Exp Brain Res (2007) 178:285–295
DOI 10.1007/s00221-006-0739-5

RESEARCH ARTICLE

Discharge rate during low-force isometric contractions influences motor unit coherence below 15 Hz but not motor unit synchronization

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Received: 21 April 2006 / Accepted: 22 September 2006 / Published online: 8 November 2006

Abstract The purpose of the study was to determine whether pairs of motor units that discharge action potentials at different rates during isometric contractions exhibit different levels of motor unit synchronization or coherence. Twelve subjects (28.6 ± 6.1 years) performed isometric contractions at target forces slightly above the recruitment threshold (1.02–20.9%) of an isolated motor unit. Based on audio feedback, subjects maintained a relatively constant discharge rate of the isolated unit for about 80 s. Intramuscular electrodes were used to record the discharge of 47 pairs of motor units at rates that ranged from 8.07 to 13.6 pps. Correlated discharge between pairs of motor units was quantified with the common input strength (CIS) index, k' index, and coherence spectrum. Greater discharge rates across pairs of motor units were predicted ($R^2 = 0.36$, $P < 0.001$) by higher coherence from 8 to 13 Hz ($r = -0.52$) and lower coherence from 0 to 4 Hz ($r = 0.37$). Indexes of motor unit synchronization (CIS and k') were strongly associated with motor unit coherence from 16 to 32 Hz (CIS: $R^2 = 0.63$; k': $R^2 = 0.4$; $P = 0.001$). The CIS index of motor unit synchronization and the motor unit coherence from 16 to 32 Hz did not vary with discharge rate. In contrast, the k' index of motor unit synchronization declined with discharge rate ($r^2 = 0.20$, $P = 0.001$). Furthermore, greater discharge rates across pairs of motor units were accompanied by higher motor unit coherence in the 8–13 Hz band and lower motor unit coherence in the 0–4 Hz band. These results demonstrate that differences in discharge rate between pairs of motor units in first dorsal interosseus during low-force, isometric contractions were associated with modulation of the correlation in the discharge times of the two motor units at frequencies less than 15 Hz.

Keywords Coherence · Cross-correlation · First dorsal interosseus

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Introduction

Comparison of the times at which action potentials are discharged by pairs of motor units during voluntary contractions often reveals that some discharges occur at about the same time. Such synchronization of discharge times has been attributed to common input that has been delivered to the spinal motor neurons either by branched axons from last order neurons (Sears and Stagg 1976; Kirkwood and Sears 1978; Datta et al. 1991) or by presynaptic synchronization of efferent fibers from the motor cortex (Smith and Fetz 1989; Farmer et al. 1993b; Baker et al. 2001; Schieber and Rivlis 2005). Accordingly, the measurement of motor unit synchronization has been used to probe the integrity of the central nervous system (CNS) in selected patient populations (Farmer et al. 1990, 1993b; Datta et al. 1991; Schmied et al. 1999) and to characterize CNS adaptations associated with various tasks (Schmied et al. 2000; Semmler et al. 2000; Kilner et al. 2002).

The proportion of nearly coincidental discharge times for pairs of motor units is classically quantified in the time domain as the peak in the cross-correlation histogram (Sears and Stagg 1976; Nordstrom et al. 1992). The magnitude of the peak has been normalized with several different indexes, including one that expresses the number of counts in the peak relative to the duration of the contraction (index CIS) and another that determines the ratio of the counts in the peak to the number of counts expected in the time defined by the duration of the peak (index k'). One of the principal differences between these two indexes is that index k' is influenced by the discharge rate of the contributing motor units during voluntary contractions, whereas index CIS is not (Nordstrom et al. 1992; Moritz et al. 2005).

The correlated discharges of motor unit pairs have also been assessed in the frequency domain as peaks in the coherence spectrum. The findings suggest that the discharge rates of pairs of motor units can be modulated in at least three bands: 0–4, 8–12, and 16–32 Hz. Modulation at 0–4 Hz, which is termed common drive, has been observed during isometric contractions and is attributed to the activation of the motor units by the same source (De Luca and Erim 1994; Myers et al. 2004). In contrast to the common drive during isometric contractions, discharge rates have been reported to be correlated at 8–12 Hz during movements with the amount of coherence increasing with movement speed (Wessberg and Kakuda 1999). In addition to the coherent oscillations that can occur at 1–12 Hz, discharge rates can be correlated from 16 to 32 Hz apparently due to periodic activity in presynaptic inputs from the motor cortex in humans (Farmer et al. 1993a, 1997; Kilner et al. 2002) and primates (Murthy and Fetz 1996).

There is evidence from experimental (Farmer et al. 1993b; Halliday and Rosenberg 1999; Kilner et al. 2002; Semmler et al. 2003, 2004) and computational (Moritz et al. 2005) studies that short-term synchronization of motor units is strongly associated with coherence from 16 to 32 Hz but not with lower frequencies in the coherence spectrum (see also Semmler et al. 1997). Furthermore, variation in discharge rate appears to increase motor unit coherence from 8 to 12 Hz (Wessberg and Kakuda 1999) but does not influence motor unit synchronization (Nordstrom et al. 1992). In contrast, a recent computational study indicates that motor unit synchronization increases when the frequency of the common input is close to the average motor unit discharge (Lowery and Erim 2005). These varied results indicate that the interactions between the discharge rate, coherence, and short-term synchronization of motor units remain unclear. The purpose of the study was to determine whether pairs of motor units that discharge action potentials at different rates during isometric contractions exhibit different levels of motor unit synchronization or coherence. Based on the associations that have been observed between short-term synchronization and coherence (Farmer et al. 1993b; Moritz et al. 2005; Semmler et al. 2003, 2004) and between discharge rate and the correlated discharge of motor units (Nordstrom et al. 1992; Wessberg and Kakuda 1999), we hypothesized that discharge rate would influence common oscillations of motor units at frequency bands lower than the 16–32 Hz band and thus would not influence short-term synchronization.

