

# Motor-Unit Coherence and Its Relation With Synchrony Are Influenced by Training

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**Semmler, John G., Martin V. Sale, François G. Meyer, and Michael A. Nordstrom.** Motor-unit coherence and its relation with synchrony are influenced by training. *J Neurophysiol* 92: 3320–3331, 2004. First published July 21, 2004; doi:10.1152/jn.00316.2004. The purpose of the study was to quantify the strength of motor-unit coherence from the left and right first dorsal interosseous muscles in untrained, skill-trained (musicians), and strength-trained (weightlifters) individuals who had long-term specialized use of their hand muscles. The strength of motor-unit coherence was quantified from a total of 394 motor-unit pairs in 13 subjects using data from a previous study in which differences were found in the strength of motor-unit synchronization depending on training status. In the present study, we found that the strength of motor-unit coherence was significantly greater in the left compared with the right hand of untrained right-handed subjects with the largest differences observed between 21 and 24 Hz. The strength of motor-unit coherence was lower in both hands of skill-trained subjects (21–27 Hz) and the right (skilled) hand of untrained subjects (21–24 Hz), whereas the largest motor-unit coherence was observed in both hands of strength-trained subjects (3–9 and 21–27 Hz). A strong curvilinear association was observed between motor-unit synchronization and the integral of coherence at 10–30 Hz in all motor-unit pairs ( $r^2 = 0.77$ ), and was most pronounced in strength-trained subjects ( $r^2 = 0.90$ ). Furthermore, this association was accentuated when using synchronization data with broad peaks ( $>11$  ms), suggesting that the 10- to 30-Hz coherence is due to oscillatory activity in indirect branched common inputs. The altered coherence with training may be due to an interaction between cortical inhibition and the number of direct common inputs to motor neurons in skill- or strength-trained hands.

## INTRODUCTION

Motor-unit synchronization and coherence represent two different types of correlated motor-unit activity that provide information on the common input to motor neurons during voluntary contractions. Motor-unit synchronization is a time-domain measure of the near coincident discharge of action potentials in pairs of motor units and provides information on the strength of branched common input to motor neurons that is mediated through the corticospinal tract (Datta and Stephens 1990; Farmer et al. 1993b; Kirkwood and Sears 1978; Sears and Stagg 1976). In contrast, motor-unit coherence is a frequency-domain measure of the strength of oscillatory input to the motor neurons that is thought to originate in cortical and subcortical areas, including the motor cortex (Baker and Baker

2003; Farmer et al. 1993a; Halliday et al. 1998). Although using different mathematical procedures, linear correlation analysis has shown an association between motor-unit synchronization and high-frequency ( $\sim 12$ – $32$  Hz) coherence, suggesting that these two phenomena may share similar mechanisms (Farmer et al. 1993a; Halliday et al. 1999; Kilner et al. 2002; Semmler et al. 2002). As such, the simultaneous measurement of motor-unit synchronization and coherence in the same pair of motor units provides a more complete description of the mechanism of common inputs to motor neurons during voluntary contractions in humans.

Acute and chronic adaptations in the strength of motor-unit synchronization are often interpreted as a change in the strategy used by the CNS to perform a particular contraction. For example, motor-unit synchronization is influenced by variations in the task performed during isometric contractions (Bremner et al. 1991; Kilner et al. 2002) and movements (Semmler et al. 2002) and is increased during the performance of attention-demanding tasks (Schmied et al. 2000). Studies involving chronic muscle use have shown that motor-unit synchronization is greater in the hand muscles of weightlifters compared with control subjects (Milner-Brown et al. 1975; Semmler and Nordstrom 1998) and is weaker in the hand muscles of musicians (Semmler and Nordstrom 1998). These observations are assumed to reflect the adaptation of corticospinal inputs to motor neurons in the expression of muscle strength and suggest a beneficial role in promoting independent and skilled muscle synergies (see Semmler 2002).

In contrast to changes in motor-unit synchronization, less is known about the training-related plasticity of descending oscillatory inputs to motor neurons (coherence) and their functional role in the fine control of muscle force (see Grosse et al. 2002; Mima and Hallett 1999; Salenius and Hari 2003 for a review). As with synchronization, motor-unit coherence can be modulated based on the requirements of the task, where reduced oscillatory input to motor neurons has been observed during concentric contractions (Kakuda et al. 1999; Semmler et al. 2002) and are strongest during steady isometric contractions that occur just after movement (Baker et al. 1997; Kilner et al. 1999). It has also been shown that coherence is modulated by the compliance of the manipulated object during a precision grip task, with increased coherence associated with increased object compliance (Kilner et al. 2000, 2002). These observations suggest that coherence in the motor system is an efficient

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strategy to maintain precise coordinated control of a large number of synergist muscles, with increased coherence present when more demanding tasks (such as gripping very compliant objects) are performed. Using this interpretation, it might be expected that long-term skilled muscle use involving fine manipulation of compliant objects (such as playing a musical instrument) would influence the level of coherence exhibited within a hand muscle, whereas chronic training involving gripping noncompliant objects (such as weightlifting) should have the opposing effect on the level of coherence observed within an intrinsic hand muscle.

The purpose of the study was to quantify the strength of motor-unit coherence from the left and right first dorsal interosseous muscles in untrained, skill-trained (musicians), and strength-trained (weightlifters) individuals who had long-term specialized use of their hand muscles. The analysis was performed on an extensive sample of motor units obtained in a previous study, where large differences in the strength of motor-unit synchronization were observed with chronic muscle use as a result of long-term training (Semmler and Nordstrom 1998). Given that there is an association between motor-unit synchronization and coherence (Farmer et al. 1993a) and reduced motor-unit synchronization is observed in skilled hands during a simple isometric contraction (Semmler and Nordstrom 1998), we expect to see reduced coherence in the hand muscles of skill-trained subjects and increased coherence in the hand muscles of strength-trained subjects when performing a simple task. The present study also afforded the opportunity to examine the association between motor-unit synchronization and coherence in a large sample of motor-unit pairs in different subjects in an attempt to obtain further information on the mechanisms responsible for the common oscillatory input to motor neurons. Of particular interest was the association between motor-unit coherence and the width of the synchronization peak, which reveals information on the relative contribution of direct and indirect common inputs to motor neurons (Kirkwood and Sears 1978; Sears and Stagg 1976). Results from this study have appeared previously in abstract form (Semmler et al. 2004).

## METHODS

The data used for the present investigation were obtained from a previous study examining the influence of training on motor-unit synchronization and motor output during low-force isometric contractions (Semmler and Nordstrom 1998). Subjects participated in a series of experiments involving separate-session measures of single motor-unit activity and index finger force fluctuations from the left and right first dorsal interosseous muscles. The data obtained from the single motor-unit experiments are the focus of the current manuscript. The original motor-unit sample obtained from these studies consisted of 544 motor-unit pairs in the left and right hands of 16 healthy adults (Semmler and Nordstrom 1998). The subjects were divided into groups based on long-term specialized use of their hand muscles. Five skill-trained subjects (age: 18–20 yr) were musicians who regularly (average of 12 h/wk for 8 yr) played a musical instrument involving skilled use of the digits of both hands (such as the piano). Five strength-trained subjects (age: 19–25 yr) were weightlifters who frequently (average of 8 h/wk for 4 yr) performed resistance training involving upper limb exercises. Six subjects (age: 23–47 yr) were untrained and had no specialized use of their hand muscles other than normal daily activities. From the original sample of 544 motor-unit pairs (Semmler and Nordstrom 1998), coherence data were obtained

from 394 motor-unit pairs in the five untrained (113 motor-unit pairs), four skill-trained (139 motor-unit pairs), and four strength-trained (142 motor-unit pairs) individuals. One untrained and one strength-trained subject was removed from the original analysis due to a small number of motor units recorded in one of the hands. One skill-trained subject was excluded due to being left-handed as measured by the Edinburgh Handedness Inventory (Oldfield 1971). All 13 subjects used in the present analysis were right-hand dominant. All subjects volunteered to participate in the study and gave informed consent to the procedures, which were conducted in accordance with the Declaration of Helsinki. The Human Research Committee at the University of Adelaide approved all experimental procedures prior to commencement of the study.

