



Fatigue- and training-related changes in 'beta' intermuscular interactions between agonist muscles



Camille Charissou^{a,b,*}, Laurent Vigouroux^a, Eric Berton^a, David Amarantini^b

^a Aix-Marseille University, CNRS, ISM UMR 7287, Marseille, France

^b Toulouse Neuroimaging Center, Université de Toulouse, Inserm, UPS, France

ARTICLE INFO

Article history:

Received 20 July 2015

Received in revised form 14 January 2016

Accepted 1 February 2016

Keywords:

Wavelet-based time–frequency coherence analysis

Intermuscular coupling

Neural adaptations

Neuromuscular performance

Strength and endurance training

ABSTRACT

The synchronous activation of the muscles involved in force production is crucial for the neuromuscular performance, but the underlying mechanisms remain to be fully elucidated. Our aim was thus to contribute to understand the mechanisms involved in the synergistic activation of agonist muscles. Through wavelet-based time–frequency analysis, this study investigated the modulation of 'beta' intermuscular interactions (IM) during maximum isometric knee extensions performed before and after repetitive submaximal fatiguing contractions. Three groups of participants were included: 9 untrained subjects (control group, CO), 10 elite rugby league players (strength-trained group, ST) and 7 trail runners (endurance-trained group, ED), engaged for 5+ years in intense strength and endurance training, respectively. Before fatigue, CO showed higher IM when compared to ED, and a trend to higher IM when compared to ST. Following fatiguing contractions, all groups showed a decline in neuromuscular performance concomitant with a change (decline) in IM values for CO only. No differences were found between ST and ED regarding to IM either before or after fatiguing contractions. These findings suggested both a form of optimization of intermuscular coupling in trained individuals and the functional importance of intermuscular coupling as a mechanism responsible for the maintenance of the neuromuscular performance.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

As a consequence of muscle redundancy (Prilutsky and Zatsiorsky, 2002), the net torque at a given joint results from the sum of the individual action of all the muscles and other structures surrounding that joint (Zajac et al., 2002). However, a challenging question that needs to be addressed is the mechanisms underlying the modulation of the synergistic activation of the muscles involved in torque production, with important applications in many areas of kinesiology.

Previous studies (Grosse et al., 2002; Farmer et al., 2007), and especially those focusing on fatigue in the 'beta' (β) band (Danna-Dos-Santos et al., 2010; Kattla and Lowery, 2010), indicated that interactions between electromyographic (EMG) signals from a muscle pair provide an index of intermuscular coordination. In line with Shinohara and Yoshitake (2009) who showed modulation of agonist muscles activation strategies with fatigue, several studies reported that muscle fatigue was associated with increased

intermuscular interactions¹ in synergistic agonist muscle pairs (Boonstra et al., 2009; Danna-Dos-Santos et al., 2010). It was thus suggested that the modulation of intermuscular interactions might be one mechanism contributing to overcome the effects of fatigue during low submaximal isometric contractions (Kattla and Lowery, 2010). The functional significance of intermuscular interactions is, however, not completely understood and how the coupling among synergistic muscles may contribute to counteract the fatigue-related decline in neuromuscular performance is yet to be investigated. Furthermore, from a motor control point of view it is widely debated (e.g., Farina et al., 2014) to what extent intermuscular interactions in β band reflects the common oscillatory input from the corticospinal tract responsible for synchronous activity patterns of synergistic agonist muscles during isometric voluntary contraction (Farmer et al., 2007; Winges et al., 2006; Gwin and Ferris, 2012). Interestingly, the changes, or the absence of changes, in neuromuscular performance following strength or endurance training (Dal Maso et al., 2012; Glowacki et al., 2004; Vila-Chã et al., 2010) have

* Corresponding author at: Institut des Sciences du Mouvement – Etienne-Jules Marey, Faculté des Sciences du Sport, CP 910, 163 av. de Luminy, F-13288 Marseille cedex 09, France. Tel.: +33 (0)4 91 17 22 55; fax: +33 (0)4 91 17 22 52.