Methods

Twelve adults (8 men and 4 women; age: 28.6 ± 6.1 years; body mass: 77.2 ± 15.4 kg; height: 172.7 ± 5.9 cm) participated in this study. All subjects were healthy, right-handed (Edinburgh Handedness Inventory; Oldfield 1971) and were moderately active (physical activity questionnaire; Paffenbarger et al. 1993). Subjects provided written, informed consent prior to participation in the study and the Human Research Committee at the University of Colorado in Boulder approved the project.

Experimental setup

Subjects were seated in an experimental chair facing a 17-in. computer monitor, which was positioned 1.6 m in front of the subject at eye level. The monitor was used to display the target force and the force exerted by the subject. All experiments were performed on the left hand (nondominant), which rested prone on a platform that was adjusted, so the shoulders were horizontal to the ground and the left arm was abducted by ~0.8 rad. A vacuum foam pad was used to immobilize the elbow and forearm (Versaform pillow, Tumble Forms, Canada). The left hand and forearm were constrained by clamps to maintain an angle of ~1.5 rad between the thumb and index finger (Taylor et al. 2003). The index finger was inserted into a splint that kept the interphalangeal joints extended. The position of the arm and index finger were continuously monitored by one of the investigators during each trial. This arrangement allowed abduction of the index finger about the metacarpophalangeal joint in the horizontal plane, a movement that is produced almost exclusively by contraction of the first dorsal interosseus muscle (Li et al. 2003).

Force recordings

The abduction force exerted by the index finger was measured with a button force transducer (Model 13, Sensotec) that was aligned with the proximal interphalangeal joint. A high sensitivity (0.051 V/N) transducer was used for contractions that were less than 20% of the maximal voluntary contraction (MVC) force, and a low sensitivity (0.0059 V/N) transducer was used to measure force during contractions that were equal to or greater than 20% MVC force. Force was digitized at 500 samples/s using Spike2 software (Cambridge Electronic Design, Cambridge, UK) and stored on a computer.

Motor unit recordings

The electrodes for the single motor unit recordings were custom fabricated. Each electrode consisted of two Formvar-insulated, stainless steel wires (50 μm diameter; California Fine Wire, Grover Beach, CA, USA). The two wires were threaded through a single-use, 27-gauge hypodermic needle, and were glued in the lumen of the needle with medical-grade cyanoacrylate glue. The wires were cut at the end of the lumen with surgical grade scissors to expose the recording surfaces. Two electrodes were inserted percutaneously about 1–2 cm apart into the first dorsal interosseus for each experiment. The hypodermic needles were left in the first dorsal interosseus muscle during the experiments so that the location of the recording electrodes could be adjusted to facilitate isolation of individual motor units. The signal from the recording electrodes was amplified (×1,000–5,000; Coulbourn isolated bioamplifier, model V75–04), band-pass filtered (0.1–8 kHz; Coulbourn bandpass filter, model V75–48), displayed on an oscilloscope (Tektronix TDS 420A), digitized at 10 *k* samples/s (1401 plus, Cambridge Electronic Design, UK), and stored on a personal computer (Dell Optiplex 6100). Motor units were detected on-line with an amplitude window discriminator (Coulbourn dual comparator window discriminator, model V21–10). Once a motor unit was detected, the position of the needle was stabilized with adhesive tape to the subject's skin.

Experimental protocol

Subjects participated in a single experiment that lasted 90–120 min. Prior to performing the experiment, each subject completed the Edinburgh Handedness Inventory form (Oldfield 1971), a physical activity questionnaire (Paffenbarger et al. 1993), and signed the consent form. After the two hypodermic needles had been inserted into the first dorsal interosseus muscle, each subject performed maximal voluntary isometric contractions (MVCs), a series of steady submaximal contractions, and another set of MVCs.

Maximal voluntary contraction

The subjects were instructed to increase the force from baseline to maximum gradually over a 3-s period and to maintain the maximal force for 2 s. After two practice trials, each subject performed three MVCs, with subsequent trials performed if the difference in peak force was greater than 5% among the three trials. The trial with the highest peak was used for analysis and the MVC was defined as the average during a 0.5-s interval around the peak force. To quantify the amount of fatigue caused by the multiple submaximal contractions, another set of MVCs was performed at the end of the experimental protocol.

Steady submaximal contractions

The purpose of these contractions was to record the discharge of one motor unit on each electrode during steady submaximal contractions that lasted about 80 s. Subjects were instructed to increase the abduction force gradually from baseline until each electrode detected at least one motor unit discharging action potentials repetitively. The recruitment threshold of each motor unit was quantified as the minimal force at which motor units discharged action potentials repetitively (>6 pps). The subject was provided with audio feedback and asked to maintain the discharge rate of one motor unit relatively constant for the duration of the contraction. To obtain a range of discharge rates, subjects were provided with visual feedback of several target forces. However, it was only possible to discriminate the discharge of 8 out of 47 pairs of motor units at more than one force. The force was displayed as a horizontal line on the monitor.