A detailed description of the experimental arrangement and procedures used to record single motor-unit activity has been described previously (Semmler and Nordstrom 1998). Briefly, the subjects' right or left arm was placed in a manipulandum, and the hand was secured by restraints to isolate the first dorsal interosseous muscle and restrict movement to all digits other than the index finger. The index finger force was measured with a force transducer aligned with the distal interphalangeal joint. Motor-unit activity was recorded with two bipolar, fine-wire electrodes that were inserted into the first dorsal interosseous muscle. Each electrode consisted of three Teflon-insulated, silver wires (45  $\mu$ m diam) that were threaded through a disposable 25-gauge needle. The activity of single motor units was examined while subjects exerted a low abduction force with the index finger for 1–7 min. The subject was provided with audio feedback on the discharge of a selected unit, which was classified during the experiment with an analog window discriminator. 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 of 14 (range: 2–31) different pairs of motor units in a given experiment. During the experiments the single motor-unit recordings were amplified (1,000 times), band-pass filtered (2 Hz to 10 kHz), and stored on tape.

The single motor-unit recordings were discriminated off-line from the taped records using a computer-based, template matching algorithm (SPS 8701; Signal Processing Systems, Malvern, SA, Australia) that identified the action potentials belonging to a particular motor unit based on waveform shape. The signal from each intramuscular electrode was analyzed separately, and the discharge times of each identified motor unit ( $\pm 125$ - $\mu$ s resolution) were stored on a computer. Interval histograms of the discharge times were constructed, and the interspike intervals of identified motor units were examined for every trial to verify discrimination accuracy. 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  $\pm$  SD and coefficient of variation of the interspike intervals were determined using a commercially available statistical package (Statview, SAS Institute).

The strength of motor-unit synchronization was determined by a cross-correlation analysis performed on pairs of 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 cumulative sum procedure (Ellaway et al. 1978), which consisted of subtracting the number of counts in the bin of interest from the mean bin count (calculated from  $-100$  to  $-30$  ms in the histogram) and continually adding the result to the previous bin, was used to identify synchronous peaks in the cross-correlation histogram. If no peak could be selected, then a standard peak width of 11 ms, centered at time 0, was used for quantification of the strength of synchrony in that motor-unit pair. The magnitude of the central synchronous peak was quantified using the synchronization index Common Input Strength (CIS) (Nordstrom et al. 1992), which represents the frequency of extra synchronous discharges in excess of chance and provides information on the strength of common inputs that are shared between the two

motor units. For each pair of motor units contributing to the cross-correlation histogram, we calculated the geometric mean of discharge rate and coefficient of variation for discharge rate.

Motor-unit-coherence was estimated in the frequency domain from the coherence spectrum between the discharge times of the pair of motor units (Farmer et al. 1993a; Rosenberg et al. 1989) and implemented in Matlab. The discriminated motor-unit data were divided into contiguous, nonoverlapping epochs of 1.28 s that comprise 256 bins. Each 5-ms bin was assigned a value of 1 when it contained a discharge and a value of 0 when it did not. The time-series data from each disjoint section were transformed into the frequency domain with a frequency resolution of 0.78 Hz. Auto- and cross-spectra (see Fig. 1) were estimated by averaging over the disjoint sections. The pooled coherence (Amjad et al. 1997) between two motor units *a* and *b* allowed us to combine several independent recordings, or segments. It was computed using the pooled auto- and cross- spectra, according to

$$|R_{ab}(\omega)|^2 = \frac{\left| \sum_{i=1}^k f_{aibi}(\omega) L_i \right|^2}{\left( \sum_{i=1}^k f_{aiai}(\omega) L_i \right) \left( \sum_{i=1}^k f_{bibi}(\omega) L_i \right)}$$

where  $f_{aiai}(\omega)$  and  $f_{bibi}(\omega)$  are the auto-spectra of the pair of processes at a given frequency  $\omega$ ,  $f_{aibi}(\omega)$  is the cross-spectrum of the pair of processes, and  $L_i$  is the number of disjoint segments

used to estimate the cross- and auto-spectrum for segment *i*. The pooled coherence values provide a normalized, unitless measure of linear association with values between 0 (completely independent) and 1 (completely dependent). The coherence values were used in the present study to infer the frequency components present in the common inputs to motor neurons. Coherence values exceeding the 95% confidence level (Rosenberg et al. 1989) for the frequencies of interest (0–100 Hz) were regarded as significant. To facilitate the comparison of coherence between groups, the coherence estimates for each pair of motor units were normalized by computing the *z* scores using the formula  $z = \sqrt{(2L)} \cdot \text{Tanh}^{-1}R$ , where *L* is the number of disjoint segments, and *R* is coherence (Brillinger 2001).

The dependent variables for each pair of motor units obtained from the study were trial duration, geometric mean discharge rate, geometric mean coefficient of variation for discharge rate, synchronization strength (CIS), synchronization peak width, and strength of coherence using *z* scores averaged over 3-Hz bins. Statistical differences for these dependent variables were assessed using a two-way ANOVA using hand (left, right) and training group (skill, strength, untrained) as factors. Tukey's post hoc tests were used to identify the location of statistical differences when appropriate. Regression analysis (linear and curvilinear) was used to examine the association between motor-unit synchronization and coherence for low (0–10 Hz) and high (10–30 Hz) frequencies. Statistical significance was designated at  $P < 0.05$ . Data are shown as means  $\pm$  SD in the text and tables.

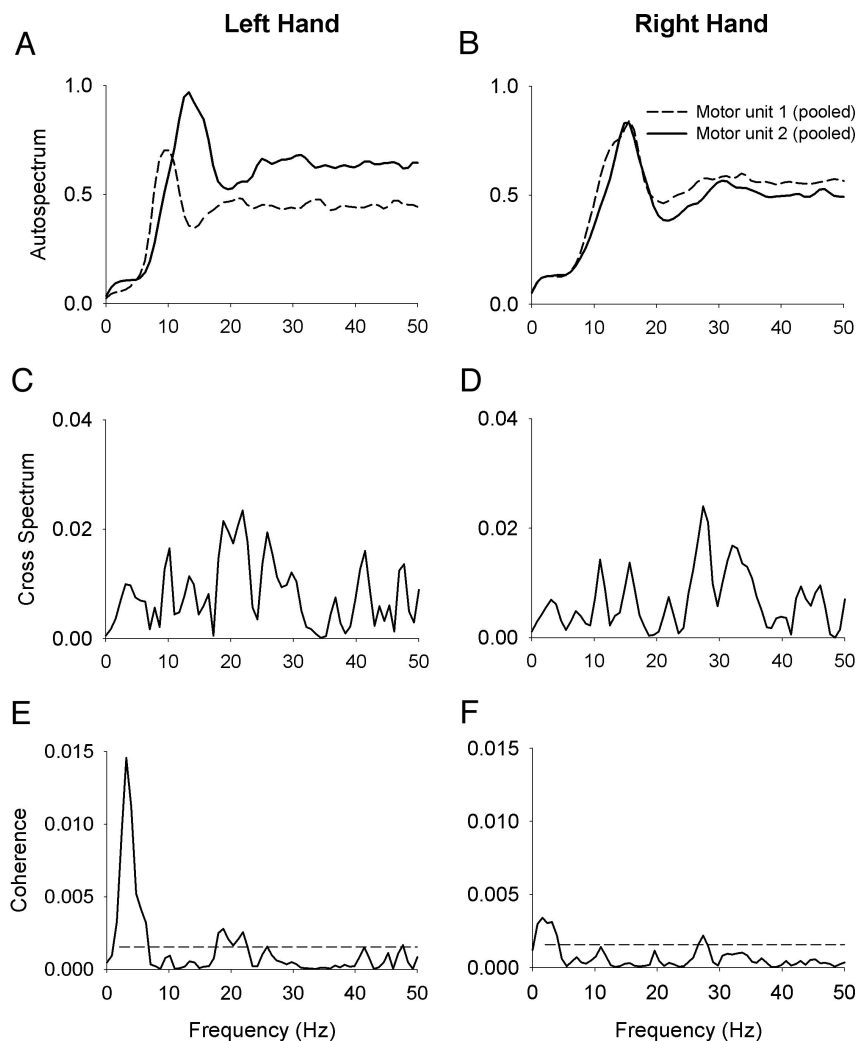


FIG. 1. Examples of pooled coherence from the left and right hand of an untrained subject. The data represent the pooled averages from 6 motor-unit pairs in the left hand and 6 motor-unit pairs in the right hand. *A* and *B*: the pooled auto-spectra from the discharge times of each pair of motor units. ---, data from the 1st motor unit of each; —, data from the 2nd motor unit. The autospectra from each motor-unit pair shows a peak between 10 and 15 Hz corresponding to the mean discharge rate of the contributing motor units. *C* and *D*: the associated cross-spectra (nonnormalized) for the pairs of motor units. *E* and *F*: the coherence functions between the pairs of motor units. ---, the 95% confidence interval. The data show that the strength of coherence was greater in the left hand, although significant coherence was still detected in the right hand of this subject. Increased strength of coherence was observed in the left hand in 4/5 untrained subjects.