E-mail address: camille.charissou@univ-amu.fr (C. Charissou).

¹ Oscillatory synchronicity in EMG activity in muscle pairs, often called 'EMG–EMG coherence' (e.g., Danna-Dos-Santos et al., 2010), has been named 'intermuscular interactions' in the present study to be consistent with literature on the correlations between electrophysiological signals (Bigot et al., 2011).

been associated with different adaptations at the peripheral level, but also with significant changes at the cortical and the corticospinal tract levels (Aagard et al., 2002; Dal Maso et al., 2012; Falvo et al., 2010; Goodwill et al., 2012; Vila-Chã et al., 2012). Although such neuromuscular adaptations can occur somewhat in opposite directions between the two training modalities (Farup et al., 2012; Mikkola et al., 2012), endurance and strength training are both thought to enhance recruitment of motor units of synergist muscles (Griffin and Cafarelli, 2005; Lucia et al., 2000). Therefore, comparing untrained participants and athletes trained for endurance or strength could provide a valuable opportunity to clarify the functional role and underlying mechanisms of intermuscular interactions.

Using the approach developed in Bigot et al. (2011) for accurate assessment of pairwise interactions between electrophysiological signals in the time–frequency domain, the present study investigated the fatigue-related modulation of β intermuscular interactions between synergist agonist muscles during maximal isometric knee extension contractions performed by untrained, strength-trained and endurance-trained participants. Our aim was to gain better understanding of the functional role of intermuscular coupling in the regulation of synergistic muscle activation during isometric maximal voluntary contraction, and to provide insights into the possible underlying mechanisms. As there are strong a priori reasons from the literature to expect significant effects of fatigue and group of participants on neuromuscular performance and intermuscular interactions, a series of planned comparisons tests was conducted to assess if differences in the dependent variables would depend on group membership and fatigue condition.

2. Methods

2.1. Participants

Twenty-six males free of known neuromuscular disorders or musculoskeletal knee injuries on their dominant side voluntarily participated in the study. The Strength-Trained group (ST) comprised ten elite rugby league players (age: 23.6 ± 2.9 years; size: 180.9 ± 4.5 cm; mass: 90.9 ± 6.3 kg; 5+ years experience at elite level) with extensive strength training experience (4–5 sessions per week over each training year), and who underwent an off-season general strength training period at the time of the experiment. The Endurance-Trained group (ED) consisted of seven trail runners (age: 37.1 ± 13.6 years; size: 173.8 ± 4.1 cm; mass: 65.0 ± 5.0 kg) engaged in heavy endurance training (>4 times per week for 5 years minimum) without experience of regular strength training. The Control group (CO) consisted of nine recreationally physically active university students not involved in any specific training program (age: 25.4 ± 5.3 years; size: 177.9 ± 7.4 cm; mass: 74.8 ± 9.1 kg). The three groups were size-matched ($F_{2,23} = 3.28$, $p > .05$), but ED was older than CO and ST (all $t < 0.02$, $p < .05$). The body mass was different between all three groups ($F_{2,23} = 28.86$, $p < .05$). The local university ethics committee approved the study and informed consent was obtained from all participants.

2.2. Recordings

The net joint torque around the dominant knee was recorded using a calibrated dynamometer (System 4 Pro, Biodex Medical Systems, Shirley, NY, USA) at 1000 Hz.

Following skin preparation (Hermens et al., 2000), surface EMG signal was recorded at 1000 Hz with a Biopac MP150 system (EMG100C amplifiers, EL503 Ag-AgCl 11 mm bipolar electrodes with a maximum 2 cm spacing; Biopac Systems Inc., Goleta, CA,

USA) from two representative knee extensors: Vastus Medialis (VM) and Rectus Femoris (RF). The reference electrode was placed on the patella of the non-dominant leg.