The length of the contraction varied from 50 to 120 s and subjects rested for 180 s between contractions at different target forces. Although the number of discharges varied (831 ± 246; Table 1), preliminary analysis indicated that motor unit synchronization (CIS and k') was not significantly different ($P > 0.2$) between 400 and 1,000 discharges for the same 14 pairs of motor units that were able to discharge for longer periods of time. The measures of motor unit synchronization from 400 discharges significantly predicted those esti-

Table 1 Discharge characteristics and target forces for the pairs of motor units during the steady submaximal contractions

Measurement	Mean ± SD	Range
Number of discharges	830 ± 248	400–1,497
Mean ISI (ms)	95 ± 12	73–124
Coefficient of variation for ISI (%)	25.52 ± 5.33	15.2–37.2
CIS (pps)	0.680 ± 0.486	0.05–1.92
k'	1.547 ± 0.465	0.97–3.4
Target force (N)	1.639 ± 1.411	0.24–6.20
Target force (% MVC)	5.781 ± 4.261	1.02–20.9
Recruitment thresholds (% MVC)	5.2 ± 5.0	0.5–19

ISI interspike interval

mated with 1,000 discharges (CIS: $r^2 = 0.65$, slope = 0.93, $P < 0.001$; k': $r^2 = 0.64$, slope = 0.92, $P < 0.001$). The number of discharges used in the current study, therefore, does not influence the estimation of motor unit synchronization.

Data analysis

Single motor units were identified based on action potential shape and amplitude (Fig. 1a). A computerized, spike-sorting algorithm (Spike2; Cambridge Electronic Design) was used to discriminate the motor units. The automatic discrimination was followed by visual inspection of the intramuscular EMG recordings and the identified discharge times and any apparent errors were corrected. The mean, SD, and coefficient of variation of the interspike intervals (ISIs) were determined using custom-designed software written in Matlab version 6.5 (The Mathworks, Natick, MA, USA). The geometric means of the ISI and the coefficient of variation for ISI were calculated for each pair of motor units (Bland 2000).

The strength of motor unit synchronization in the time domain was quantified by the index CIS (Nordstrom et al. 1992) and the index k' (Ellaway 1978; Halliday et al. 2003). For each motor unit pair, a cross-correlation histogram, with a bin width of 1 ms, was constructed by comparing each discharge time of the reference motor unit with all discharge times by the other unit within ±100 ms (Nordstrom et al. 1992). As in previous studies (Semmler et al. 2004), the motor unit discharging at the lower rate was considered the reference motor unit. The cumulative sum procedure (Ellaway 1978), which subtracts the number of counts in each bin from the mean bin count (M) and continually adds the result to the previous bin, was used to identify synchronous peaks in the cross-correlation histogram (Fig. 1b). Inflections in the cumulative sum of the histogram defined the width of the central peak and

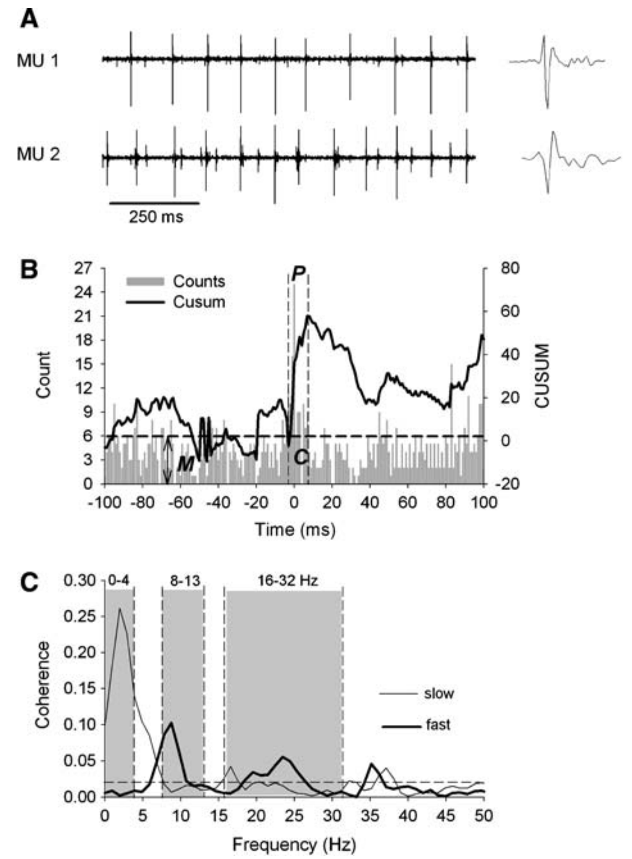

Fig. 1 Representative motor unit discharges (**a**) and the corresponding methods used to estimate the strength of motor unit synchronization (**b**) and motor unit coherence (**c**). The waveforms for the two motor units are shown beside each train of action potentials in *A*. Indexes CIS and k' were quantified from the cross-correlation histogram (**b**; *gray bars*; resolution 1 ms) and its corresponding cusum (**b**; *thick line*). *M* represents the average count in the bins from −100 to −30 ms. Inflections in the cusum around time 0 were used to denote the beginning and end of the peak in the cross-correlation histogram (*dashed vertical lines*). For this record, the peak began at −4 ms and ended at 7 ms. Region *C* indicates the number of counts expected in the peak of the histogram due to chance, which was estimated as the product of *M* and the width of the peak. Region *P* represents the number of counts in the peak in excess of those due to chance. Indexes CIS and k' were derived from the sizes of regions *C* and *P*. Correlated motor unit activity was also quantified as peak values in three frequency bands (0–4, 8–13, and 16–32 Hz; *gray areas*) of the coherence spectrum (**c**: graphed resolution is 0.5 Hz). *Slow* indicates the coherence between two motor units discharging at a geometric mean interspike interval (ISI) of 110 ms, whereas *fast* denotes the coherence between two motor units discharging at a geometric mean ISI of 90 ms. The *dashed horizontal lines* indicate the following: **b** values *above the line* indicate correlated discharges in excess of those due to chance; **c** values *above the line* indicate significant coherence

the number of counts in the central peak above those due to chance (average number of counts from −100 to −70 ms) was calculated; region *C* denotes counts due to chance, whereas region *P* indicates counts in excess of chance. Index CIS (pps) was calculated as the ratio of P to the duration of the contraction (60–120 s in the current study; (Nordstrom et al. 1992). Index k' corresponded to the ratio of the counts in regions P and C (Ellaway and Murthy 1985; Nordstrom et al. 1990). Motor unit discharges, which exhibited ISIs that were longer than 250 ms and shorter than 20 ms, were excluded from the cross-correlation analysis.

