

Fatigue related changes in electromyographic coherence between synergistic hand muscles

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Abstract The aim of this study was to examine coherence between surface electromyographic (EMG) signals from two index finger flexor muscles, the first dorsal interosseous (FDI) and flexor digitorum superficialis (FDS), during and immediately following sustained, fatiguing isometric contraction. Coherence was observed between the FDI and FDS EMG signals in the tremor (8–12 Hz), beta (15–35 Hz) and gamma (35–60 Hz) bands in all subjects. A significant increase in EMG–EMG coherence in the beta and gamma frequency bands was observed immediately following the fatiguing contraction. No significant difference was observed in the tremor band coherence before and after fatigue. Coherence was observed between EMG and force in the tremor band during both the pre- and post-fatigue contractions and a significant increase in the FDI EMG-force coherence post-fatigue was observed. It is suggested that the increase in beta and gamma band coherence with fatigue may be due to increased levels of corticomotoneuronal drive to both muscles. Alternatively, the increased EMG–EMG coherence may reflect an increased contribution of peripheral afferents to coupling across the muscle with fatigue. Although the functional significance is not clear, the increase in coherence may help to overcome reduced motoneuron excitability with fatigue, to bind together different sensorimotor elements or to coordinate force generation across muscles in a more synergistic manner as the force generating capacity of the muscle is decreased.

Keywords Coherence · Synchronization · Muscle fatigue · Motor unit

Introduction

Analysis of the coherence between electromyographic (EMG) signals provides a means of examining the characteristics of common neural inputs to co-contracting muscles during voluntary contraction. Coherent activity has been reported under various conditions, across a range of frequencies, between both surface and intramuscular EMG signals from the hand and forearm muscles (Baker et al. 1997; Kilner et al. 1999; Farmer et al. 2007), and between the firing times of individual motor units within the same and different muscles (Farmer et al. 1993; Semmler et al. 2004). The central nervous system oscillatory drives responsible for this coherent activity are typically characterized within four different frequency bands. These include a low frequency 1–3 Hz oscillation, that may also be observed as the common modulation of motor-unit firing times known as ‘common drive’ (De Luca and Erim 1994; Myers et al. 2004), oscillations at the frequency of physiological tremor (8–12 Hz) (McAuley and Marsden 2000) and within the beta (15–30 Hz) and gamma (30–60 Hz) frequency ranges (Conway et al. 1995; Mima and Hallett 1999; Omlor et al. 2007).

The similarity between EMG–EMG coherence and well-established corticomuscular coherence (Conway et al. 1995; Salenius et al. 1997) suggests that the common motoneuronal activity within 15–30 Hz frequency range is likely to be, at least partially, cortical in origin. In primates, it has been observed that coherence between EMG signals in the 20–30 Hz range exhibits the same task-dependence as coherence between EMG signals and

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local field potentials recorded from the motor cortex (Baker et al. 1997). Similar results have subsequently been confirmed in human subjects (Kilner et al. 1999). Previous studies have demonstrated a correlation between short-term motor-unit synchronization and beta band coherence in both experimental (Farmer et al. 1993; Semmler et al. 2002) and simulated (Moritz et al. 2005; Lowery et al. 2007) data, indicating that the two phenomena, measured in the time and frequency domains, respectively, share the same underlying mechanism. Significant corticomuscular coherence has also been observed within the frequency range of physiological tremor, which suggests the contribution of efferent components involving the cortex in addition to peripheral feedback mechanisms (McAuley and Marsden 2000).

Electromyographic beta band coherence and motor-unit synchronization have been shown to depend on a variety of factors including attention (Schmied et al. 2000; Kristeva-Feige et al. 2002), task learning and training (Semmler et al. 2004; Perez et al. 2006), hand dominance (Schmied et al. 1994; Semmler and Nordstrom 1995), neurological disorders (Grosse et al. 2002) and changes following spinal cord injury or stroke (Powers et al. 1989; Davey et al. 1990). Little is known, however, about the effects of muscle fatigue on short-term motor-unit synchronization or coherence. Fatigue is an ongoing process that describes the reduction in the force generating capacity of muscle as a result of previous activation (Bigland-Ritchie et al. 1986). It encompasses a number of changes occurring at both the central and peripheral level. Although synchronization of motor-unit activity is commonly suggested as a means of maintaining force output as muscle fatigues, direct evidence of changes in synchronization during or following fatiguing contractions is limited and experimental findings have been somewhat controversial. While a number of studies have reported no change in synchronization with muscle fatigue in the masseter and vastus lateralis (Nordstrom et al. 1990; Contessa et al. 2009), an increase in motor-unit synchronization and low frequency (0–10 Hz) coherence has been observed in the biceps brachii muscle both immediately after, and 24 h after, fatiguing eccentric exercise (Dartnall et al. 2008). Application of an indirect measure of motor-unit synchronization, based on the skewness of the surface EMG signal, has provided further evidence of increased motor-unit synchronization during fatiguing isometric contraction of the biceps muscle (Holtermann et al. 2009).

A small number of studies have examined changes in corticomuscular coherence during and immediately following muscle fatigue. An increase in beta band (13–32 Hz) coherence between MEG and EMG signals from the extensor communis digitorum has been reported following fatiguing isometric contraction, indicating

increased coupling between synchronized cortical neurons and the motoneuron pool (Tecchio et al. 2006). In contrast, during sustained voluntary elbow flexion, Yang et al. (2009) reported a reduction in EEG–EMG coherence in the 15–35 Hz range, which suggests a weakening of corticomuscular coupling during fatigue. Direct comparison of the results of these studies is complicated by the fact that the distal muscles of the hand and forearm are known to have stronger cortical connections (Phillips and Porter 1964; Palmer and Ashby 1992), and thus higher levels of motor-unit synchronization (De Luca et al. 1993; Farmer et al. 1993), than more proximal muscles including the biceps.

Changes in coherence or synchronization across simultaneously active muscles during fatiguing contractions have not yet been examined. Analysis of EMG–EMG coherence across muscles may provide insight into the temporal modulation of oscillatory activity at the cortical level and central nervous system control strategies for maintaining force output as muscle fatigues. The purpose of this study was, therefore, to investigate changes in coupling across synergistic hand muscles as a result of isometric fatiguing contraction. Coherence between surface EMG signals from two index finger flexor muscles, the first dorsal interosseous (FDI) and the flexor digitorum superficialis (FDS), were compared during, before and immediately after a sustained isometric fatiguing contraction.

Methods

Subjects

The experiment was performed on the right-hand of 15 healthy, right-hand dominant subjects (10 males and 5 females, mean age 25 years, range 25–34 years) with no known neuromuscular disorders or musculoskeletal injuries of the hand. All subjects gave their written informed consent before the study. The study was approved by the Human Research Ethics Committee, University College Dublin.

Experimental setup

Subjects were seated in a specially designed chair with a force transducer mounted on a custom-built rig attached to the chair. Their elbow joint angle was positioned at 90° in a rigid support with the upper arm vertical, next to the trunk, and the forearm positioned parallel to the ground. The subject's back was supported, as was the back of the upper arm, underneath the forearm and the elbow. The forearm was pronated with the palm resting on a horizontal platform. The index finger was inserted into a splint that kept the interphalangeal joints extended. This arrangement

allowed flexion of the index finger about the metacarpophalangeal joint, a movement that is produced by contraction of the FDI and FDS muscles. Digits 3–5 and thumb of the right-hand were secured in such a way that only the force exerted by the index finger was recorded. The position of the arm and index finger were continuously monitored during each trial. The force exerted by the index finger and the target force level was displayed to the subject on a monitor placed at eye level.