All measurements were made with the participants seated in the dynamometer chair. The trunk and hips were firmly stabilized with straps to minimize extraneous movements. The thigh and shank on the dominant side were secured with straps to hold the knee and hip angles at 90° and 110° respectively. Torque and EMG data were automatically synchronized in the MP150 unit, recorded using AcqKnowledge software (Biopac, Systems Inc., Goleta, CA, USA) and analyzed offline.

2.3. Protocol

Following active warm-up, the experimental design consisted in three consecutive steps:

1. The participants performed three 5 s maximum voluntary contractions during isometric knee extension, with the rest period between each contraction set to 15 s as in Ferri-Morales et al. (2014).
2. The participants completed a fatiguing protocol of the knee extensors consisting of ten submaximal knee extension isometric contractions sustained to exhaustion a rest interval of 1 min between each contraction (Pääsuke et al., 1999). The target torque was set at 40% of the highest torque calculated on a 2 s window among the three maximum voluntary contractions performed at step 1.
3. The participants performed maximum voluntary contractions immediately after the fatiguing protocol with the same procedure as in step 1.

For all contractions, the participants were provided strong verbal encouragement and visual feedback of the produced torque.

2.4. Data processing

All computations were done using Matlab (Mathworks, Natick, MA, USA). All filters were zero-lag Butterworth type.

2.4.1. Maximum knee joint torque

The net torque recorded at the knee was low-pass filtered at 100 Hz with a 6th-order filter (Zhang et al., 2010). The maximum knee extension torque (MVC) was defined as the average torque during a 2 s window in which the mean torque of the three maximum voluntary contractions was highest.

2.4.2. Holding time

For each fatiguing contraction, the holding time (HT) was defined as the duration between the first instant when the actual torque exceeded 90% target torque for more than 3 s and the first instant when the participant did no longer sustain this effort for the same period.

2.4.3. Intermuscular interactions

EMG signals recorded during maximum voluntary contractions were high-pass filtered at 3 Hz with a 4th-order filter. In each fatigue condition, intermuscular interactions between unrectified high-pass-filtered EMG signals from VM and RF muscles were calculated in the time–frequency domain and their magnitude subsequently quantified using the WavCrossSpec software for wavelet coherence analysis (Bigot et al., 2011) (see Appendix A for further explanation and equations used for calculations; see Fig. 1 for an illustration of the processing steps). The magnitude of β intermuscular interactions (IM) was defined as the volume under magnitude-squared coherence values in the 15–35 Hz frequency