## RESULTS

The motor-unit discharge properties and synchronization data for the pairs of motor units that were used in the coherence analysis are shown in Table 1. Significant differences between training groups and a group  $\times$  hand interaction were observed in the ANOVA for all dependent variables except for the geometric mean CV, where only a hand effect was observed. Significant differences in the ANOVA were further explored with a Tukey's post hoc test. These data show that the duration of the contraction was significantly greater in untrained subjects ( $132.1 \pm 59.6$  s) compared with skill-trained subjects ( $114.8 \pm 117.1$  s), and it was greater in the right hand of untrained subjects compared with the right hand of skill-trained and untrained subjects. The motor units were discharging faster (geometric mean discharge rate) in the right hand of untrained subjects compared with the left hand of untrained subjects and both hands of skill-trained subjects. No difference in the variability of motor-unit discharge (geometric mean coefficient of variation) was observed between any of the groups but was significantly greater in the right ( $18.3 \pm 3.5\%$ ) compared with the left ( $17.1 \pm 3.6\%$ ) hand in all subjects. As reported previously (Semmler and Nordstrom 1998), the mean strength of motor-unit synchronization (index CIS) for both hands combined was greatest in strength-trained subjects ( $0.51 \pm 0.47$ ), intermediate in untrained subjects ( $0.33 \pm 0.34$ ), and least in skill-trained subjects ( $0.16 \pm 0.20$ ). Furthermore, the strength of motor-unit synchronization was greatest in the right hand of strength-trained subjects and least in the left hand of skill-trained subjects. A significant difference in the strength of synchronization between right and left hands was only observed for the untrained subjects. Finally, the width of the central synchronous peak in the cross-correlation histogram was different between subject groups with the skill-trained subjects ( $12.6 \pm 3.9$  ms) expressing a significantly narrower peak compared with untrained ( $14.5 \pm 5.8$  ms) and strength-trained subjects ( $15.0 \pm 4.9$  ms). The largest peak width was observed in the right hand of strength-trained subjects and was significantly different from both hands of skill-trained subjects. The removal of 149 motor-unit pairs from the original study

did not substantially influence the motor-unit discharge properties from each of the three subject groups, as similar findings were reported previously (Semmler and Nordstrom 1998).

A coherence analysis is shown for the left and right hands of one untrained subject in Fig. 1. The data represent the pooled coherence from six motor units in the left hand and a randomly selected six motor units (out of a total of 24 motor units) in the right hand. The peak in the power-spectra for each pair of motor units (Fig. 1, A and B) corresponds to the mean discharge times of the contributing motor units, which were 9.4 Hz (motor unit 1) and 13.3 Hz (motor unit 2) for the left hand and 15.6 Hz for motor units in the right hand. The typical pattern of motor-unit coherence that is observed during isometric contractions consists of a large-amplitude low-frequency peak ( $\sim 1$ – $10$  Hz) and a smaller-amplitude high-frequency peak ( $\sim 15$ – $30$  Hz). The coherence analysis (Fig. 1, E and F) shows a significant low-frequency peak at 3.1 Hz in the left hand and 1.6 Hz in the right hand, and a significant high-frequency peak at 18.8 Hz for the left hand and 27.3 Hz for the right hand. However, the integral of *significant* coherence was approximately three times larger in the left hand (0.036 vs. 0.013) within the low-frequency band and approximately four times larger in the left hand (0.017 vs. 0.005) within the high-frequency band.

The strength of motor-unit coherence in left and right hands of skill-trained, strength-trained and untrained subjects is shown in Fig. 2. The pooled coherence values are shown for descriptive purposes in A–C, whereas the mean z-scores are shown for use in statistical analysis in D–F. For these data, the number of contiguous 1.28-s epochs used to create the pooled coherence was greater in untrained ( $132 \pm 60$ ) compared with skill-trained subjects ( $115 \pm 48$ ), and was significantly greater in the right hand of untrained subjects ( $143 \pm 52$ ) compared with the right hand of skill-trained ( $114 \pm 47$ ) and strength-trained ( $111 \pm 48$ ) subjects. The typical pattern of motor-unit coherence, consisting of a low- and high-frequency peak, was most obvious in the left hand of untrained subjects (Fig. 2A) and both hands of strength-trained subjects (Fig. 2C). In contrast, the coherence was reduced in the right hand of

TABLE 1. Discharge characteristics and ANOVA comparisons for the motor-unit pairs that were used in the coherence analysis

n	Untrained		Skill Trained		Strength Trained		ANOVA Comparisons		
	Left (n = 54)	Right (n = 59)	Left (n = 66)	Right (n = 73)	Left (n = 66)	Right (n = 76)	Group (df = 2,388)	Hand (df = 1,388)	Interaction (df = 2,388)
Trial duration, s	120.4 $\pm$ 65.4	142.8 $\pm$ 51.9 <sup>a</sup>	115.6 $\pm$ 49.7	114.0 $\pm$ 46.9	124.6 $\pm$ 76.2	110.5 $\pm$ 47.7	F = 3.0 P < 0.05	F = 0.2 NS	F = 3.3 P < 0.05
Geometric mean rate, Hz	11.1 $\pm$ 1.8	11.9 $\pm$ 1.4 <sup>b</sup>	10.9 $\pm$ 1.2	11.0 $\pm$ 1.1	11.2 $\pm$ 1.0	11.1 $\pm$ 1.8	F = 1.5 NS	F = 4.7 P < 0.01	F = 3.5 P < 0.05
Geometric mean CV, %	16.8 $\pm$ 3.2	18.0 $\pm$ 5.1	17.4 $\pm$ 3.9	17.7 $\pm$ 2.5	17.1 $\pm$ 3.6	19.1 $\pm$ 2.7	F = 10.6 P < 0.01	F = 1.5 NS	F = 1.9 NS
Synchrony Index CIS, impulses/s	0.46 $\pm$ 0.34 <sup>c</sup>	0.22 $\pm$ 0.31	0.10 $\pm$ 0.18	0.21 $\pm$ 0.20	0.45 $\pm$ 0.44 <sup>d</sup>	0.56 $\pm$ 0.49 <sup>e</sup>	F = 36.1 P < 0.001	F = 0.04 NS	F = 10.1 P < 0.001
Peak width, ms	14.9 $\pm$ 5.7	14.3 $\pm$ 5.8	12.5 $\pm$ 4.0	12.7 $\pm$ 3.8	13.8 $\pm$ 4.1	16.0 $\pm$ 5.3 <sup>f</sup>	F = 8.9 P < 0.001	F = 1.6 NS	F = 3.1 P < 0.05

Values for untrained, skill-trained, and strength-trained subjects are means  $\pm$  SD. ANOVA comparisons show F and P values between subject groups, hands, or the group  $\times$  hand Interaction. df, degrees of freedom for the main comparison and the residual. CIS, common input strength; CV, coefficient of variation. Subscript letters represent comparisons with Tukey's post hoc test when a significant group  $\times$  hand interaction was observed. <sup>a</sup> P < 0.05 compared with the right hand of skill-trained and strength-trained subjects. <sup>b</sup> P < 0.05 compared with the left hand of untrained and P < 0.01 compared with strength trained subjects and both hands of skill trained subjects; <sup>c</sup> P < 0.01 compared with the right hand of untrained subjects and both hands of skill trained subjects; <sup>d</sup> P < 0.01 compared with the right hand of untrained subjects and both hands of skill trained subjects; <sup>e</sup> P < 0.01 compared with the right hand of untrained and both hands of skill trained subjects; <sup>f</sup> P < 0.01 compared with both hands of skill-trained subjects.

