approximately 1–10 Hz) and high (approximately 15–30 Hz) frequency bands, which presumably originates in the somatosensory cortex, primary motor cortex, or brain stem (Conway et al. 1995; Farmer et al. 1993a,b; Halliday et al. 1998). In the present study, we have confirmed the existence of coherence in these frequency bands in both young and old adults. However, two noteworthy observations can be made from the current data. First, motor-unit coherence was enhanced in the range of approximately 5–9 Hz compared with young adults (85% greater in old adults at 5 Hz). Second, the older adults expressed an additional oscillatory

**FIG. 1.** Examples of cross-correlation (A, B) and coherence analysis (C) in a pair of motor units from 1 young and 1 old adult. A, B: the strength of motor-unit synchronization measured with the synchrony index common input strength (CIS) was similar for the young (A, 1.11 impulses/s) and old (B, 1.17 impulses/s) subjects. The dashed horizontal line in each case represents the mean number of counts outside of the central peak region, whereas the 2 vertical dotted lines signify the location of the central peak. C: from the same pairs of motor units, the strength of coherence was greater in the old adult (thick line), particularly at frequencies of 5–10 and 15–25 Hz. No substantial coherence was observed for the motor-unit pair in the young subject (thin line) above 5 Hz. The dashed line represents the 95% confidence interval for both subjects.

**FIG. 2.** Mean strength of coherence for each frequency (A) and averaged over 5-Hz bins (B) in young (thin line) and old (thick line) adults. A: the mean strength of motor-unit coherence was greater in old adults at 4.7, 8.5, 12.4, 13.2, 35.7, 44.2, and 48.8 Hz. Standard error bars have been plotted for every fifth data point (3.9 Hz). B: the largest differences in coherence between young and old adults were observed at low frequencies.
Nonetheless, because oscillatory activity in descending drive has been associated with fluctuations in motor output (Halliday et al. 1999; Wessberg and Kakuda 1999), the increased motor-unit coherence observed in old adults is a possible contributor to the reduced steadiness that is often observed in these subjects (Enoka et al. 2003; Semmler et al. 2000).

When motor neurons consistently discharge action potentials at similar times during a voluntary contraction, the correlated activity can occur through the following two mechanisms (Farmer et al. 1993a,b; Kirkwood and Sears 1978; Sears and Stagg 1976): 1) the presence of branched inputs from a common source (motor-unit synchronization); and 2) modulation of branched input by a common oscillator (motor-unit coherence).

The two types of common input can be distinguished by time- and frequency-domain analysis from the discharge times of pairs of motor units. Although these two measures of common input to motor neurons are mathematically equivalent (Rosenberg et al. 1989), they emphasize different aspects of the same data. For example, we have shown that one motor unit contains from one young and one old adult in Fig. 1 with similar synchronization in the time domain, but different coherence in the frequency domain. The use of the coherence analysis, in addition to the synchronization data for these motor-unit pairs, suggests the following interpretation. For the motor-unit pair in the old adult, the common inputs to the motor neurons oscillated at specific frequencies, and this was revealed as peaks in the coherence spectrum at approximately 5–10, 15–25, and 25–35 Hz (thick line in Fig. 1C). In contrast, the synchronous common inputs for the pairs of motor units in the young subject were more random and were distributed over a wide range of frequencies, producing relatively little coherence in the frequency domain (thin line, Fig. 1C). This suggests that differences between common inputs that occur at a specific frequency are not reliably detected by quantification of the central peak in the cross-correlation histogram. Furthermore, compared with conventional cross-correlation techniques, it is likely that a coherence analysis is a more sensitive method to provide a complete description of shared common inputs to motor neurons.

DISCLOSURES

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REFERENCES