Correlations in the frequency domain were examined with the coherence spectrum (Rosenberg et al. 1989). Briefly, discharge times from each pair of motor units were partitioned into contiguous, nonoverlapping epochs of 1.28 s that each comprised 1,024 bins (sampling frequency = 400 samples/s). Each 2.5-ms bin was then given a value of 1 when it contained a discharge time, and a value of 0 when it did not. These time-series data were transformed into the frequency domain with a resolution of 0.39 Hz (sampling frequency = 400 samples/s and window size = 1,024). Auto- and cross-spectra were estimated, and a coherence estimate was computed. Significant peaks were identified as values that exceeded the 95% confidence intervals relative to the zero value. Based on previous studies that examined common oscillations for a pair of motor units (Farmer et al. 1997; Mima and Hallett 1999; Brown 2000) and the purpose of this study, three frequency bands in the coherence spectrum were analyzed: 0–4 Hz (Myers et al. 2004), 8–13 Hz (Vallbo and Wessberg 1993; Wessberg and Kakuda 1999), and 16–32 Hz (Farmer et al. 1993a; Farmer 1998). The highest coherence (peak value) was determined for each frequency band.

The discharge of the motor unit pairs was characterized with the geometric mean of the ISI, geometric mean coefficient of variation and standard deviation for ISI, force level (N or % MVC), indexes CIS and k', peak and median value in the coherence spectrum, and peak values in the three bands of interest in the coherence spectrum. The associations between two variables (e.g., geometric mean of the ISI and CIS) were examined with bivariate regression analyses. The strength of the association is reported as the squared Pearson product–moment correlation coefficient (r^2), which indicates the proportion of variance for the criterion variable (typically referred as the dependent variable; e.g., CIS) that is accounted for by its linear relation with the predictor variable (typically referred as the independent variable; e.g., geometric mean of the ISI; (Green and Salkind 2002). Multiple regression analyses and the associated part correlations (r) were used to examine the contribution of each coherence band to the CIS, k', force level, and geometric mean of the ISI. The goodness of fit of the model, which indicates how well the linear combination of the predictor variables (e.g., peak values in coherence band) predicted the criterion variable (e.g., geometric mean of the ISI), was given by the squared multiple correlation (R^2). The relative importance of the predictors was estimated with the part correlations (r), which provide the correlation between a predictor and the criterion, removing the effects of all other predictors in the regression equation from the predictor but not the criterion (Green and Salkind 2002). A positive sign of the part correlation indicates that the predictor and the criterion are positively related, whereas a negative sign indicates that they are inversely related. All regression analyses were performed with SPSS software (SPSS version 13.0)

The discharge characteristics (described above) for pairs of motor units that were recorded at two discharge rates were compared with a Wilcoxon nonparametric t test (Z scores) and a Monte Carlo 99% confidence interval. The Monte Carlo simulation to estimate the confidence interval was performed by the SPSS software (SPSS version 13.0). The interaction of discharge rate (slow vs. fast discharge rates) and frequency band in the coherence spectrum (0–4, 8–13, and 16–32 Hz) was examined with a repeated-measures analysis of variance (ANOVA) followed by appropriate (dependent and independent t tests with Bonferroni corrections) post hoc analyses. The alpha level for all statistical tests was set at 0.05 (except the nonparametric tests) and coherence analyses were significant above 95% confidence intervals from zero (Rosenberg et al. 1989; Farmer et al. 1997). Data are indicated as mean ± SD in the text and tables and as mean ± SEM in the figures.

Results

The aim of this study was to determine whether pairs of motor units that discharge action potentials at different discharge rates exhibit different levels of motor unit synchronization and coherence. The correlated activity for pairs of motor units was quantified with motor unit synchronization from the cross-correlation histogram (time domain) and the coherence spectrum (frequency domain).

The discharge times of 47 pairs of motor units in the first dorsal interosseus muscle of 12 subjects were recorded at forces that ranged from 1.02 to 20.9% MVC force (Table 1). MVC force was similar ($P = 0.3$) at the beginning (mean ± SD: 34.1 ± 11.8 N) and end (33.6 ± 10.4 N) of the experiment, which indicates that the results were not influenced by muscle fatigue. The geometric mean discharge rate across the 47 pairs of motor units ranged from 8.07 to 13.6 pps (10.7 ± 1.33 pps) and 830 ± 248 discharges were discriminated for the pairs of motor units. The indexes

CIS and k' did not vary significantly ($r^2 < 0.02$, $P > 0.4$) with force (N or % MVC). Furthermore, the geometric mean coefficient of variation for ISI ranged from 15.2 to 37.2% (25.5 ± 5.3%) and was not significantly associated with the geometric mean ISI ($r^2 = 0.03$, $P = 0.2$), whereas the geometric mean SD for ISI ranged from 12.9 to 34.4 ms (23.9 ± 5.2 ms) and did increase with geometric mean ISI ($r^2 = 0.15$, $P = 0.01$). Neither index of ISI variability, however, was significantly associated with either index of synchronization: index CIS (CV: $r^2 = 0.07$, $P = 0.08$; SD: $r^2 = 0.02$, $P = 0.35$) and index k' (CV: $r^2 = 0.01$, $P = 0.6$; SD: $r^2 = 0.04$, $P = 0.2$).