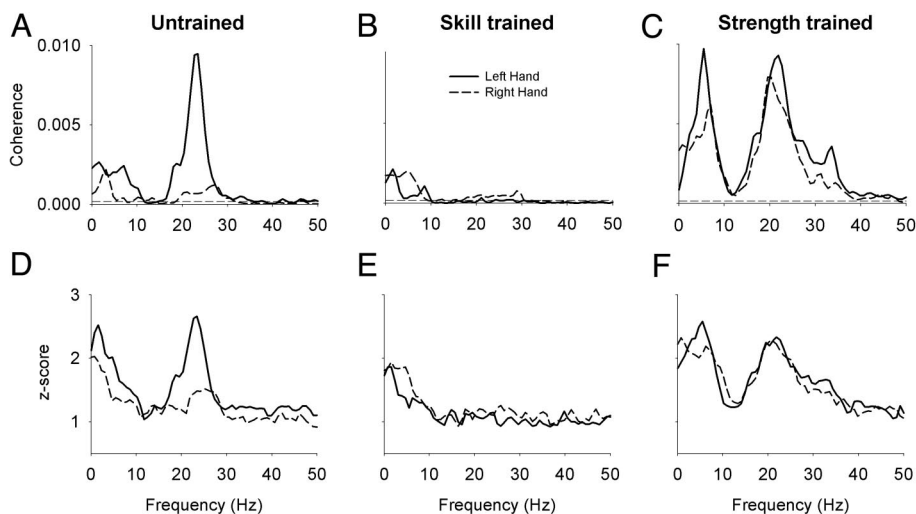


FIG. 2. The strength of motor-unit coherence in left and right hands of skill-trained, strength-trained, and untrained subjects is shown in Fig. 2. A–C: the pooled coherence values; D–F: the mean  $z$  scores. ---, the approximate 95% confidence interval for both plots. These data show that the strength of motor-unit coherence was lower in both hands of skill-trained subjects (21–27 Hz, see Table 2) and the right hand of untrained subjects (21–24 Hz), whereas the largest motor-unit coherence was observed in both hands of strength-trained subjects (3–9 Hz and 21–27 Hz).

untrained subjects (Fig. 2A) and both hands of skill-trained subjects (Fig. 2B), particularly at high (10–30 Hz) frequencies.

For statistical purposes, the mean coherence  $z$  scores shown in Fig. 2, D–F, were averaged over 3-Hz bins, and a summary of the statistical analysis of these data is shown in Table 2. These data reveal substantial differences in motor-unit coherence between subject training groups and hands. Significant between-hand differences were observed in all subjects at 21–24 Hz, and a significant interaction in the ANOVA shows that motor-unit coherence was greater in the left compared with the right hand of untrained subjects at these frequencies. When comparing the area under the pooled coherence plot (integral) for left and right hands of untrained subjects within these frequency bands, the coherence was  $\sim 10$  times greater in the left hand (0.022) compared with the right hand (0.002). This pattern of increased coherence for the left compared with the right hand was observed in 4/5 untrained subjects. No between-hand differences in motor-unit coherence were detected in the skill- or strength-trained subjects (Fig. 2, E and F, and Table 2).

The data in Fig. 2 and Table 2 also clearly show that motor-unit coherence is influenced by chronic muscle use and training. Although significant group differences were observed in the ANOVA at all frequencies except 0–3 Hz, the most

striking differences between subject groups existed at frequencies from 21 to 27 Hz. Within this high-frequency band, there was increased motor-unit coherence in strength-trained and untrained subjects compared with skill-trained subjects. A significant group  $\times$  hand interaction from 21 to 27 Hz indicated that motor-unit coherence was greater in left and right hands of strength-trained subjects compared with the left and right hands of skill-trained subjects. Furthermore, a significant group  $\times$  hand interaction at 21–24 Hz indicated that motor-unit coherence was greater in the right hand of strength-trained subjects compared with the right hand of untrained subjects, and the left hand of untrained subjects was greater than the left hand of skill-trained subjects. Conversely, these results suggest that there is reduced motor-unit coherence within these high-frequency bands in both hands of skill-trained subjects (21–27 Hz) and the right hand of untrained subjects (21–24 Hz) compared with strength-trained subjects. Within the low-frequency range (0–10 Hz), the largest differences between training groups were observed between 3 and 9 Hz, where motor-unit coherence was greater in strength-trained subjects compared with untrained and skill-trained subjects. A significant interaction at 3–6 Hz revealed increased coherence in the left hand of strength-trained subjects compared with the left hand of skill-trained subjects. When considering all group  $\times$  hand

TABLE 2. Summary of two-way ANOVA comparisons between training groups, hands, and the group  $\times$  hand interaction for coherence  $z$  scores averaged over 3-Hz bins up to 30 Hz

Frequency, Hz	Group (df = 2,388)	Hand (df = 1,388)	Interaction (df = 2,388)
0–3	$F = 0.03$ , NS	$F = 1.5$ , NS	$F = 1.1$ , NS
3–6	$F = 7.1$ , $P < 0.01^*$	$F = 0.7$ , NS	$F = 4.0$ , $P < 0.05^{**LH}$
6–9	$F = 17.4$ , $P < 0.001^*$	$F = 0.5$ , NS	$F = 0.6$ , NS
9–12	$F = 6.4$ , $P < 0.01^*$	$F = 1.0$ , NS	$F = 2.0$ , NS
12–15	$F = 5.9$ , $P < 0.01^{**}$	$F = 0.3$ , NS	$F = 0.01$ , NS
15–18	$F = 22.1$ , $P < 0.001^*$	$F = 1.1$ , NS	$F = 0.3$ , NS
18–21	$F = 24.1$ , $P < 0.001^*$	$F = 1.9$ , NS	$F = 1.8$ , NS
21–24	$F = 24.5$ , $P < 0.001^\dagger$	$F = 7.1$ , $P < 0.01^\ddagger$	$F = 6.4$ , $P < 0.01^\ddagger_{UT*RH,LH}$
24–27	$F = 26.3$ , $P < 0.001^\dagger$	$F = 1.2$ , NS	$F = 4.1$ , $P < 0.05^{**RH,LH}$
27–30	$F = 18.6$ , $P < 0.001^*$	$F = 0.01$ , NS	$F = 1.5$ , NS

df, degrees of freedom for the main independent variable and the residual. NS, not significant. <sup>LH</sup>, left hand. <sup>RH</sup>, right hand. <sup>UT</sup>, untrained subjects. \*Significantly greater in strength-trained subjects compared with untrained and skill-trained subjects. \*\*Significantly greater in strength-trained subjects compared with skill-trained subjects.  $^\dagger$ Significantly greater in strength-trained and untrained subjects compared with skill-trained subjects.  $^\ddagger$ Significantly greater in the left hand compared with the right hand.

comparisons within the low- and high-frequency bands, these data show increased motor-unit coherence in both hands of strength-trained subjects, intermediate coherence in the left hand of untrained subjects, and reduced coherence in both hands of skill-trained subjects and the right hand of untrained subjects (Table 2).

These differences in motor-unit coherence between training groups and hands occurred despite equivalent numbers of motor-unit pairs in each subject group and hand (Table 1), and the level of coherence required to reach statistical significance (Fig. 2, A–C, --- horizontal) was similar for each group and hand. Furthermore, although there was a large variation in the range of motor-unit pairs obtained from each subject and hand, a reasonable sample of motor units was obtained from each subject in the training groups. For the skill- and strength-trained groups, where the largest coherence differences existed, each subject contributed an equivalent number of motor-unit pairs to the overall pooled average. For example, there was an average of 17 (range, 8–31) motor-unit pairs in the left and 18 (12–26) motor-unit pairs in the right hand of skill-trained subjects, and an average of 17 (13–19) motor-unit pairs in the left and 19 (14–22) motor-unit pairs in the right hand of strength-trained subjects. This number of motor-unit pairs is more than sufficient to reliably describe the strength of common input within a given muscle (see Semmler and Nordstrom 1999).