Force and surface electromyographic recordings

The isometric flexion force exerted by the index finger was measured using a 6 *df* force transducer (Nano 17, ATI, USA) that was aligned with the proximal interphalangeal joint. Bipolar surface EMG signals were recorded from both the FDI and FDS muscles using 8 mm diameter Ag/AgCl electrodes (Ambu, Neonatal electrode, N-00-S/25) separated with a 10 mm inter electrode distance. The skin was prepared by gentle abrasion and cleansing with alcohol. A pair of electrodes was placed directly above the FDI muscle. A second pair of electrodes was located above the FDS muscle, mid-way between the medial epicondyle and the radial styloid process. The surface EMG signals were amplified with a gain of 1,000 (Grass P511 AC amplifier), band-pass filtered (3–1,000 Hz) with a sampling rate of 2.5 kHz. The force signal was low-pass filtered at 100 Hz. Both of these signals were recorded on a PC equipped with a data acquisition interface (Spike 2 v6.07, Cambridge Electronic Design, Cambridge, UK).

Experimental protocol

Following familiarization with the load cell and experimental setup, each subject performed a series of isometric index finger flexion contractions. The subject first performed three isometric maximum voluntary contractions (MVCs) and the subject's maximal voluntary contraction was calculated as the average value of the maximum force recorded over three successive contractions where the maximum force values lay within 10% of one another. The subject was then instructed to conduct a series of six, 10 s duration, non-fatiguing isometric contractions following the target force level at 10% MVC. Successive contractions were separated from one another by 10 s. This was followed by a sustained fatiguing contraction at 30% MVC until task failure, which was defined as the point at which the force decreased below 10% of the target force for >2 s. This was immediately followed by another series of six, 10 s duration non-fatiguing isometric contractions at 10% MVC. The non-fatiguing isometric contractions were conducted at 10% MVC to avoid further fatiguing the subjects before, and immediately after, the sustained

fatiguing contractions. An example of the EMG data recorded from the FDI and FDS and the force generated during the experiment for a single subject is presented in Fig. 1.

Data Analysis

EMG RMS amplitude and median frequency

The root mean square (RMS) value of the EMG signal and the median frequency of the EMG power spectrum were calculated during the sustained fatiguing contraction for non-overlapping 0.5 s duration epochs. The RMS value and median frequency were normalized with respect to their values at the beginning of the fatiguing contraction for each subject and the change in both parameters was examined to assess the progression of muscle fatigue.

Coherence analysis

The magnitude squared coherence, $C_{xy}(f)$ between the two EMG signals recorded from the FDI and FDS muscles, $x(t)$ and $y(t)$, for a given frequency f was calculated as (Bendat and Piersol 1986)

$$C_{xy}(f) = \frac{|S_{xy}(f)|^2}{S_{xx}(f)S_{yy}(f)} \quad (1)$$

where $S_{xy}(f)$ is the cross spectrum and $S_{xx}(f)$ and $S_{yy}(f)$ are the auto spectra of $x(t)$ and $y(t)$.

$C_{xy}(f)$ varies between zero and one, where one indicates a perfect linear relationship between $x(t)$ and $y(t)$ and zero indicates that the two signals are not linearly related at that frequency. The coherence estimate was considered significant at $P < \alpha$ where

$$Z = 1 - \alpha^{1/(L-1)} \quad (2)$$

where L is the total number of disjoint segments used to calculate the coherence (Rosenberg et al. 1989) and $\alpha = 0.05$ (i.e., above 95% confidence interval). Equation 2 is valid for non-overlapping segments with taper. The significance level for overlapped segments with taper after some modifications based on Welch (1967) was adapted as described by Terry and Griffin (2008).

$$Z_{\text{ovlp}} = 1 - \alpha^{1/(wL^* - 1)} \quad (3)$$

$$L^* = \text{floor} \left[\frac{(L-1)}{(1-\text{ovlp})} \right] + 1 \quad (4)$$

where the variable *ovlp* is the percentage of segment overlap and L^* is the number of overlapped segments; w is a weighting factor that is dependent on the amount of overlap and taper type. For tapered segments with window

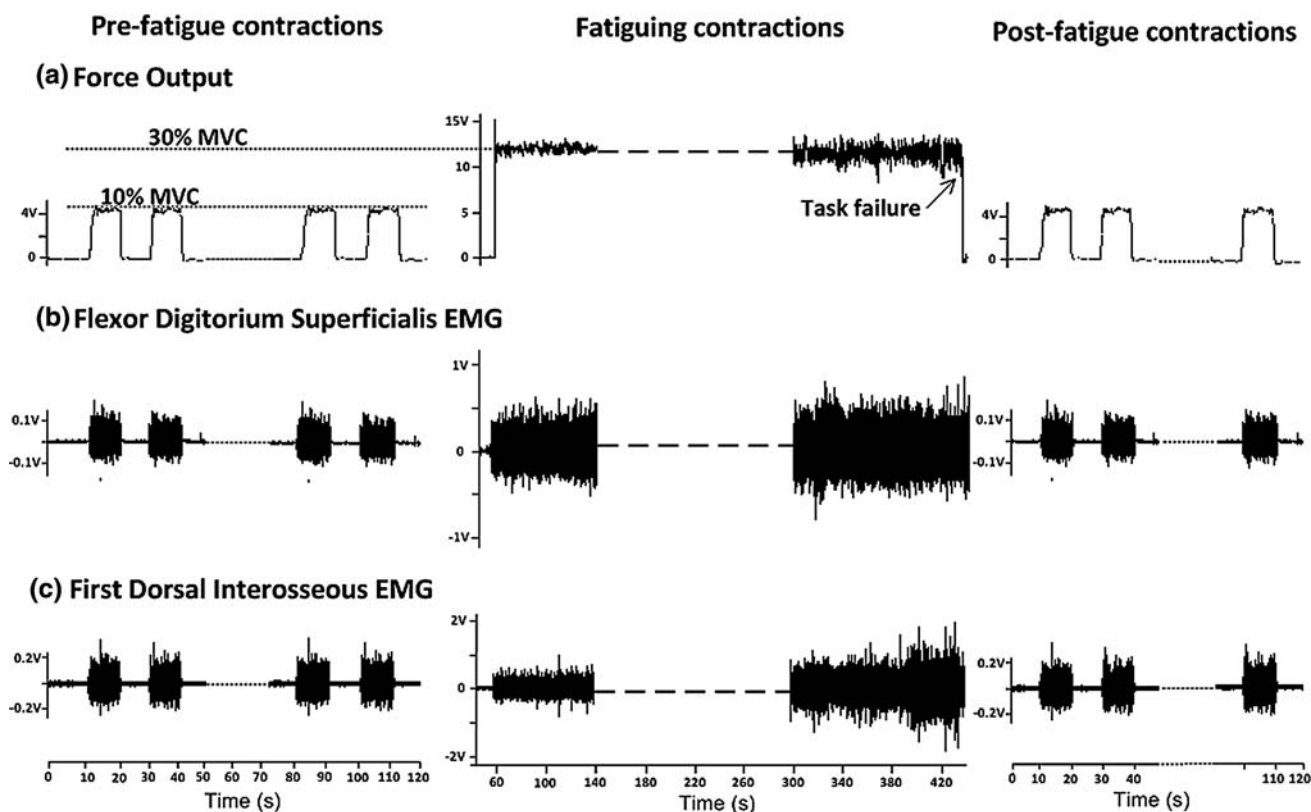


Fig. 1 a Force output and b, c EMG signal recorded from the FDI and FDS muscle in a representative subject during the fatiguing contraction at 30% MVC and during the pre- and post-fatigue contractions at 10% MVC