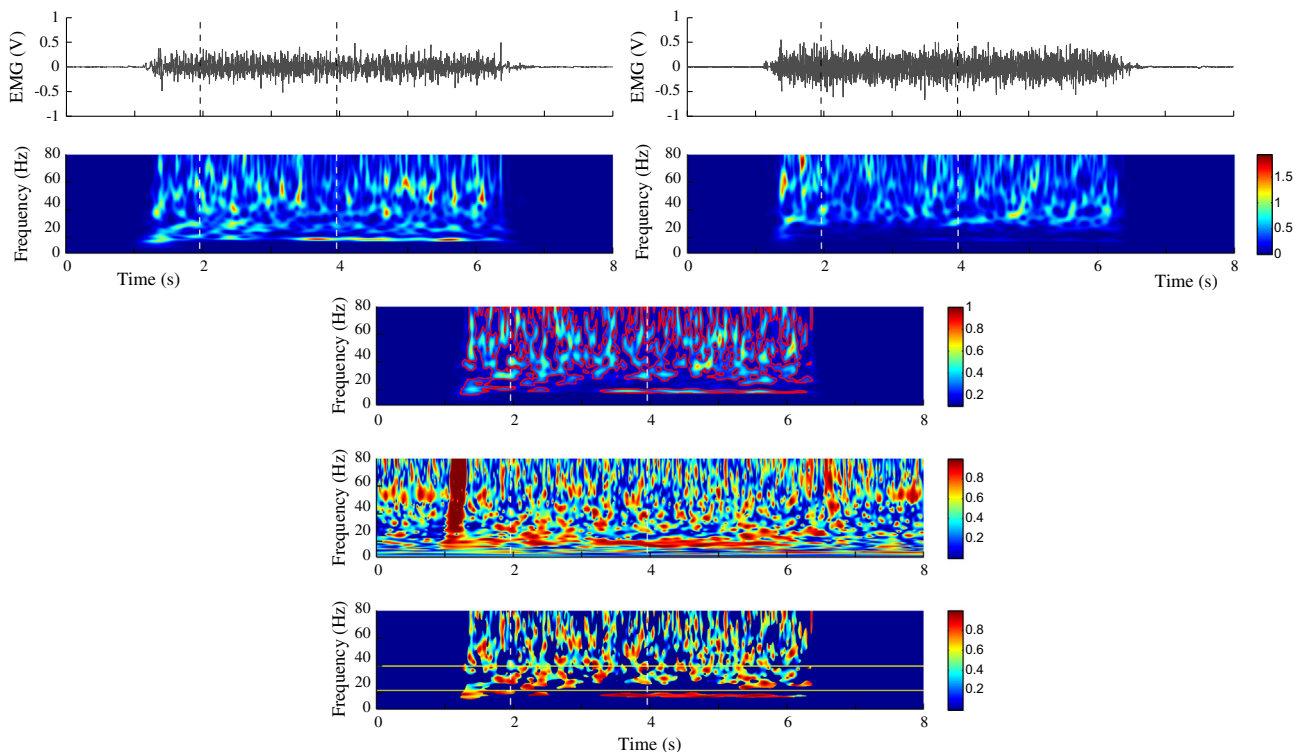


Fig. 1. Illustration of the different steps used for time–frequency analysis of intermuscular interactions from a representative CO participant in the PRE fatigue condition. In each graph, the dashed vertical lines mark the beginning and the end of the 2 s period where the produced torque is maximum. First row: mean EMG signals from VM (left) and RF (right) muscles. Second row: wavelet auto-spectra of EMG time-series from VM (left) and RF muscles (right). Third row: wavelet cross-spectrum between the two EMG time-series; the red contours identify the areas in the time–frequency plane where the correlation between the EMG signals is significant. Fourth row: wavelet magnitude-squared coherence between the two EMG time-series. Fifth row: wavelet magnitude-squared coherence between the two EMG time-series where the correlation between the EMG signals is significant; the horizontal lines delimit the 15–35 Hz ‘beta’ frequency band. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

band (Kattla and Lowery, 2010; Semmler et al., 2013) where the correlation between EMG time-series was detected significant on the wavelet cross-spectrum (Bigot et al., 2011).

2.5. Statistics

All dependent variables were tested for normality (Shapiro-Wilk test, $\alpha = .05$) and square root transformation was performed to achieve normal distribution when necessary (Borcard, 1998; Daumas, 1982). All data met the assumption of homogeneity of variances (Levene’s test, all $p > .05$).

Given the numerous previously published studies on fatigue or central and neuromuscular adaptations to training (see, e.g., Introduction), planned comparisons through linear contrasts between means were conducted to assess between-Group differences on HT during the fatiguing contractions, and to test for Group differences on MVC and IM in each fatigue condition (PRE, POST) according to their theoretical relevance (Howell, 2006).

Independent *t*-tests were used to assess between-Group differences between repetition 1 and 10 in HT decrease expressed as a proportion and transformed using arcsin square root transformation (De Muth, 2006).

Data are reported as mean \pm SD within the text and as mean \pm SE in Figs. 3–5. Significance was set at $p < .05$; a *p*-value between .05 and .10 was considered a trend.

3. Results

Fig. 2 shows typical profiles of knee isometric extension torque and time–frequency maps of intermuscular interactions between EMG signals from VM and RF muscles.