To investigate the relation between motor-unit synchronization and coherence, the strength of motor-unit synchronization (index CIS) was compared with coherence within the two commonly observed frequency bands of 0–10 and 10–30 Hz. Because there was no consensus on the most appropriate measure to quantify coherence, motor-unit synchronization was compared with the maximum coherence (Farmer et al. 1993a), the mean coherence (Kilner et al. 2002), and the integral of coherence within these frequency bands. The coefficient of determination ( $r^2$ ) values for motor-unit synchronization and coherence using these three measures are shown in Table 3. As demonstrated previously (Farmer et al. 1993a; Kilner et al. 2002), the strength of the association was consistently greater between motor-unit synchronization and coherence within the high-frequency band (10–30 Hz) with all three quantitative procedures. Furthermore, the strongest associa-

tions were consistently observed when using the integral of coherence at both low (0–10 Hz) and high (10–30 Hz) frequencies. Because of this, all subsequent analyses between motor-unit synchronization and coherence have used the integral of coherence at 0–10 and 10–30 Hz.

For all motor units combined ( $n = 394$ ), the strongest association between motor-unit synchronization and coherence was observed within the high-frequency band (10–30 Hz), and the best fit was created with a third-order polynomial function of the form  $y = 0.78 - 0.41x + 0.28x^2 - 0.03x^3$ . A strong curvilinear association between synchronization and coherence at 10–30 Hz was also observed for all motor units in the left and right hands (Table 3) with the strongest relation in the right hand. The most striking differences in the association between motor-unit synchronization and coherence were observed when motor-unit pairs were separated between subject groups, and these data are shown in Fig. 3. Closer examination of the subject group data indicates that the curvilinear association between motor-unit synchronization and coherence was strongly influenced by the strength-trained subjects. With both hands combined (Fig. 3 and Table 3), the association between synchronization and coherence in the 10- to 30-Hz frequency band was strongest for the strength-trained subjects (Fig. 3F, —,  $y = 0.10 - 0.20x + 0.46x^2 - 0.76x^3$ ), intermediate and linear for the untrained subjects (Fig. 3B,  $y = 0.05 + 0.24x$ ), and least for the skill-trained subjects (Fig. 3D,  $y = 0.07 + 0.07x$ ). The correlations in the low-frequency band were weak and similar for all groups ( $r^2$  values from 0.13 to 0.25). When separated for hands (Fig. 3 and Table 3), the strongest association in the 10- to 30-Hz frequency band was observed for the right hand of strength-trained (Fig. 3F, ---) and untrained subjects (Fig. 3B, ---), and the left hand of skill-trained subjects (Fig. 3D, ···). In the 0- to 10-Hz frequency band, the strongest association was observed for the right hand of untrained subjects (Fig. 3A, ---), and the left hand of skill-trained (Fig. 3E, ···) subjects, and the left hand of strength-trained subjects.

Aside from the size of the central peak in the cross-correlation histogram, a second feature that provides discriminative information on motor-unit synchronization is the width of the central synchronous peak. A two-way ANOVA indicated a significant difference in peak width

TABLE 3. Coefficient of determination ( $r^2$ ) values between motor unit synchronization (index CIS) and three different measures of coherence at 0–10 and 10–30 Hz

	<i>n</i>	Coherence (0–10 Hz)			Coherence (10–30 Hz)		
		Maximum	Mean	Integral	Maximum	Mean	Integral
Both hands	394	0.07	0.15	0.18	0.31	0.58*	0.77*
Left hand	186	0.08	0.13	0.14	0.29	0.43	0.63*
Right hand	208	0.09	0.18	0.22	0.50*	0.77*	0.87*
Untrained	113	0.10	0.19	0.18	0.26	0.37	0.53
Skill	139	0.09	0.11	0.13	0.05	0.11	0.11
Strength	142	0.09	0.21	0.25	0.74*	0.88*	0.90*
Untrained left	54	0.02**	0.03**	0.03**	0.17	0.24	0.31
Untrained right	59	0.24	0.87*	0.90*	0.22	0.53	0.77
Skill left	66	0.07	0.14	0.14	0.06**	0.11	0.11
Skill right	73	0.11	0.11	0.13	0.03**	0.09	0.09
Strength left	66	0.16	0.39	0.45	0.51	0.86*	0.89*
Strength right	76	0.07	0.14	0.17	0.64	0.89*	0.90*

\*Best fit with a third-order polynomial function. All other values were determined with a simple linear regression analysis. \*\* Non-significant correlation with all other values statistically significant at  $P < 0.05$ .

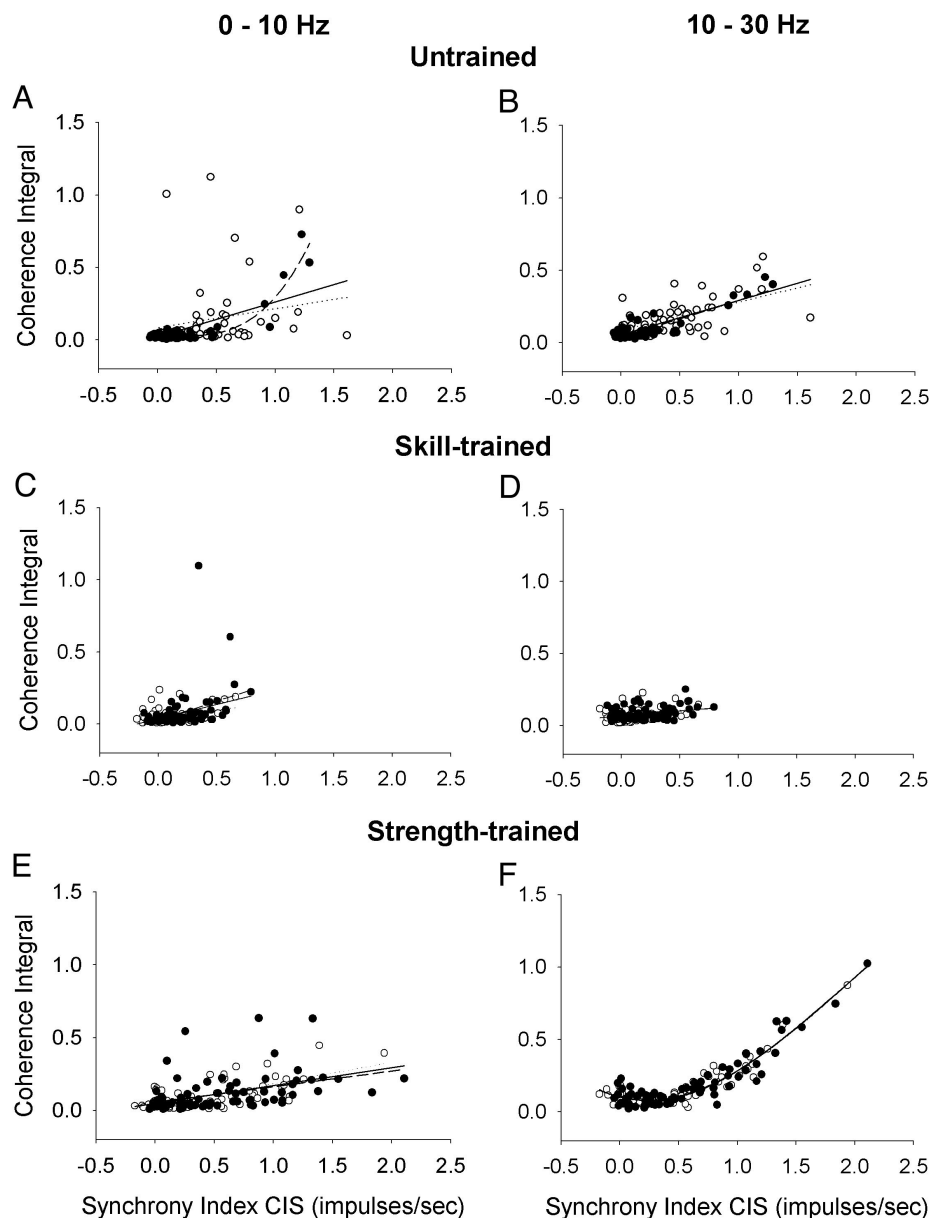


FIG. 3. Relation between motor-unit synchronization (index CIS) and the integral of coherence in the 0- to 10-Hz (A, C, E) and 10- to 30-Hz (B, D, F) frequency bands. Data are shown for left ( $\circ$ ) and right ( $\bullet$ ) hands of untrained (A and B), skill-trained (C and D), and strength-trained (E and F) subjects. Significant linear or curvilinear (3rd-order polynomial) associations are shown between synchronization and coherence for all motor units (—) and motor units in the left ( $\cdots$ ) and right ( $---$ ) hands. These data show that the strongest association between synchronization and coherence occurred at the 10- to 30-Hz frequency band, particularly in strength-trained subjects (F; curvilinear association,  $r^2 = 0.90$ ,  $P < 0.001$ ). The correlations in the low-frequency band were weak and similar for all groups ( $r^2$  values from 0.13 to 0.25). No consistent differences in the strength of the association were observed between hands within each subject group.