W and $nfft$ segment elements, the weighting factor is calculated from

$$w = \frac{1}{1 + 2w'} \tag{5}$$

$$w' = \left\{ \frac{\sum_{k=1}^{ovlp \times nfft} w(k) \times w(k + (1 - ovlp) \times nfft)}{\sum_{k=1}^{nfft} w^2(k)} \right\}^2 \tag{6}$$

The coherence was calculated for a segment length of 2,048 samples 50% overlap, using a Hanning window. This combination of segment taper and overlap has been shown to yield significantly higher coherence values than other taper and overlap combinations (Terry and Griffin 2008). The EMG data during the six, 10 s contractions pre-fatigue were concatenated and the coherence between the FDI and FDS muscles was examined. The coherence between the EMG data during the post-fatigue contractions was similarly calculated, as was the coherence between force and EMG data pre- and post-fatigue. The EMG data during the fatiguing contractions was divided into two and the coherence between the FDI and FDS was also compared during the first half and second half of the contraction.

Statistical analysis

Statistical analysis was performed using SPSS 15.0 for windows (SPSS). The sum of the EMG–EMG coherence values that lay above the 95% significance level in each of the tremor (8–12 Hz), beta (15–35 Hz) and gamma (35–60 Hz) frequency bands during the first half and second half of the fatiguing contractions, and during the pre- and post-fatigue contractions were analyzed for statistical significance. The Shapiro–Wilk test for normality was performed and it was found that the data were not normally distributed. A non-parametric, Wilcoxon signed-rank test was, therefore, used to determine significance. EMG–EMG coherence and EMG-force coherence was considered significantly different between the first half and second half of the fatiguing contractions or between the pre- and post-fatigue contractions for P values <0.05.

Results

The average duration of the fatiguing contraction was 430.00 ± 130.22 s (mean \pm SD). A progressive reduction in the median frequency of the EMG power spectrum and an increase in the EMG RMS amplitude was observed in

all subjects in both the FDI and FDS muscles, during the fatiguing contraction (Fig. 2). The median frequency and the RMS amplitude of the FDI EMG signal during the first 10 s of the fatiguing contraction were 136.36 ± 3.08 Hz and 0.120 ± 0.006 V, respectively, and 120.32 ± 3.40 Hz and 0.167 ± 0.012 V during the last 10 s of the fatiguing contraction. The median frequency and the RMS amplitude of the FDS EMG signal were 130.32 ± 3.04 Hz and 0.038 ± 0.002 V, during the first 10 s of the fatiguing contraction, and 107.68 ± 4.34 Hz and 0.050 ± 0.003 V during the last 10 s of the fatiguing contraction. Figure 2a presents the normalized EMG RMS amplitude and Fig. 2b the normalized EMG median frequency during the fatiguing contraction of the FDI muscle, averaged over all subjects. The observed progressive decrease in the EMG median frequency and increase in the RMS amplitude are consistent with changes in the EMG signal typically observed during submaximal isometric fatiguing contractions (Merletti et al. 1990).

The magnitude of the force fluctuations increased with fatigue and was greatest toward the end of the fatiguing contraction. The average value of the coefficient of variation of the force was 9.7% during the last 10 s of the fatiguing contraction, compared with 5.3% during the first 10 s of the fatiguing contraction.

Examples of power spectra of the FDI and FDS EMG signals during the pre- and post-fatigue contractions for a single representative subject are presented in Fig. 3a, b. The corresponding coherence spectra are presented in Fig. 3c.

During the sustained fatiguing contraction at 30% MVC, significant coherence was observed in 14 subjects in the tremor band (8–12 Hz) and in all subjects in the beta (15–35 Hz) and gamma (35–60 Hz) bands during the first half of the fatiguing contraction. Significant coherence was also observed in all subjects in the tremor band and in 14 subjects in the beta and gamma bands during the second

half of the fatiguing contraction. At 10% MVC, significant coherence was observed in 9 subjects in the tremor band and in 13 subjects in the beta and gamma bands during the pre-fatigue contraction. During the post-fatigue contraction significant coherence was observed in 11 subjects in the tremor, 12 subjects in the beta and in 14 subjects in the gamma bands.

An increase in EMG coherence across the FDI and FDS muscles during the second half of the fatiguing contraction was observed in 13 subjects in the tremor band, 10 subjects in the beta band and 7 subjects in the gamma band. An increase in the coherence post-fatigue, when compared with the pre-fatigue contraction, was observed in 5 subjects in the tremor band and in 11 subjects in the beta and gamma frequency bands (Table 1). Figure 4 presents an example of the coherence spectrum between the FDI and FDS EMG signals for two representative subjects during the first half and second half of the fatiguing contraction and during the isometric contractions pre- and post-fatigue.

Statistical analysis revealed a significant increase in EMG coherence across the second half of the fatiguing contraction compared to first half of the fatiguing contraction in the tremor band only ($P = 0.020$), with no significant increase in coherence in the beta ($P = 0.112$) and gamma ($P = 0.609$) frequency bands. A significant increase in EMG coherence during the post-fatigue contraction, compared with the pre-fatigue contractions, was observed in both the beta ($P = 0.048$) and gamma ($P = 0.020$) frequency bands. No significant increase in coherence was observed in the tremor band ($P = 0.754$). Figure 5 presents the mean value of the integral of the coherence lying above the 5% significance level in the tremor, beta and gamma bands, averaged over all subjects, during the first half and second half of the fatiguing contractions (Fig. 5a) during the isometric contractions pre- and post-fatigue (Fig. 5b).