3.1. Maximum knee joint torque (MVC)

Before fatigue (Fig. 3, PRE), planned comparisons revealed that MVC was higher in ST than in both CO and ED ($F_{1,23} = 9.76$ and $F_{1,23} = 14.03$ respectively, $p < .05$), with no significant difference between CO and ED ($F_{1,23} = 0.66$, $p > .05$). After fatigue (Fig. 3, POST), ST had higher MVC than both CO and ED ($F_{1,23} = 17.32$ and $F_{1,23} = 15.61$ respectively, $p < .05$), without significant difference between CO and ED ($F_{1,23} = 0.00$, $p > .05$). MVC was lower after than before fatigue in all groups, with a significant decrease by 25.84% for CO, 20.53% for ED and 18.20% for ST (all $F_{1,23} = 37.88$, $p < .05$; Fig. 3).

3.2. Holding time (HT)

Planned comparisons showed that mean HT over all participants significantly decreased from 106.15 ± 38.53 s to 45.26 ± 15.12 s between the first and the tenth contraction ($F_{1,23} = 101.54$, $p < .05$; Fig. 4a). Subsequent analysis revealed that HT was longer in ED than in CO for the last contraction ($F_{1,23} = 4.74$, $p < .05$), without any significant difference between ST and ED ($F_{1,23} = 2.75$, $p > .05$) and ST and CO ($F_{1,23} = 0.46$, $p > .05$). The proportion of HT decrease between contraction 1 and 10 was higher in CO than in both ED and ST ($t = 2.67$ and $t = 2.21$ respectively, $p < .05$), without significant difference between ED and ST ($t = 0.87$, $p > .05$) (Fig. 4b).

3.3. β intermuscular interactions

Areas in the time–frequency plane where β intermuscular interactions were significant were detected in all participants, both before and after fatigue.