between subject groups ( $P = 0.002$ ), where the broadest peaks were observed in the strength-trained subjects ( $15.0 \pm 4.9$  ms) and the narrowest in the skill-trained subjects ( $12.6 \pm 3.9$  ms). Furthermore, a significant group  $\times$  hand interaction ( $P = 0.047$ ) revealed a difference between hands in the strength-trained subjects (Table 1). Because of these group and hand differences in the width of the central synchronous peak, the association between motor-unit synchronization and coherence was re-examined separating motor-unit pairs that had a narrow central peak ( $\leq 11$  ms) compared with those with a broad central peak ( $> 11$  ms). When separating motor units based on peak width, the largest difference in the association was observed at high frequencies (10–30 Hz). For all motor-unit pairs, the relation between motor-unit synchronization and coherence between 10 and 30 Hz was stronger using peak widths  $> 11$  ms ( $n = 175$ ,  $r^2 = 0.81$ ,  $P < 0.001$ ) compared with those  $\leq 11$  ms ( $n = 219$ ,  $r^2 = 0.07$ ,  $P < 0.001$ ). When separating

between hands, the largest differences for peak width were observed with coherence at 10–30 Hz in the right hand (narrow,  $n = 112$ ,  $r^2 = 0.05$ ,  $P < 0.05$ ; broad,  $n = 96$ ,  $r^2 = 0.91$ ,  $P < 0.001$ ) compared with the left hand (narrow,  $n = 107$ ,  $r^2 = 0.09$ ,  $P < 0.01$ ; broad,  $n = 79$ ,  $r^2 = 0.62$ ,  $P < 0.001$ ). This occurred despite no significant difference (2-way ANOVA) in the width of the central synchronous peak between right and left hands for narrow (right,  $10.8 \pm 0.8$  ms; left,  $10.7 \pm 1.0$ ) or broad peaks (right,  $18.5 \pm 5.0$  ms; left,  $17.6 \pm 4.7$ ) in all subjects. For coherence at 0–10 Hz, stronger correlations were also observed using broad compared with narrow peaks, but the difference was marginal within this frequency range compared with 10–30 Hz.

When distinguishing between training groups, a substantial difference in the strength of the association between motor-unit synchronization and maximal coherence at 10–30 Hz was observed between narrow ( $\leq 11$  ms) and broad ( $> 11$  ms) synchronization peaks (Fig. 4). The largest difference in the strength of the



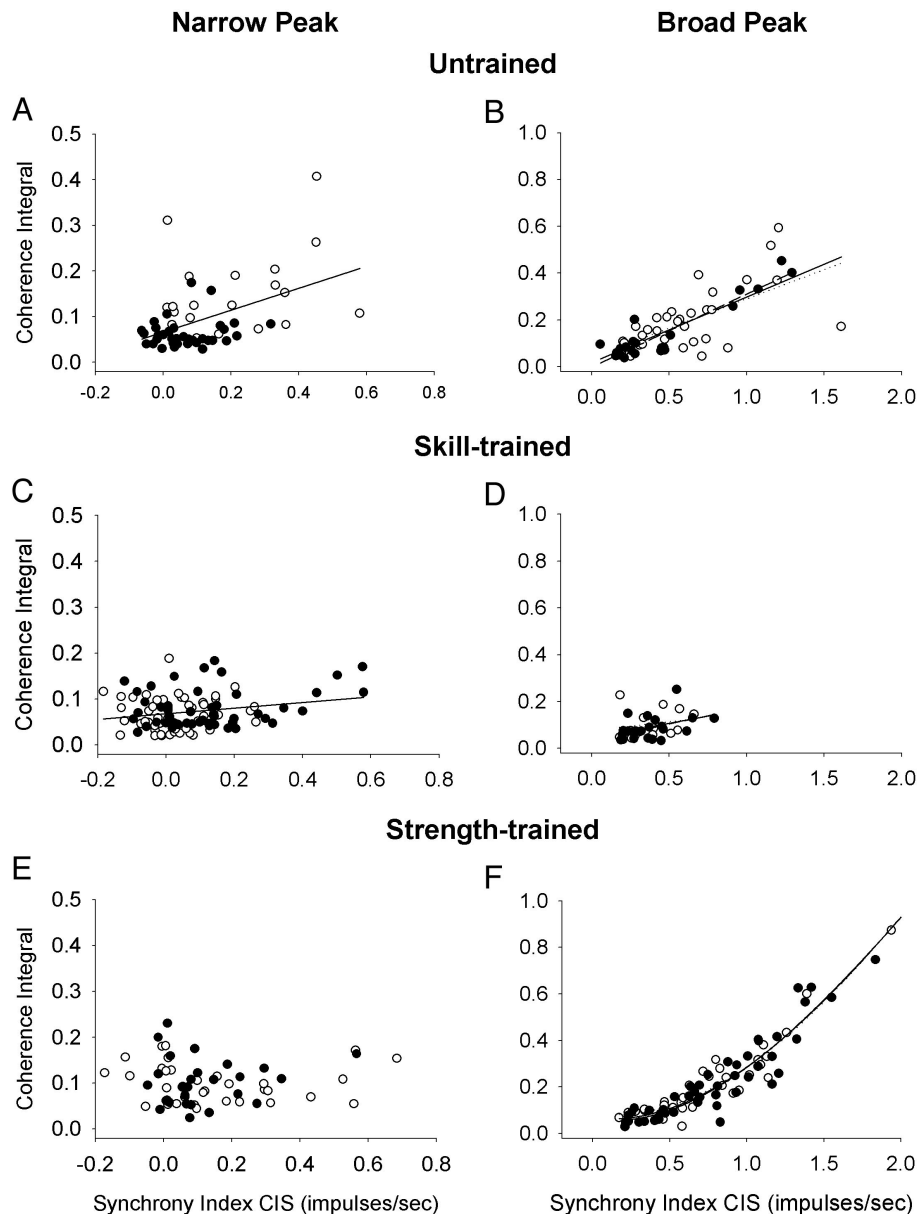


FIG. 4. Relation between motor-unit synchronization and the integral of coherence in the 10- to 30-Hz frequency band for narrow (A, C, E) and broad (B, D, F) synchronization peaks. Data are shown for left ( $\circ$ ) and right ( $\bullet$ ) hands of untrained (A and B), skill-trained (C and D), and strength-trained (E and F) subjects. Significant linear or curvilinear (3rd-order polynomial) associations are shown between synchronization and coherence for all motor units (—) and motor units in the left ( $\cdots$ ) and right ( $---$ ) hands. The strongest relation between motor-unit synchronization and coherence was observed with broad synchronization peak widths, particularly in strength trained (curvilinear association in F;  $r^2 = 0.91$ ,  $P < 0.001$ ) and untrained (— in B;  $r^2 = 0.57$ ,  $P < 0.001$ ) subjects.

association was observed in the strength-trained subjects (narrow,  $n = 60$ ,  $r^2 = 0.005$ ,  $P > 0.05$ ; broad,  $n = 82$ ,  $r^2 = 0.91$ ,  $P < 0.001$ ; Fig. 4, E and F), whereas no differences were observed for the skill-trained subjects (narrow,  $n = 102$ ,  $r^2 = 0.05$ ,  $P < 0.05$ ; broad,  $n = 37$ ,  $r^2 = 0.12$ ,  $P < 0.05$ ; Fig. 4, C and D). Furthermore, the largest differences between narrow and broad peaks occurred in the right hand of untrained (narrow,  $n = 37$ ,  $r^2 = 0.03$ ,  $P > 0.05$ ; broad,  $n = 37$ ,  $r^2 = 0.85$ ,  $P < 0.001$ ), skill-trained (narrow,  $n = 49$ ,  $r^2 = 0.07$ ,  $P > 0.05$ ; broad,  $n = 24$ ,  $r^2 = 0.20$ ,  $P < 0.05$ ), and strength-trained subjects (narrow,  $n = 26$ ,  $r^2 = 0.01$ ,  $P > 0.05$ ; broad,  $n = 50$ ,  $r^2 = 0.92$ ,  $P < 0.001$ ). No consistent differences were observed between narrow and broad synchronization peaks for maximal coherence at 0–10 Hz when distinguishing for hands or training groups. These data indicate that the strongest correlations between motor-unit synchronization and coherence in the 10- to 30-Hz band occur with broad synchronization peak widths, particularly in strength trained and untrained subjects.