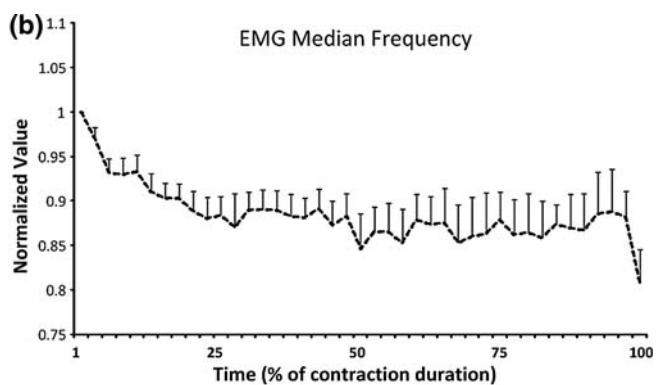
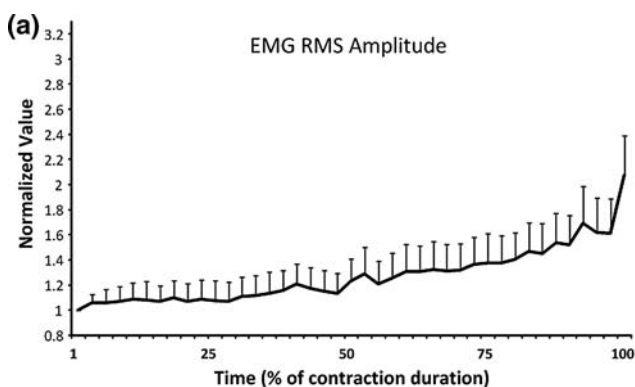


Fig. 2 **a** EMG RMS amplitude and **b** power spectrum median frequency (mean \pm standard error) plotted as a percentage of contraction time during the sustained fatiguing contraction of the

FDI muscle. The data have been normalized with respect to the values at the beginning of the contraction and have been averaged over all 15 subjects

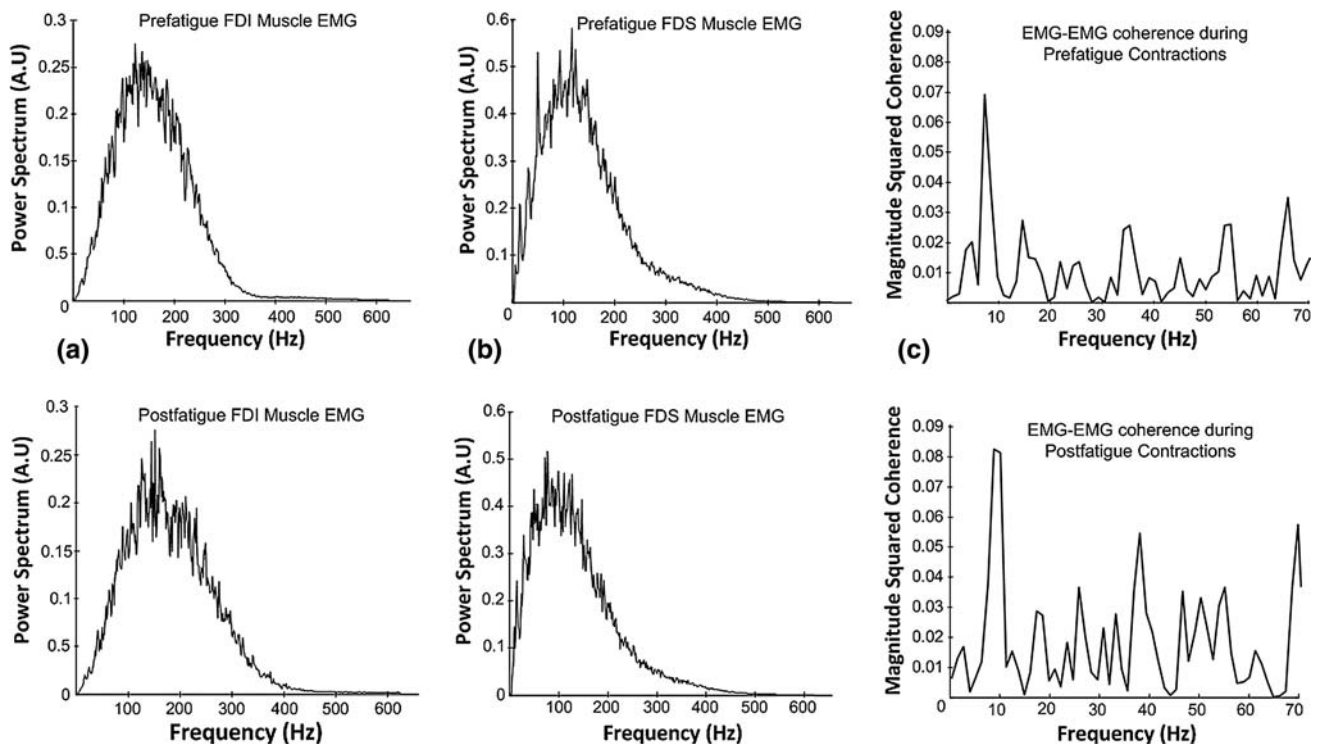


Fig. 3 Power spectra of **a** FDI and **b** FDS EMG signals during pre- and post-fatigue contractions. The corresponding coherence spectra between the FDI and FDS EMG signals during the pre- and post-fatigue contractions are presented in **c**

Table 1 The duration of the fatiguing contraction for each individual subject and the corresponding change in EMG coherence for each frequency band

Subject	Contraction duration (s)	Tremor band (8–12 Hz)	Beta band (15–35 Hz)	Gamma band (35–60 Hz)
1	428	–	Increase	Increase
2	249	–	Increase	Increase
3	553	Increase	Increase	Increase
4	99	Decrease	Increase	Decrease
5	497	Increase	Increase	Increase
6	544	Increase	Increase	Increase
7	287	Increase	Increase	Increase
8	393	Decrease	Increase	Increase
9	500	Decrease	Decrease	Increase
10	500	Decrease	Increase	Decrease
11	454	Increase	–	Decrease
12	377	Decrease	Decrease	Increase
13	519	Decrease	Increase	Increase
14	498	Decrease	Decrease	Decrease
15	552	–	Increase	Increase

The frequency at which the peak coherence occurred in each of the tremor, beta and gamma frequency bands did not change following the fatiguing contractions ($P = 0.074$), ($P = 0.814$) and ($P = 0.802$), respectively. The average peak coherence frequency during the pre-fatigue contractions was 8.60 ± 1.23 , 25.38 ± 7.97 and 47.63 ± 8.40 Hz and during the post-fatigue contraction, $10.01 \pm$

1.20 , 26.01 ± 7.15 and 45.49 ± 7.90 Hz, in the tremor, beta and the gamma bands, respectively.

Figure 6a, b presents the coherence between the EMG and force during the pre- and post-fatigue contractions for a single representative subject. Significant coherence between EMG and force was observed in the tremor band in most subjects, with little coherence observed in the beta or