Motor unit discharge rate and common oscillations

The geometric mean ISI was linearly associated ($r^2 = 0.26$, $P < 0.001$) with force level (% MVC), indicating that, on average, force increased with the rate at which the 47 pairs of motor units discharged action potentials. The association between geometric mean ISI and force level, however, was best described with an exponential equation ($R^2 = 0.36$, $P < 0.001$; Fig. 2). To determine the common oscillations of the motor units that occurred with increased drive to the motor neuron pool (projected from discharge rate), the geometric mean ISI (criterion variable) was predicted from the three coherence bands of interest (predictor variables). The geometric mean ISI was best predicted ($R^2 = 0.36$, $P < 0.001$; Fig. 3) with the peak values in the 0–4 Hz ($r = 0.37$) and 8–13 Hz ($r = -0.52$) bands of the coherence spectrum. The predictive equation was $0.095 - (0.120 \times$ peak in the 8–13 Hz band$) + (0.06 \times$ peak in the 0–4 Hz band). The coherence band from 16 to 32 Hz (or 4–8 and 32–50 Hz) did not contribute significantly to the prediction of motor unit discharge.

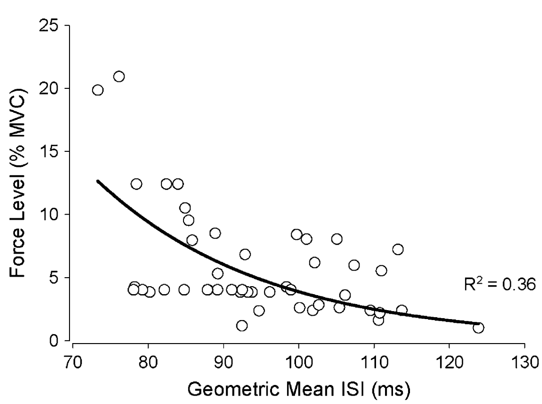

Fig. 2 Relation between discharge rate and force level (% MVC) for the 47 pairs of motor units. The force was slightly above recruitment threshold for each unit. The geometric mean ISI was negatively associated with force level ($R^2 = 0.36$, $P < 0.001$), indicating that motor units recorded with a higher discharge rate were, on average, recorded at a higher force level

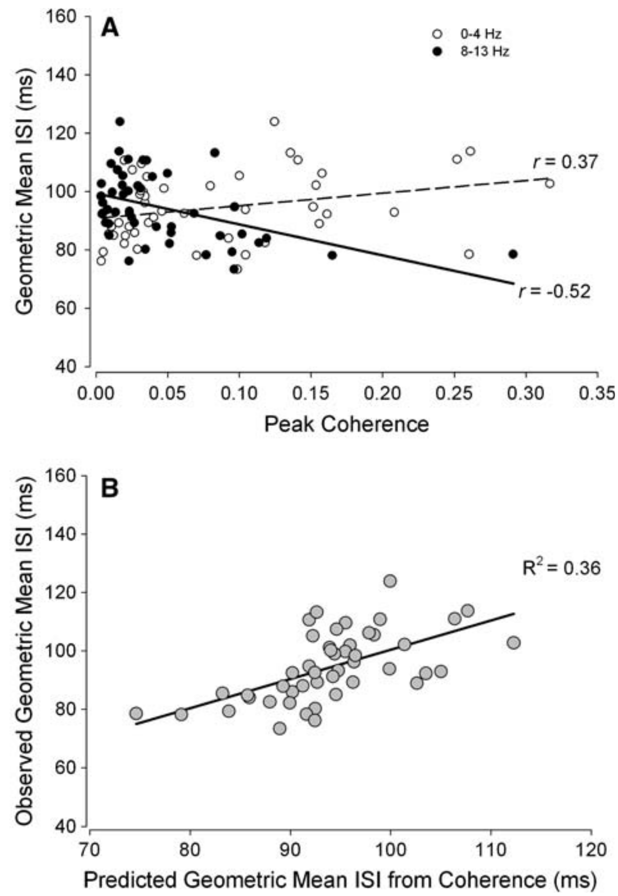

Fig. 3 The association between the geometric mean ISI and peak coherence. Each *point* in **a** represents the association between the peak coherence (0–4 Hz: *open circle*; 8–13 Hz: *filled circle*) and geometric mean ISI. The ISI was predicted ($R^2 = 0.36$, $P < 0.001$; **b**) from the coherence in the 0–4 Hz band ($r = 0.37$) and the coherence in the 8–13 Hz band ($r = -0.52$). The r values on the graph denote the part correlations derived from the multiple regression model

Thus, higher discharge rates (lower geometric mean ISIs) across the sample of motor unit pairs were accompanied by higher peak values in the 8–13 Hz band and lower peak values in the 0–4 Hz band. The results were similar when the coherence within the bands was calculated as the percent of the total coherence from 0 to 50 Hz

The influence of discharge rate on coherence was also similar in the eight pairs of motor units that were recorded at two significantly different ISIs (105.5 ± 9.7 vs. 94.1 ± 10.1 ms; $Z = -2.38$, $P = 0.008$). The frequency that indicated the median of the coherence spectrum increased significantly ($Z = -2.38$, $P = 0.006$) from 4.88 ± 1.93 Hz at the slow discharge rate to 6.59 ± 2.89 Hz during the faster discharge rate (Fig. 4). This shift to higher frequencies appeared to be related to a significant decrease in coherence from 0 to 4 Hz (0.17 ± 0.08 vs. 0.08 ± 0.08; $P = 0.001$) and an increase