## DISCUSSION

The purpose of the study was to quantify the strength of motor-unit coherence from the left and right first dorsal interosseous muscles in untrained, skill-trained (musicians), and strength-trained (weightlifters) individuals who had long-term specialized use of their hand muscles. The analysis was performed on data collected for a previous study, where significant differences were observed in the strength of motor-unit synchronization between subjects in these three groups (Semmler and Nordstrom 1998). In the present study, we found that motor-unit coherence was also influenced by different long-term patterns of hand muscle use, as reduced motor-unit coherence was observed in the dominant (skilled) hand of untrained subjects and both hands of skill-trained subjects (musicians), whereas the strongest coherence was observed in both hands of strength-trained subjects. Furthermore, a strong curvilinear association was observed between motor-unit synchronization and the integral of high-frequency (10–30 Hz)



coherence in strength-trained subjects, and this was most prominent when using broad ( $>11$  ms) synchronization peak widths.

Motor-unit coherence is a measure of common oscillatory inputs to motor neurons that is quantified in the frequency domain. The typical pattern of coherence during low-force isometric contractions in humans is an increased common oscillation from 0 to 10 Hz and  $\sim 15$ –30 Hz (Farmer et al. 1993a), although the pattern can be more complex during slow movements (see Kakuda et al. 1999; cf. Semmler et al. 2002). Indirect evidence from patients with peripheral and CNS lesions indicate that the oscillatory activity, at least within the high-frequency band ( $\sim 15$ –30 Hz), is conveyed via branched corticospinal inputs (Farmer et al. 1993a). There is also increasing evidence that coherence between the motor cortex and muscle at 15–30 Hz is at least partially responsible for muscle-muscle and single motor-unit coherence. For example, both the cortico-muscular and muscle-muscle coherence show similar task-dependent alterations during different phases of a precision grip task (Kilner et al. 1999). Furthermore, cortico-muscular coherence, muscle-muscle coherence, and single motor-unit coherence at 15–30 Hz are all increased with increased compliance of the gripped object (Kilner et al. 2000, 2002). Based on these findings, it is generally accepted that motor-unit coherence at  $\sim 15$ –30 Hz reflects oscillatory activity from the motor cortex. Other CNS oscillations have been observed at frequencies of 10 Hz (Pfurtscheller and Neuper 1992; Stancak et al. 1997) and 40–50 Hz (Brown et al. 1998), but it is not yet known how these different frequencies interact within the cortex to produce a functional outcome, although they do not seem to be correlated with motor output (Conway et al. 1995; but see Raethjen et al. 2002). Nonetheless, the motor-unit coherence observed during isometric contractions is likely to reflect the integration of multiple oscillators from different cortical and sub-cortical areas, with a considerable oscillatory input from the primary motor cortex, in the descending command to muscles. It has been proposed that the functional significance of this oscillatory neurophysiological activity is to provide a “binding” mechanism to more efficiently activate task-related groups of neurons that are distributed over wide neural networks (Farmer 1998; McAuley and Marsden 2000).

#### *Motor-unit coherence is influenced by training*

Despite numerous examples of hemispheric differences that are evident within the CNS (see Hammond 2002 for review), this represents the first study to show left-right differences in the descending oscillatory input to motor neurons during isometric contractions in humans. Greater coherence was observed in the left hand in 4/5 untrained right-handed subjects (Fig. 1), and it is interesting to note that the one subject with the contrary finding also was the only subject to display greater motor-unit synchronization in the right hand (Semmler and Nordstrom 1998). The largest difference between hands was observed at 21–24 Hz, where the coherence was  $\sim 10$  times larger in the left hand compared with the right hand in these subjects. The difference in coherence within this high-frequency band suggests that the strength of common oscillatory inputs, originating predominantly from the motor cortex (Baker and Baker 2003; Conway et al. 1995; Halliday et al. 1998; Salenius et al. 1997), was reduced in the dominant (right)

hand during the performance of a simple index finger abduction task in subjects with no specialized use of their hand muscles. In support of this finding, Stancak and Pfurtscheller (1997) showed reduced  $\sim 20$ -Hz motor cortex oscillations over the left hemisphere of right-handed subjects before extension movements of the opposing index finger. The possibility exists that the reduced 21- to 24-Hz motor-unit coherence observed in the dominant hand of right-handed subjects may be caused by reduced inhibitory mechanisms within the dominant sensorimotor cortex. For example, a recent modeling study has indicated that inhibitory interneurons play a critical role in the oscillations produced by local cortical circuits with the strength of the oscillations related to the number of inhibitory connections involved (Pauluis et al. 1999). This observation was supported by Baker and Baker (2003), who used diazepam (GABA agonist) to enhance the size of cortical inhibitory postsynaptic potentials and showed an increase in  $\sim 20$  Hz coherence within the sensorimotor cortex, indicating that the cortical oscillations were related to the strength of intracortical inhibition. This mechanism of reduced coherence in the right hand is supported by the finding of reduced intracortical inhibition in the dominant hand of right-handed subjects at rest (Ilic et al. 2004), although others have reported the opposite result (Hammond et al. 2004), and hemispheric differences in intracortical inhibition have not been assessed during a voluntary contraction.

In the present study, we have found that motor-unit coherence was influenced by skilled muscle use, as reduced motor-unit coherence was found in the dominant (skilled) hand of right-handed subjects and both hands of skill-trained subjects (musicians). The largest differences with muscle use were again observed within the high-frequency band (21–27 Hz), indicating that one possible neural adaptation to long-term skilled muscle use is a reduced contribution of common oscillatory inputs from the motor cortex to hand muscle motor neurons when the skilled hand is used to perform simple isometric contractions. There are a number of possible mechanisms that could be responsible for reduced common oscillatory inputs to motor neurons in skilled hands. For example, a recent computer simulation study has shown that the presence of strong active dendritic conductances on neurons decreases coherence when the input is delivered through common branched input or common modulation of random inputs (Taylor and Enoka 2004). Furthermore, modeling of cortical circuits showed that inhibitory interneurons play a key role in producing cortical oscillations with the strength of the oscillations related to increasing inhibition, whereas the frequency of the oscillation depended on the time course of the inhibition (Pauluis et al. 1999). Interestingly, the reduced oscillatory activity in skilled hands cannot be a combination of both mechanisms because the presence of inhibition combined with active dendritic conductances produces an increase in coherence (Taylor and Enoka 2004). Another contributing factor to the reduced coherence during isometric contractions in skilled hands could be due to the oscillatory activity occurring through a greater number of independent inputs, which are less likely to produce significant coherence peaks compared with common-branched inputs (Taylor and Enoka 2004). The finding in highly trained musicians of reduced interhemispheric (Ridding et al. 2000) and within-hemisphere inhibition (Nordstrom and Butler 2002) and lower strength of common inputs compared

with independent inputs (Table 1) (Semmler and Nordstrom 1998) suggests that cortical inhibition and common modulation of random inputs both play an important role in the reduced coherence in skilled hands. Although the converse could explain the increased coherence that is observed in strength-trained subjects, the influence of chronic weightlifting on cortical inhibition is not known. Furthermore, the actual physical stimulus that promoted the changes in motor-unit coherence in skill- and strength-trained subjects in the present study is unclear, as the hand muscles of these subjects were not specifically trained in isolation. It still remains to be determined if skill and strength training are the sole determinants of changes in motor-unit coherence or if it is related to some other measure of neuromuscular performance such as asymmetrical (musicians) compared with symmetrical (weightlifters) bilateral contractions or quantitative differences in daily muscle activity levels between subject groups measured with long-term electromyographic (EMG) recordings (see Kern et al. 2001).