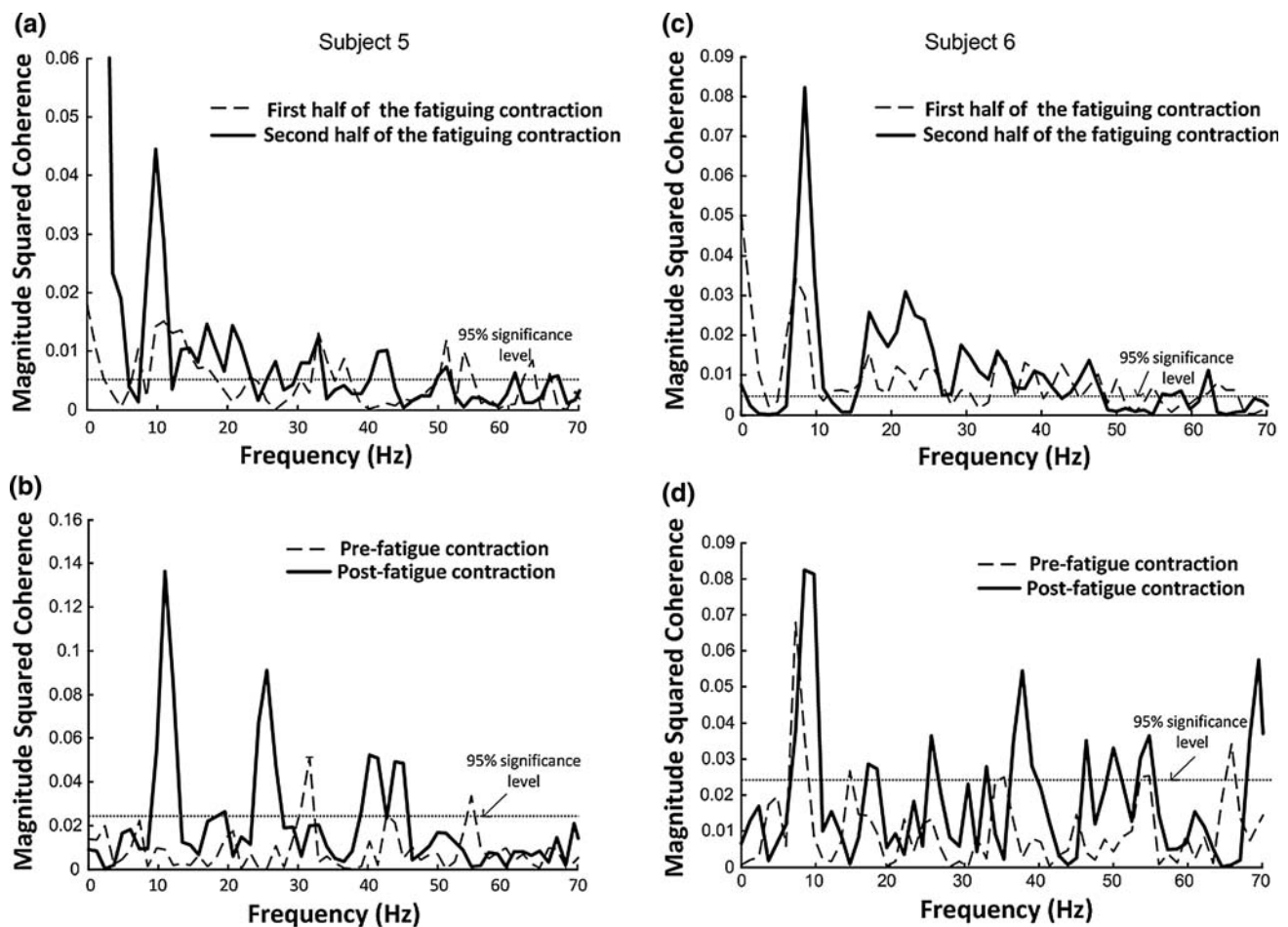


Fig. 4 Coherence between the FDI and FDS EMG data for two representative subjects (subjects 5 and 6) during the first (*dashed line*) and second (*solid line*) half of the fatiguing contraction (**a, c**) and during pre-fatigue (*dashed line*) and post-fatigue (*solid line*)

contractions (**b, d**) which corresponds to the concatenated EMG data during the six, 10 s contractions. The *horizontal line* indicates the 95% significance level

gamma bands. The frequency at which the peak coherence occurred in the pre-fatigue contractions was 9.36 ± 1.83 and 9.16 ± 1.55 Hz and during the post-fatigue contraction, 9.21 ± 1.36 and 9.59 ± 1.40 Hz, in the FDI EMG and force and in the FDS EMG and force, respectively. A significant increase in the coherence between the FDI EMG and force was observed in the tremor band ($P = 0.023$), post-fatigue when compared to pre-fatigue (Fig. 6c). No significant increase in coherence was observed between the FDS EMG and force ($P = 0.158$) (Fig. 6d).

Discussion

The aim of this study was to examine changes in the coherence between EMG signals from synergistic hand muscles before and immediately after fatigue. The FDI and FDS muscles were chosen as the focus of the study as both muscle are index finger flexors and are sufficiently far apart

that cross-talk between EMG signals from the two may be assumed to be negligible. As the relationship between crosstalk, the unwanted detection of signals from muscles other than muscle of interest, and the correlation or coherence between two surface EMG signals is complex, cross-talk could lead to high levels of spurious coherence across a wide range of frequencies (Lowery et al. 2003).

Electromyographic signals are non-stationary during fatiguing contractions and vary with respect to time due to alterations in parameters such as motor-unit recruitment, firing patterns and muscle fiber conduction velocity. Traditional coherence measures based on Fourier analysis cannot provide information about the progression of coherent activity over time and, therefore, may not provide the best means of examining variations in neuromuscular coupling as muscle fatigues. Therefore, in this study the EMG signals were compared during low level, non-fatiguing contractions before, and immediately after, the sustained fatiguing contractions following the approach

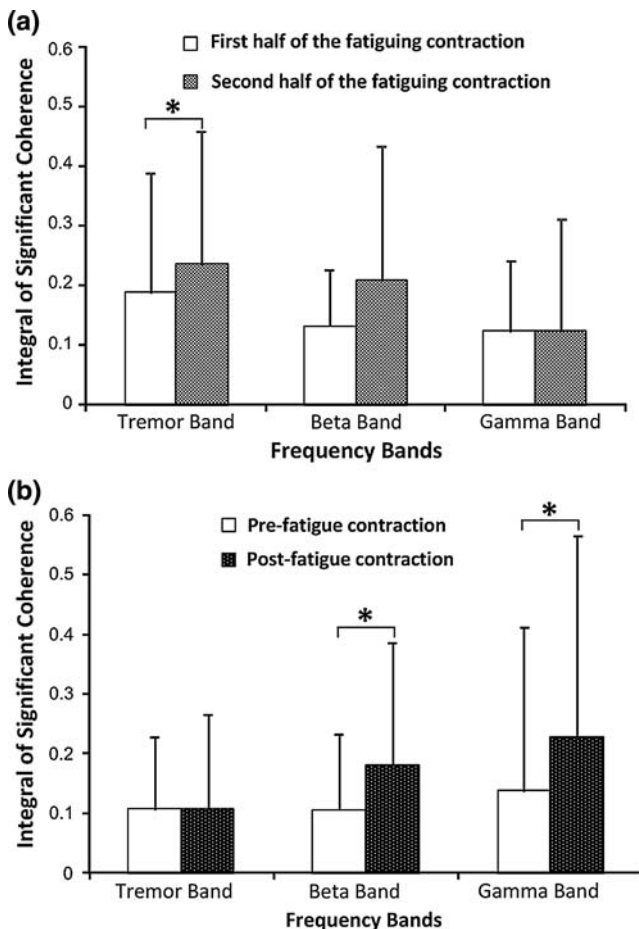


Fig. 5 Mean and standard deviation of the integral of the significant coherence during **a** the first and second half of the fatiguing contraction **b** the pre- and post-fatigue contractions. The data has been averaged over all subjects. A statistically significant increase in coherence during the post-fatigue contraction was observed in the beta (15–35 Hz) and gamma (35–60 Hz) bands. Statistically significant difference between the two groups is indicated with an *asterisk* ($P < 0.05$)

used by Tecchio et al. (2006) to examine the short-term effects of fatigue on corticomuscular coupling. The recovery process after fatigue will, however, also influence the EMG signals and may possibly effect the coherence observed after the fatiguing contraction. Analysis of coherence during the first and second half of the fatiguing contraction was also included to allow comparison with previous studies (Yang et al. 2009).