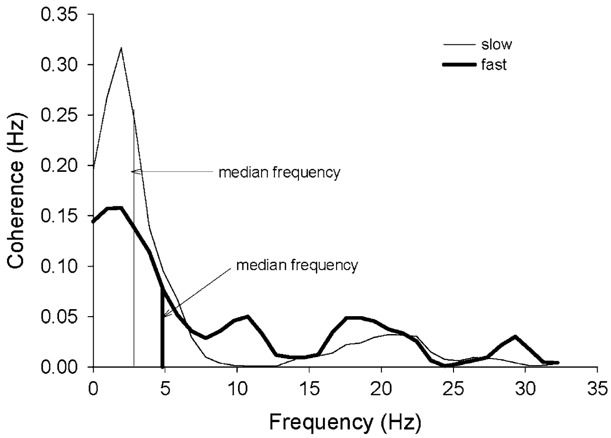

Fig. 4 Representative coherence spectra for the same pair of motor units at two different discharge rates. The geometric mean ISI was 110 ms for the slow discharge and 95 ms for the fast discharge. The median frequency of the coherence spectrum shifted to higher frequencies (from 3.1 to 4.9 Hz) with increased discharge rate. This appeared to be related to increases in coherence from 8 to 13 Hz and decreases in coherence from 0 to 4 Hz

(significant for $P < 0.1$) in coherence from 8 to 13 Hz (0.03 ± 0.03 vs. 0.04 ± 0.03; $P = 0.09$). There was no change in the coherence band from 16 to 32 Hz (0.03 ± 0.02 vs. 0.03 ± 0.02; $P = 0.2$). Therefore, the effect of increased drive to the motor neuron pool appears to be similar across different pairs of units and between the same pairs of motor units.

Motor unit synchronization and discharge rate

Although there was a significant association ($P = 0.001$) between CIS and k', the two indexes did not convey identical information ($r^2 = 0.63$). The contribution of discharge rate to each index of motor unit synchronization was examined with bivariate linear regressions between the geometric mean ISI and the indexes of motor unit synchronization. The geometric mean ISI was not significantly associated with the CIS index ($r^2 = 0.01$, $P > 0.2$; Fig. 5a), whereas it significantly contributed to the k' index of motor unit synchronization ($r^2 = 0.20$, $P < 0.001$, Fig. 5b). The influence of variation in discharge rate was also examined in eight pairs of motor units that were recorded at two different discharge rates. The CIS ($Z = -1.33$) and k' ($Z = -1.54$) indexes did not differ ($P > 0.1$) for the slow and fast discharge rates (CIS: 0.88 ± 0.43 vs. 0.66 ± 0.41; k': 1.69 ± 0.36 vs. 1.51 ± 0.34).

Motor unit synchronization and coherence

The two motor unit synchronization indexes were also predicted from the coherence spectrum. The major

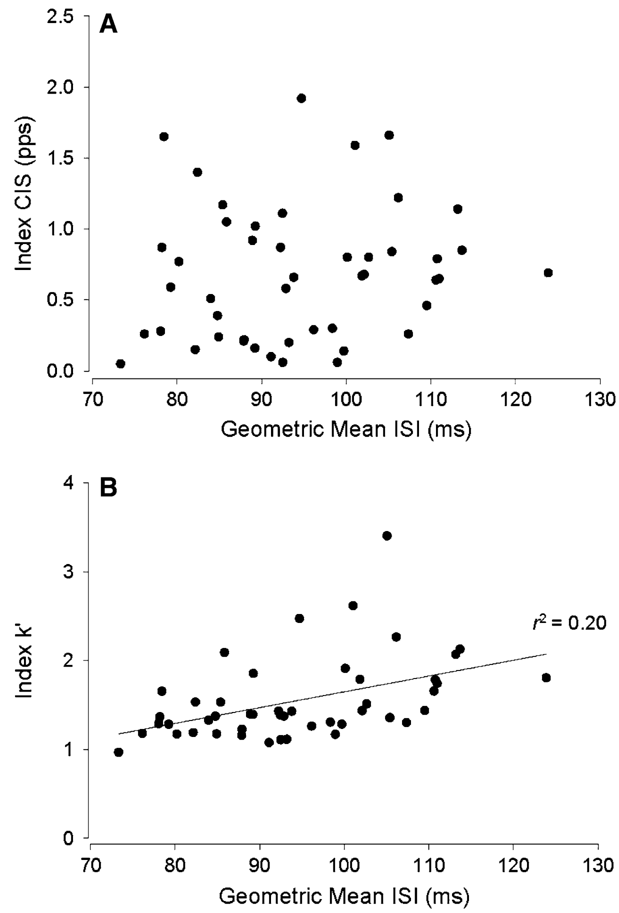

Fig. 5 The association between discharge rate and indexes of motor unit synchronization. The geometric mean ISI was not associated with the CIS index ($r^2 = 0.01$, $P > 0.2$; **a**), but was significantly associated with the k' index ($r^2 = 0.2$, $P < 0.01$; **b**)

predictor for both the CIS index ($R^2 = 0.63$, $P < 0.001$; Fig. 6a) and the k' index ($R^2 = 0.40$, $P < 0.001$; Fig. 6b) was the peak in the 16–32 Hz band of the coherence spectrum. Although there was a weak, significant association between CIS and coherence bands from 0 to 4 Hz ($r^2 = 0.10$, $P < 0.001$) and 8–13 Hz ($r^2 = 0.10$, $P < 0.001$), the addition to the prediction of CIS was small (R^2 change = 0.07). Furthermore, the addition of the geometric ISI to the 16–32 Hz coherence improved the prediction of the k' index ($R^2 = 0.60$, R^2 change = 0.20, $P < 0.001$; Fig. 6c) but not the prediction of CIS index (R^2 change = 0.07) of motor unit synchronization.