There is substantial evidence of the task-related nature of cortico-muscular coherence, but the functional significance of the descending neural oscillations remains controversial. Previous studies have demonstrated that cortico-muscular coherence in the 15- to 30-Hz range is absent during movement and increases during periods of maintained steady isometric contractions (Feige et al. 2000; Kilner et al. 1999). Furthermore, the 15- to 30-Hz cortico-muscular coherence is most marked just after the grasp of an object has been adjusted and declines over long periods of a steady grasp but is increased with the compliance of a grasped object (Kilner et al. 2000, 2002). These findings suggest that the oscillations may represent an efficient sensorimotor control mechanism used to maintain steady grasp of a compliant object. In support of this, the sensorimotor cortex hand area is altered with long-term training for skilled hand use in musicians (Elbert et al. 1995; Krings et al. 2000) and Braille readers (Pascual-Leone et al. 1993). Although the functional significance of use-dependent adaptations in the descending oscillatory inputs to motor neurons is speculative, the reduced coherence in skilled hands may represent a more efficient strategy to control the neurons involved in the isometric contraction, allowing for greater degrees of freedom during more complex tasks if the need arises. When confronted with a more difficult task, it is possible that greater coherence would be observed in skilled hands, given that a systematic variation in the relative EMG power in low- and high-frequency bands has been observed in older adults depending on whether the task was a simple constant force or more demanding rhythmical contraction (Sosnoff et al. 2004; Vaillancourt and Newell 2003). One possible functional outcome of altered oscillatory inputs to motor neurons with chronic muscle use is the effect on physiological tremor (Halliday et al. 1999; McAuley and Marsden 2000; Raethjen et al. 2002). We have previously shown that tremor amplitude is reduced in musicians and increased in weightlifters (Semmler and Nordstrom 1998) in a study that included the subjects used in the present study. Nonetheless, the functional significance of the altered cortical oscillations that are a feature of the descending input to motor neurons in skill- and strength-trained hands remains to be more clearly elucidated.

### *Broad peak synchronization is related to high-frequency coherence*

Motor-unit synchronization and coherence represent two different statistical procedures to quantify common input to motor neurons. Motor-unit synchronization reveals similarities in the timing of discharge between a pair of motor units, whereas motor-unit coherence reveals common periodicities within the two motor-unit spike trains. Synchronized motor-unit discharge in the time domain is believed to arise from the presynaptic fibers that branch to provide common inputs to the motor neurons (Datta and Stephens 1990; Datta et al. 1991), with one source of common input arising from corticospinal neurons (Farmer et al. 1993a; Schmied et al. 1999). In contrast, it is a commonly held view that motor-unit coherence results from oscillatory activity of common inputs or modulation of separate inputs that are driven by a common oscillator (Farmer 1998; Farmer et al. 1993a; Semmler et al. 2002) within the cortex or brain stem with effects on motor neurons mediated at least in part by corticospinal neurons (Baker and Baker 2003; Baker et al. 1997; Conway et al. 1995; Farmer et al. 1993a). Recently, an alternative view has emerged from computer-simulation data indicating that the strength of motor-unit synchronization and coherence between neurons can be differentially influenced by the pattern of common input and the interaction between the level of dendritic conductances and inhibitory input (Taylor and Enoka 2004). However, given that the high-frequency oscillation ( $\sim 15$ – $30$  Hz) and the central peak in the cross-correlation histogram is abolished by stroke (Farmer et al. 1993a,b), this has been widely accepted as evidence that branched inputs from the corticospinal pathway contribute to both of these phenomena. Furthermore, the mechanisms that lead to motor-unit synchronization likely do not include common oscillatory modulation of independent inputs (Taylor and Enoka 2004).

As in previous studies (Farmer et al. 1993a; Halliday et al. 1999; Kilner et al. 2002; Semmler et al. 2002) we have confirmed that there is a close association between the strength of motor-unit synchronization and high-frequency (10–30 Hz) coherence. However, we have found that the association is greater when the integral of coherence is used rather than when the maximum (Farmer et al. 1993a) or mean (Kilner et al. 2002) coherence is used. The strongest correlations between motor-unit synchronization and the integral of coherence is not surprising given that the synchrony index CIS is also based on calculation of the area of the central synchronous peak in the cross-correlation histogram (Nordstrom et al. 1992). Furthermore, we have found that there is a strong curvilinear association between synchronization and coherence that is most prominent in strength-trained subjects (Fig. 3F,  $r^2 = 0.9$ ). These data indicate that a substantial proportion of the variability in common oscillatory activity was due to branched common inputs at high (10–30 Hz) frequencies, and the stronger the branched input the greater the effect on coherence within this frequency band. In contrast, there was a weak association between motor-unit synchronization and coherence at 10–30 Hz in skill-trained subjects, suggesting that the majority of the common oscillations within this frequency band were occurring through other mechanisms not involving common input to the motor neurons, such as oscillations through independent inputs to the motor neurons in skilled hands. An

alternative view is that the strength of common input was not varied between subject groups, but the intrinsic properties of the neurons and the level of background inhibition were altered with chronic muscle use. For example, it is possible that reduced synchronization and coherence in skilled hands could be due to the presence of active dendritic conductances and low levels of inhibition, whereas the increased synchronization and coherence in strength-trained subjects could be due to active dendritic conductances and high levels of background inhibition (Taylor and Enoka 2004). However, the significance of the computer-simulation data from Taylor and Enoka (2004) depends on the prevalence of active dendritic conductances in motor neurons that are monitored during motor-unit experiments in humans. Despite the significance of persistent inward currents for the input-output characteristics of the neuron (Binder and Powers 1999; Lee and Heckman 2000; Lee et al. 2003), the evidence for the presence of active dendritic conductances in human motor neurons during low-force voluntary contractions is inconclusive (Collins et al. 2002; Gorassini et al. 1998; Keen et al. 2002; Kiehn and Eken 1997).

The width of the central synchronous peak in the cross-correlation histogram is often used to distinguish between direct common input onto motor neurons and indirect common input that involves one or more interposed neurons. Because direct common input is more likely to evoke action potentials that discharge within a few milliseconds of each other, it produces a narrow peak in the cross-correlation histogram compared with the broader peak produced by indirect common input (Kirkwood and Sears 1978; Sears and Stagg 1976). Therefore the width of the central peak can provide information on the relative contribution of direct and indirect common inputs to motor neurons. When separating the synchronization data into narrow ( $\leq 11$  ms) and broad ( $> 11$  ms) peaks, we found that the association between motor-unit synchronization and coherence at 10–30 Hz was greater when using broad ( $> 11$  ms) synchronization peak widths (Fig. 4). Furthermore, a clear difference in the strength of the association was observed between narrow and broad peaks in strength-trained subjects (Fig. 4, *E* and *F*), who displayed the widest synchronization peaks (15.0 ms) compared with the untrained (14.5 ms) and skill-trained (12.6 ms) subjects. These data suggest that the majority of the 10- to 30-Hz coherence occurs through oscillatory activity in indirect branched common inputs. The possibility also exists that broad duration synchronization and 10- to 30-Hz coherence could be produced by branched corticospinal inputs that are modulated by presynaptic cortical oscillations at the appropriate frequency. This type of oscillatory activity would produce multiple peaks and troughs in the cross-correlation histogram with a lead/lag time at the primary oscillatory frequency, which would have a tendency to slightly broaden the estimate of peak width using the CUSUM procedure (see Fig. 6 in Farmer et al. 1997). Such an interpretation is supported by recent evidence in patients with mirror movements, suggesting that the fast-conducting direct corticospinal inputs contribute to EEG/EMG coherence at  $\sim 22$  Hz (Farmer et al. 2004).

In conclusion, we have performed a coherence analysis on pairs of motor units in the left and right hands of untrained, skill-trained (musicians), and strength-trained (weightlifters) subjects during the performance of a simple isometric contraction. We found that the strength of common oscillatory inputs

to motor neurons (coherence) was reduced in the dominant hand of untrained subjects and both hands of skill-trained subjects, whereas it was enhanced in both hands of strength-trained subjects. The alterations in the strength of coherence in these subjects may be due to the interaction of different levels of cortical inhibition and the number of direct common inputs to motor neurons (motor-unit synchronization) in skill- and strength-trained hands. Furthermore, there was a strong curvilinear association between motor-unit synchronization and the integral of coherence at 10–30 Hz, which was accentuated in the strength-trained subjects. This association was strengthened when using synchronization data with broad peaks ( $> 11$  ms), suggesting that the 10- to 30-Hz coherence is due to oscillatory activity in indirect branched common inputs.

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