In the present study, significant coherence between EMG signals from the FDI and FDS muscle was observed in the tremor, beta and gamma bands during isometric finger flexion (Fig. 4). This is consistent with the idea that the synaptic motoneuron inputs are organized according to hand function and the findings of previous experimental studies (Kilner et al. 1999). The presence of beta band EMG coherence between the two muscles is also in agreement with the observation of widespread motor-unit

synchronization between motor-units in different finger and hand muscles acting synergistically to produce movement in a given direction and may reflect branched inputs to the motor units from pyramidal tract neurons (Bremner et al. 1991). Baker et al. (1997) have similarly reported that changes in beta band EMG–EMG coherence in primates reflects changing levels of synchronous drive from the corticospinal system and exhibits a similar task-dependence to corticomuscular coupling as estimated using EEG–EMG coherence. MEG/EEG–EMG coherence in the gamma band has been observed primarily during strong isometric or during dynamic contractions, with experimental evidence indicating that it may also be cortical in origin (Brown et al. 1998; Omlor et al. 2007). In contrast, the origin of physiological tremor is likely to be multi-factorial, with components due to the stretch-reflex, mechanical resonance and cortical drives (McAuley and Marsden 2000).

During the sustained fatiguing contraction, EMG amplitude increased and the EMG median frequency progressively decreased (Fig. 2). These changes are typical of myoelectric manifestations of fatigue during submaximal isometric contractions and confirm the progression of muscle fatigue during the sustained contraction. The decrease in the median frequency observed is primarily due to the reduction in muscle fiber conduction velocity, while the increase in the RMS amplitude reflects increasing motor-unit recruitment and firing rates in order to maintain the force level as the muscle fatigues (Lowery et al. 2003).

A statistically significant increase in the EMG coherence between the FDI and FDS muscles was observed in both the beta and gamma frequency bands during the post-fatigue contractions, when compared to pre-fatigue contractions (Fig. 5b) and in the tremor band during second half of the fatiguing contraction when compared to first half of the fatiguing contraction (Fig. 5a). The increase in beta band coherence is consistent with the results reported by Tecchio et al. (2006) who observed an increase in beta band coherence between MEG–EMG signals in response to short-term fatigue of the extensor communis digitorum. The results presented in Fig. 5b indicate that the level of beta and gamma band synchronization across the FDI and FDS muscles increased in response to muscle fatigue, possibly due to stronger coupling between motor cortical neurons and the motor units of both muscles. In contrast, Yang et al. (2009) reported a decrease in corticomuscular coherence between EEG and EMG signals from the elbow flexor muscles during fatigue, indicating weakening of cortical inputs to the muscle system. A possible explanation for the difference between the results observed in the present study and by Tecchio et al. (2006), and those reported by Yang et al. (2009), is the different organization of corticomuscular connections among the muscles of the hand and forearm and the elbow flexor muscles.

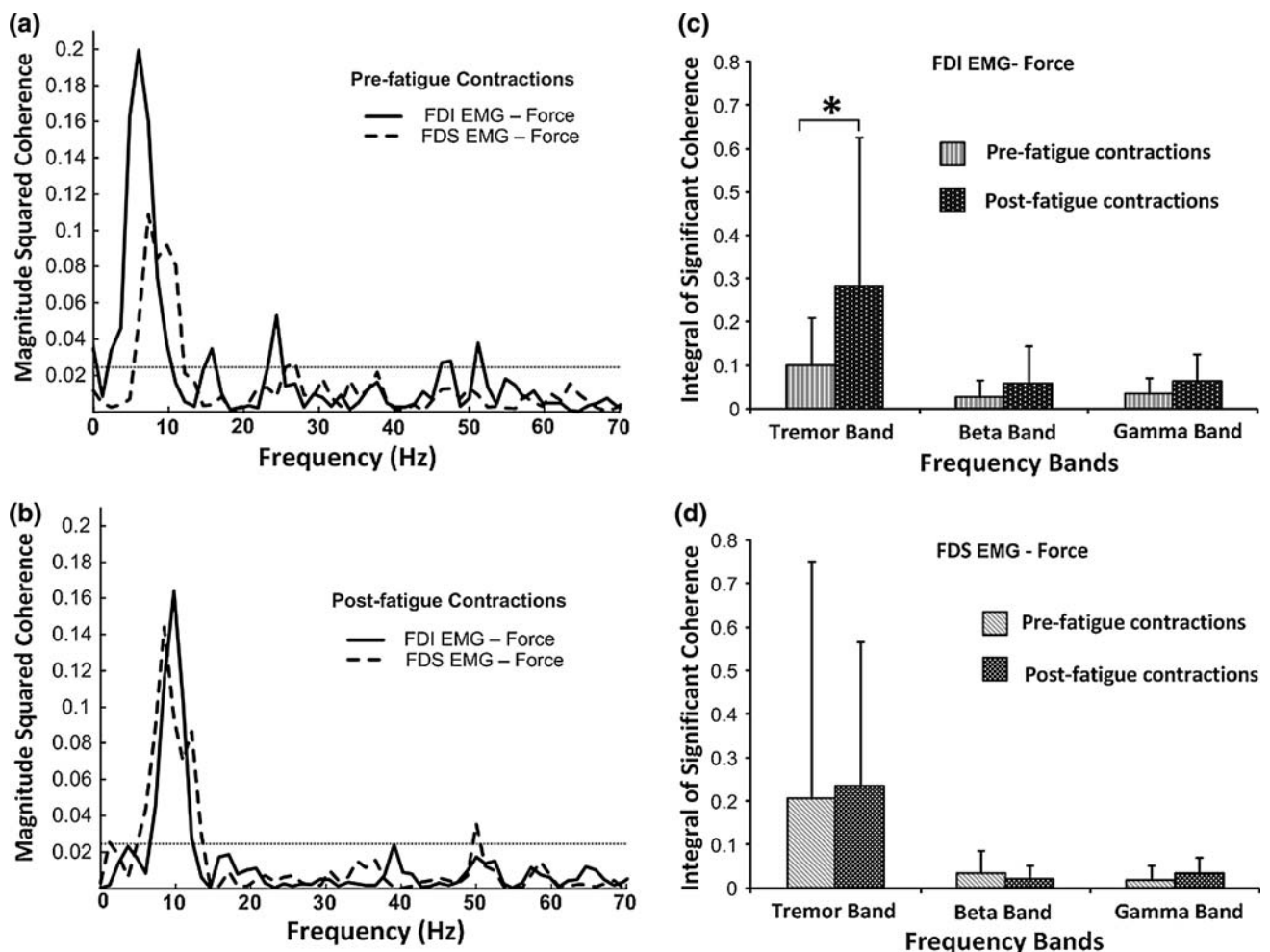


Fig. 6 Coherence between EMG and force during **a** pre-fatigue contraction and **b** post-fatigue contraction for a single representative subject. *Solid line* corresponds to FDI EMG–force coherence and *dashed line* corresponds to FDS EMG–force coherence. The *horizontal line* indicates the 95% significance level. The mean value of the

integral of the significant coherence between the FDI EMG and force (**c**) and between FDS EMG and force (**d**) in the tremor, beta and gamma bands, averaged over all subjects, during the pre- and post-fatigue contractions

Corticomotoneuronal connections to distal muscles have been shown to be stronger than those to more proximal muscles (Phillips and Porter 1964; Palmer and Ashby 1992). Levels of motor-unit synchronization and beta band coherence have subsequently been observed to be higher among motor units of smaller distal muscles, including the FDI and finger extensors, than among motor units of larger proximal muscles, such as the biceps brachii and deltoid (De Luca et al. 1993; Farmer et al. 1993). The contrasting behavior of beta band coherence in the finger extensor and elbow flexor muscles may possibly reflect different levels of corticomuscular coupling to these muscles. Alternatively, the increased EMG–EMG coherence may reflect an increased contribution of peripheral afferents to coupling across the muscle with fatigue.