Discussion

The purpose of the study was to determine whether pairs of motor units that discharged action potentials at different rates during isometric contractions exhibited different levels of motor unit synchronization or coher-

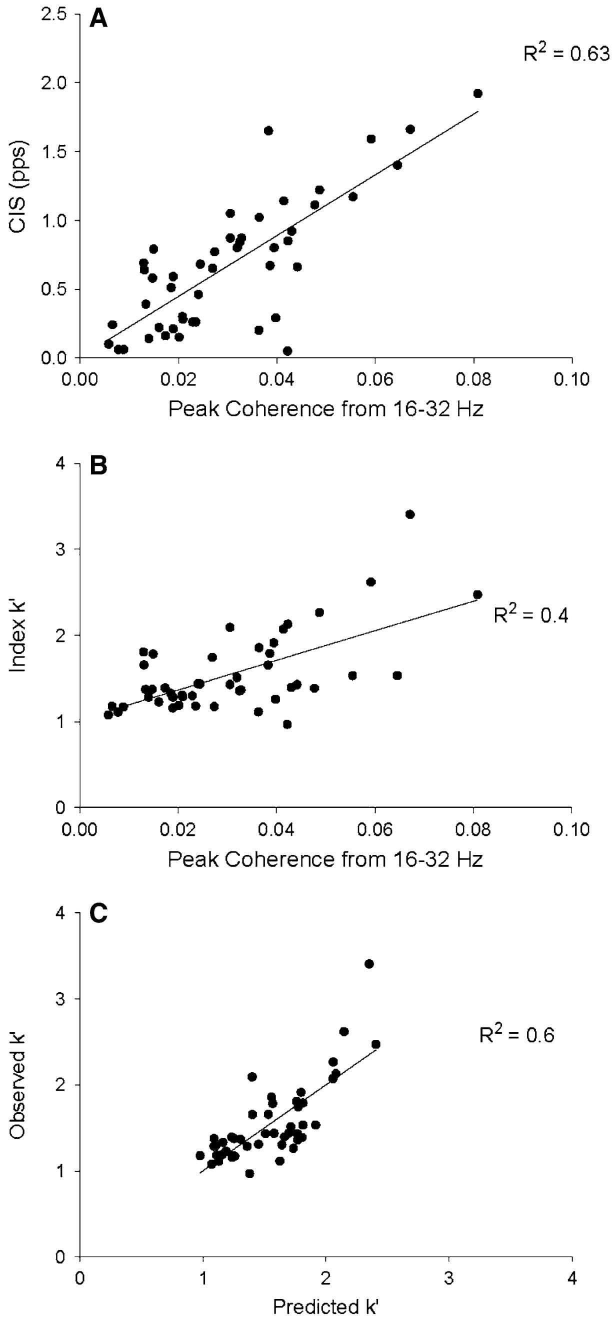

Fig. 6 The association between indexes of motor unit synchronization and coherence. Both the CIS index ($R^2 = 0.63$, $P < 0.001$; **a**) and k' index ($R^2 = 0.4$, $P < 0.001$; **b**) were associated with peak coherence from 16 to 32 Hz. The linear combination of geometric mean ISI and coherence from 16 to 32 Hz improved the prediction of the k' index ($R^2 = 0.6$, $P < 0.001$; C) but not the CIS index

ence. The correlated discharge of motor units was assessed in the time domain as short-term synchronization and in the frequency domain with the coherence spectrum. The findings agree with previous work and demonstrate that short-term synchronization of motor unit discharge is best predicted with motor unit coherence from 16 to 32 Hz (Farmer et al. 1993a) and does not change with discharge rate (Nordstrom et al. 1992; Moritz et al. 2005). The main finding of the current study was that greater discharge rates were accompanied by greater common oscillations between two motor units from 8 to 13 Hz and lower common oscillations between two motor units from 0 to 4 Hz.

Common oscillations and motor unit discharge

The findings of the current study demonstrate that a higher discharge rate, which presumably was caused by a larger descending drive onto the motor neuron pool (see Fig. 2) during the voluntary contractions (Schieber and Rivlis 2005), did not influence the amount of short-term synchronization or coherence of motor unit discharge from 16 to 32 Hz. Rather, an increase in discharge rate augmented the amount of correlated activity from 8 to 13 Hz and decreased the common oscillations between two motor units at low frequencies (<4 Hz). These results, which were derived from sustained isometric contractions at various forces, extend the observations of Wessberg and Kakuda (1999) that increases in movement speed were accomplished by an increase in the mean rate and 8–12 Hz coherence of motor unit discharge. The results of the current study are also consistent with prior observations on the independence of short-term synchronization and common low-frequency modulation of discharge rate (Farmer et al. 1993b; Semmler et al. 1997; Moritz et al. 2005).

Although most experimental studies demonstrate that corticomuscular coherence around 20 Hz (Conway et al. 1995; Salenius et al. 1997; Kilner et al. 2000) and correlated motor unit activity from 6 to 12 Hz can be related to self-oscillations in the monosynaptic stretch reflex loop (Christakos et al. 2006), three findings suggest that the 8–13 Hz coherence between two motor units may be due to a distinct oscillatory input to the motor neuron pool. First, the 8–14 Hz oscillations recorded in the primary motor cortex (M1; local field potentials) of primates during steady isometric contractions were coherent with discharge of corticospinal motor neurons (pyramidal tract neurons) (Baker et al. 2003). The coherent oscillatory signals between the motor cortex and muscle at ~10 Hz have also been demonstrated during steady contractions in human subjects (Marsden et al. 2001; Gross et al. 2002). Second, the amount of coherence of motor unit discharge at 8–13 Hz appears to increase in conjunction with larger descending input to the motor neuron pool, as observed during movements at various speeds (Wessberg and Kakuda 1999) and during sustained isometric contractions at different target forces (current study). Third, the correlated motor unit activity at 8–13 Hz was not associated with peaks in the 0–4 and 16–32 Hz bands, which indicates that this drive is independent of other oscillatory inputs to the motor neuron pool. Thus, the significant increase in peak coherence at 8–13 Hz observed in the current study most likely corresponds to an excitatory oscillatory input to the motor neuron pool.