Oscillations in the gamma band and around the Piper Rhythm (40 Hz) are typically observed during strong

voluntary contractions (Brown et al. 1998). In this study, however, increased coherence in the gamma band was observed at only 10% MVC post-fatigue (Figs. 3, 4). The target force of 10% of the maximum voluntary force measured in the unfatigued muscle likely represents a higher percentage of the maximum force that is attainable in the fatigued muscle. A possible explanation for the similarity between the gamma band coherence observed at 10% MVC post-fatigue and gamma coherence observed during strong voluntary contractions may, therefore, lie in the increase in neuromuscular drive which is necessary to maintain this force when the muscle is fatigued.

Although coherence increased in the majority of subjects with fatigue, the variability observed across subjects was high. A high variation in the level of motor-unit synchronization across subjects was similarly observed by Bremner et al. (1991), who noted that certain subjects

consistently exhibited higher levels of synchronization than others. The variability may be due to limitations of coherence as a measure of common motoneuronal inputs, intrinsic differences in corticomuscular coupling across subjects or a combination of both.

While tremor and force fluctuations increased during the second half of the fatiguing contraction, no significant difference in the coherence between EMG signals at the frequency of physiological tremor was observed post-fatigue (Fig. 5). The augmentation of tremor during fatiguing contractions likely does not depend upon central fatigue alone, but derives partially from peripheral afferent inputs. The difference in behavior at the tremor frequency may, therefore, reflect the different origin of common motoneuronal inputs at the tremor and beta or/and gamma frequency bands.

Significant coherence between EMG and force was observed in the tremor band during both the pre- and post-fatigue contractions (Fig. 6) with relatively little coherence observed between EMG and force in the beta and gamma bands. This is predicted by the results of model simulations which indicate that low frequency neural inputs (typically <10 Hz) have the greatest influence on force variability due to the mechanical low-pass filtering effect of muscle (Lowery and Erim 2005). The observation of strong coupling between force and EMG within the tremor band, but not at the higher frequencies associated with motor-unit synchronization, is consistent with the observation of previous studies that there is no association between increases in force variability and motor-unit synchronization during fatiguing contraction (Semmler et al. 2000; Contessa et al. 2009). A statistically significant increase in the coherence between FDI EMG and force was observed in the tremor band post-fatigue. However, no significant increase in the FDS EMG and force with fatigue was observed. This difference may be due to the presence of stronger corticospinal projections to the FDI than to the FDS (Palmer and Ashby 1992). As tremor is multifactorial in origin, with both cortical and peripheral stretch-reflex loop components, the relative contribution of both to tremor in the FDI and FDS is likely quite different. It is possible that cortical inputs at the tremor frequency increase as the muscle fatigues causing an increase in coherence between FDI EMG and force, but little or no change in FDS EMG and force coherence. Alternatively, the different behavior may reflect differences in the activity of the Ia afferents, relative changes in muscle length in the FDI and FDS or alterations in the relative contribution of both muscles to force production as the muscles fatigues.

Whether increased coherence with fatigue has a functional role or simply reflects changes in cortical or other neural firing patterns is not clear. If EMG–EMG coherence within the beta and gamma frequency bands reflects an increase in synchronized corticospinal common inputs to

the motoneuron pool across the muscles, one possibility may be that synchronization of motoneuron inputs may help to overcome reduced excitability of the motoneuron pool during fatigue. Synchronized inputs are more effective at recruiting neurons than asynchronous inputs (Murthy and Fetz 1994). Failure to activate spinal motoneurons and a reduction in motoneuron excitability following muscle fatigue has been illustrated using transcranial magnetic stimulation (Andersen et al. 2003). Increased synchronization or coherence may thus act as a component of the descending corticospinal command to overcome this reduced excitability and recruit additional motoneurons. Alternatively, it has been suggested that gamma oscillations may reflect binding of functionally associated cortical elements including visual attention, motor planning and cognition (Brown 2000). It is possible that integration of information across these elements may increase in order to maintain force output as the muscle fatigues. Greater subject attention may also be required with fatigue. Motor-unit synchronization has been shown to increase with increased attention (Schmied et al. 2000), whether this may have a functional role or simply reflects alterations in common inputs to the motoneuron pool is not known. Finally, the central nervous system may control muscles acting synergistically as a functional unit (De Luca and Erim 2002). Synchronization of motor-unit firings may act to coordinate force generation across the muscles which may help to maintain the target force level more efficiently as the muscle fatigues.

In conclusion, beta and gamma band coherence across the FDI and FDS muscles was observed to increase immediately following fatigue. This suggests an increase in common neural input across these muscles, which may be cortical in origin. The functional significance of the increase in coherent activity may be to overcome reduced excitability of the motoneuron pool, to increase binding across sensorimotor elements or to facilitate contraction in a more synergistic manner as the force generating capacity of the muscle is decreased with fatigue.

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References

- Andersen B, Westlund B, Krarup C (2003) Failure of activation of spinal motoneurons after muscle fatigue in healthy subjects studied by transcranial magnetic stimulation. *J Physiol* 551:345–356
- Baker SN, Olivier E, Lemon RN (1997) Coherent oscillations in monkey motor cortex and hand muscle EMG show task-dependent modulation. *J Physiol* 501(Pt 1):225–241
- Bendat J, Piersol A (1986) *Random data: analysis and measurement procedures*. Wiley Interscience, New York

- Bigland-Ritchie B, Cafarelli E, Vollestad NK (1986) Fatigue of submaximal static contractions. *Acta Physiol Scand Suppl* 556:137–148
- Bremner FD, Baker JR, Stephens JA (1991) Variation in the degree of synchronization exhibited by motor units lying in different finger muscles in man. *J Physiol* 432:381–399
- Brown P (2000) Cortical drives to human muscle: the Piper and related rhythms. *Prog Neurobiol* 60:97–108
- Brown P, Salenius S, Rothwell JC, Hari R (1998) Cortical correlate of the Piper rhythm in humans. *J Neurophysiol* 80:2911–2917
- Contessa P, Adam A, De Luca J (2009) Motor unit control and force fluctuation during fatigue. *J Appl Physiol* 107(1):235–243
- Conway BA, Halliday DM, Farmer SF, Shahani U, Maas P, Weir AI, Rosenberg JR (1995) Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man. *J Physiol* 489(Pt 3):917–924
- Dartnall TJ, Nordstrom MA, Semmler JG (2008) Motor unit synchronization is increased in biceps brachii after exercise-induced damage to elbow flexor muscles. *J Neurophysiol* 99:1008–1019
- Davey NJ, Ellaway PH, Friedland CL, Short DJ (1990) Motor unit discharge characteristics and short term synchrony in paraplegic humans. *J Neurol Neurosurg Psychiatry* 53:764–769
- De Luca CJ, Erim Z (1994) Common drive of motor units in regulation of muscle force. *Trends Neurosci* 17:299–305
- De Luca CJ, Erim Z (2002) Common drive in motor units of a synergistic muscle pair. *J Neurophysiol* 87:2200–2204
- De Luca CJ, Roy AM, Erim Z (1993) Synchronization of motor-unit firings in several human muscles. *J Neurophysiol* 70:2010–2023
- Farmer SF, Bremner FD, Halliday DM, Rosenberg JR, Stephens JA (1993) The frequency content of common synaptic inputs to motoneurons studied during voluntary isometric contraction in man. *J Physiol* 470:127–155
- Farmer SF, Gibbs J, Halliday DM, Harrison LM, James LM, Mayston MJ, Stephens JA (2007) Changes in EMG coherence between long and short thumb abductor muscles during human development. *J Physiol* 579:389–402
- Grosse P, Cassidy MJ, Brown P (2002) EEG-EMG, MEG-EMG and EMG-EMG frequency analysis: physiological principles and clinical applications. *Clin Neurophysiol* 113:1523–1531
- Holtermann A, Gronlund C, Karlsson JS, Roeleveld K (2009) Motor unit synchronization during fatigue: described with a novel sEMG method based on large motor unit samples. *J Electromyogr Kinesiol* 19:232–241
- Kilner JM, Baker SN, Salenius S, Jousmaki V, Hari R, Lemon RN (1999) Task-dependent modulation of 15–30 Hz coherence between rectified EMGs from human hand and forearm muscles. *J Physiol* 516(Pt 2):559–570
- Kristeva-Feige R, Fritsch C, Timmer J, Lucking CH (2002) Effects of attention and precision of exerted force on beta range EEG-EMG synchronization during a maintained motor contraction task. *Clin Neurophysiol* 113:124–131
- Lowery MM, Erim Z (2005) A simulation study to examine the effect of common motoneuron inputs on correlated patterns of motor unit discharge. *J Comput Neurosci* 19:107–124
- Lowery MM, Stoykov NS, Kuiken TA (2003) A simulation study to examine the use of cross-correlation as an estimate of surface EMG cross talk. *J Appl Physiol* 94:1324–1334
- Lowery MM, Myers LJ, Erim Z (2007) Coherence between motor unit discharges in response to shared neural inputs. *J Neurosci Methods* 163:384–391
- McAuley JH, Marsden CD (2000) Physiological and pathological tremors and rhythmic central motor control. *Brain* 123(Pt 8):1545–1567
- Merletti R, Knaflitz M, DeLuca CJ (1990) Myoelectric manifestations of fatigue in voluntary and electrically elicited contractions. *J Appl Physiol* 69:1810–1820
- Mima T, Hallett M (1999) Electroencephalographic analysis of cortico-muscular coherence: reference effect, volume conduction and generator mechanism. *Clin Neurophysiol* 110:1892–1899
- Moritz CT, Barry BK, Pascoe MA, Enoka RM (2005) Discharge rate variability influences the variation in force fluctuations across the working range of a hand muscle. *J Neurophysiol* 93:2449–2459
- Murthy VN, Fetz EE (1994) Effects of input synchrony on the firing rate of a 3-conductance cortical neuron model. *Neural Comput* 6:1111–1126
- Myers LJ, Erim Z, Lowery MM (2004) Time and frequency domain methods for quantifying common modulation of motor unit firing patterns. *J Neuroeng Rehabil* 1:2
- Nordstrom MA, Miles TS, Turker KS (1990) Synchronization of motor units in human masseter during a prolonged isometric contraction. *J Physiol* 426:409–421
- Omlor W, Patino L, Hepp-Reymond MC, Kristeva R (2007) Gamma-range corticomuscular coherence during dynamic force output. *Neuroimage* 34:1191–1198
- Palmer E, Ashby P (1992) Corticospinal projections to upper limb motoneurons in humans. *J Physiol* 448:397–412
- Perez MA, Lundbye-Jensen J, Nielsen JB (2006) Changes in corticospinal drive to spinal motoneurons following visuo-motor skill learning in humans. *J Physiol* 573:843–855
- Phillips CG, Porter R (1964) The pyramidal projection to motoneurons of some muscle groups of the baboon's forelimb. *Prog Brain Res* 12:222–245
- Powers RK, Vanden Noven S, Rymer WZ (1989) Evidence of shared, direct input to motoneurons supplying synergist muscles in humans. *Neurosci Lett* 102:76–81
- Rosenberg JR, Amjad AM, Breeze P, Brillinger DR, Halliday DM (1989) The Fourier approach to the identification of functional coupling between neuronal spike trains. *Prog Biophys Mol Biol* 53:1–31
- Salenius S, Portin K, Kajola M, Salmelin R, Hari R (1997) Cortical control of human motoneuron firing during isometric contraction. *J Neurophysiol* 77:3401–3405
- Schmied A, Vedel JP, Pagni S (1994) Human spinal lateralization assessed from motoneuron synchronization: dependence on handedness and motor unit type. *J Physiol* 480(Pt 2):369–387
- Schmied A, Pagni S, Sturm H, Vedel JP (2000) Selective enhancement of motoneuron short-term synchrony during an attention-demanding task. *Exp Brain Res* 133:377–390
- Semmler JG, Nordstrom MA (1995) Influence of handedness on motor unit discharge properties and force tremor. *Exp Brain Res* 104:115–125
- Semmler JG, Steege JW, Kornatz KW, Enoka RM (2000) Motor-unit synchronization is not responsible for larger motor-unit forces in old adults. *J Neurophysiol* 84:358–366
- Semmler JG, Kornatz KW, Dinunno DV, Zhou S, Enoka RM (2002) Motor unit synchronisation is enhanced during slow lengthening contractions of a hand muscle. *J Physiol* 545:681–695
- Semmler JG, Sale MV, Meyer FG, Nordstrom MA (2004) Motor-unit coherence and its relation with synchrony are influenced by training. *J Neurophysiol* 92:3320–3331
- Tecchio F, Porcaro C, Zappasodi F, Pesenti A, Ercolani M, Rossini PM (2006) Cortical short-term fatigue effects assessed via rhythmic brain-muscle coherence. *Exp Brain Res* 174:144–151
- Terry K, Griffin L (2008) How computational technique and spike train properties affect coherence detection. *J Neurosci Methods* 168:212–223
- Welch P (1967) The use of fast Fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. *IEEE Trans Audio* 15:70–73
- Yang Q, Fang Y, Sun CK, Siemionow V, Ranganathan VK, Khoshknabi D, Davis MP, Walsh D, Sahgal V, Yue GH (2009) Weakening of functional corticomuscular coupling during muscle fatigue. *Brain Res* 1250:101–112