Another interesting finding was the decrease in the modulation of motor unit discharge from 0 to 4 Hz with higher discharge rate. This low-frequency modulation of the motor unit discharge rate corresponds to the common drive principle (De Luca et al. 1982; De Luca and Erim 1994; Myers et al. 2004). Common drive has been observed within a muscle (Garland and Miles 1997; Semmler et al. 1997) and among synergistic (De Luca and Erim 2002) and antagonistic muscles (De Luca and Mambrito 1987). Although there is no clear evidence of the systems that contribute to the low-frequency oscillations in motor unit activity (Brown 2000), common drive has been proposed to be included in the descending input to the motor neuron pool (Kamen and De Luca 1992) and proprioceptive feedback (Garland and Miles 1997). The conclusion that common drive arises from supraspinal sources was supported by the observation that facial muscles, which lack muscle spindles, exhibit similar low-frequency modulation of the motor unit discharge as do limb muscles (Kamen and Deluca (1992). Furthermore, Garland and Miles (1997) found that the amount of common drive in the flexor digitorum profundus muscle was reduced when the afferent feedback from its muscle receptors was reduced by the posture of the fingers and wrist that disengaged the deep finger flexor muscle from its normal action on the fourth finger. The findings of the current study that low-frequency modulation of motor unit discharge (common drive) decreased with an increase in the net excitation of the motor neuron pool, however, do not provide any insight on the origin of common drive.

Motor unit synchronization and discharge rate

In agreement with the hypothesis, there was no significant change in either motor unit synchronization or coherence at 16–32 Hz with variation in discharge rate. As observed previously (Nordstrom et al. 1992; Moritz et al. 2005), the magnitude of the CIS index did not change with an increase in discharge rate during voluntary contractions, whereas the values for the k' index decreased. For example, Nordstrom et al. (1992) reported a moderate relation ($r^2 = 0.25$) between the geometric mean ISI and index k' for 80 pairs of motor units in first dorsal interosseus discharging at rates that ranged from 6.1 to 17.4 pps (median 11.8 pps). The current study found a similar relation ($r^2 = 0.20$) for 47 pairs of motor units in first dorsal interosseus discharging at rates that ranged from 8.07 to 13.6 pps (10.7 ± 1.33 pps). These results appear to contrast with previous observations (Kamen and Roy 2000) that CIS and k' values for 114 pairs of motor units in first dorsal interosseus were greater during maximal contractions compared with those at 50% of maximum: CIS for young adults, 3.80 ± 2.84 vs. 2.5 ± 1.32; CIS for old adults, 3.00 ± 0.80 vs. 2.4 ± 1.51. The differences between our findings and those of Kamen and Roy (2000) may be due to the following three reasons: First, the data of Kamen and Roy (2000) is grouped in two force levels 50 and 100%, which may not be the optimal way to understand the relation between force level and motor unit synchronization. Inclusion of other force levels may reveal a different relation between force level and motor unit synchronization. In contrast, the data in the current study are presented as a continuous set ranging from 1 to 20%. Second, many motor units are concurrently active during stronger contractions, which could impair the precision of motor unit discrimination. Third, the motor units recorded at 100% were recruited at much lower threshold than those in the current study. The experimental results of Nordstrom et al. (1992) and the current study are consistent with a computational study that found the magnitude of short-term synchronization was greatest during low-force contractions (≤15% MVC) and decreased at higher forces (Moritz et al. 2005).

Furthermore, both indexes of motor unit synchronization were associated with the peak in the 16–32 Hz band of the coherence spectrum, and there was no significant modulation at 16–32 Hz with variation in discharge rate. These results are consistent with experimental (Farmer et al. 1993a, b; Semmler et al. 2004) and computational (Moritz et al. 2005) studies that demonstrated the association between CIS and coherence in the 16–32 Hz band. The findings of the current study, however, suggest that the peak coherence from 16 to 32 Hz is a stronger predictor for the CIS index ($r^2 = 0.63$) than for the k' index ($r^2 = 0.4$). This difference may be due to the influence of the discharge rate on the calculation of the k' index but not on the calculation of the CIS index (Nordstrom et al. 1992; Moritz et al. 2005).

A recent computational model indicates that motor unit synchronization, as quantified with index CIS, increases when the frequency of the common input is close to the average motor unit discharge (Lowery and Erim 2005). In the current study, the discharge rate of the motor units ranged from 8 to 13 pps and was predicted from an increase in the modulation of the motor units at the 8–13 Hz coherence band. Nonetheless, there was no significant change in motor unit synchronization (as quantified with index CIS) with increases in discharge rate within the limited range of discharge rates and forces examined in the current study. Furthermore, although there was a weak association ($r^2 = 0.1$) between the 8–13 Hz coherence and CIS, the addition of the 8–13 Hz band to the 16–32 Hz band barely improved the prediction of the CIS ($R^2 = 0.63$ to $R^2 = 0.68$). Therefore, in agreement with previous studies (Farmer et al. 1993a, b; Semmler et al. 2004), these results suggest that the amplitude of motor unit synchronization is influenced primarily by common modulation of motor unit discharge at 16–32 Hz and less so by common oscillations close to the discharge rate of the motor units.

In summary, the current study has demonstrated that a higher mean discharge rate for pairs of motor units is accompanied by higher motor unit coherence from 8 to 13 Hz and lower motor unit coherence from 0 to 4 Hz. Motor unit synchronization (index CIS) and coherence at 16–32 Hz, which were correlated, did not vary with discharge rate. This observation indicates that variation in discharge rate is accompanied by changes in the correlated activity of two motor units at frequencies less than 15 Hz.

Acknowledgments An award (NS42734) to RME from the National Institute of Neurological Disorders and Stroke supported this work. The authors thank Dr. John Semmler for his comments on an initial draft of the manuscript.

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