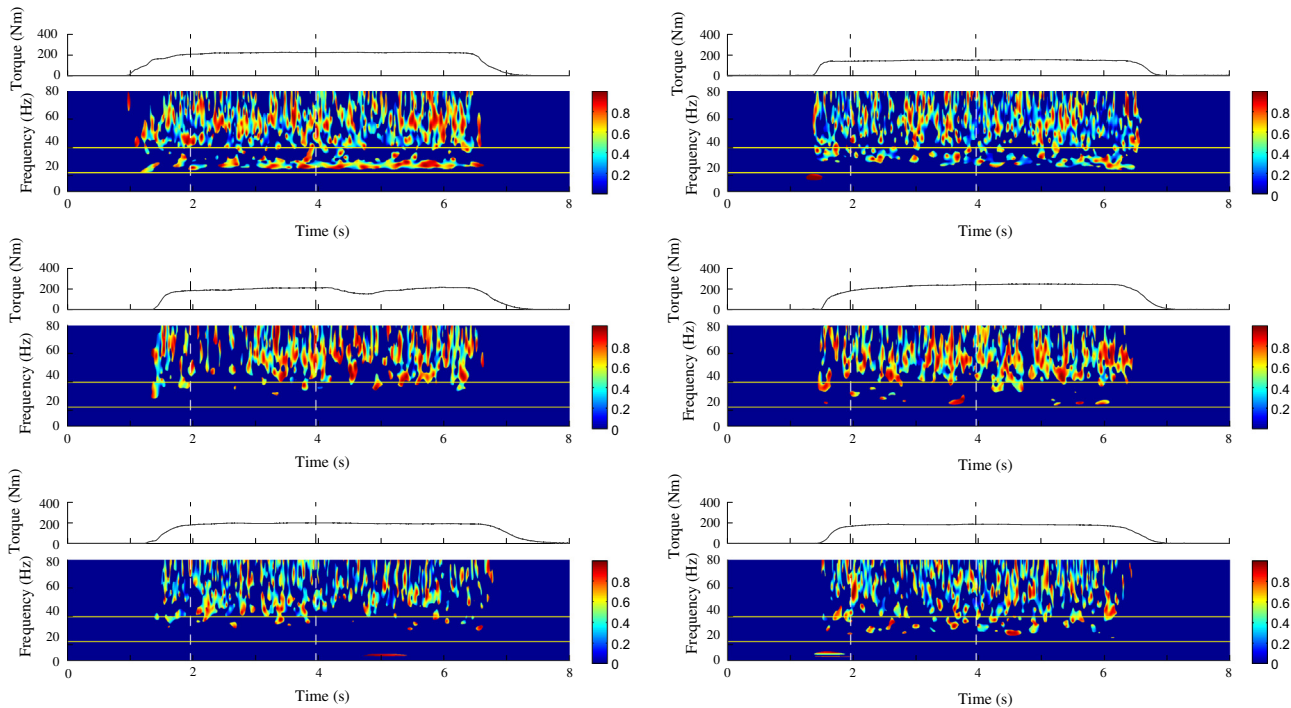


Fig. 2. Typical knee net joint torque and map of intermuscular interactions between VM and RF muscles in the PRE (left panels) and POST (right panels) fatigue conditions for representative control (CO, upper panels), strength-trained (ST, middle panels) and endurance-trained (ED, lower panels) participants. In each panel, the upper graph shows the mean torque-time curve during maximal isometric knee extension, from 1 s before to 1 s after the 6 s contraction; the lower graph shows time–frequency plots of magnitude-squared coherence values where the correlation between EMG time-series was detected significant on the wavelet cross-spectrum, with the horizontal lines delimiting the 15–35 Hz ‘beta’ frequency band. On all graphs, dashed vertical lines mark the beginning and the end of the 2 s period where the produced torque is maximum. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Before fatigue, the statistical analysis revealed that IM was higher in CO than in ED ($F_{1,23} = 5.06$, $p < .05$) and indicated a tendency for higher IM in CO than in ST ($F_{1,23} = 2.96$, $p = .09$) (Fig. 5b).

IM significantly decreased in CO after fatigue ($F_{1,23} = 4.93$, $p < .05$), whereas it remained stable between pre- and post-fatigue in both ED and ST ($F_{1,23} = 0.49$ and $F_{1,23} = 1.44$ respectively, $p > .05$), resulting in similar IM between groups after fatigue (CO vs. ED: $F_{1,23} = 0.44$, CO vs. ST: $F_{1,23} = 0.17$, ED vs. ST: $F_{1,23} = 1.13$; $p > .05$) (Fig. 5a).

4. Discussion

This study investigated the modulation of β intermuscular interactions between knee agonists during maximum isometric voluntary extensions performed before and after repetitive sub-maximal fatiguing contractions by untrained subjects and elite rugby league players and trail runners engaged for 5+ years in intense strength and endurance training, respectively. Through the time–frequency analysis of intermuscular interactions, we aimed to contribute to the understanding of the functional role and potential mechanisms underlying the regulation of synergistic activation of agonist muscles involved in torque production.

4.1. Maximum torque and holding time

The results on MVC revealed higher knee maximum torque in ST than in CO and ED before and after fatigue, and a significant decrease of MVC in all groups after fatigue. These findings replicate Pääsuke et al. (1999) and agree with those showing greater training outcomes in strength-trained than in endurance-trained individuals (Glowacki et al., 2004; Vila-Chã et al., 2010). These changes in MVC can be readily explained by both morphological and neural adaptations to strength training (Folland and

Williams, 2007) carried out by elite rugby league players in our ST group. The absence of difference in MVC between CO and ED agreed with Vila-Chã et al. (2010) but contrasts with Dal Maso et al. (2012) and Lattier et al. (2003) who reported similar MVC in endurance-trained and strength- or power-trained individuals. This apparent discrepancy may be explained by between-studies differences in the sport disciplines practiced by the participants.

The results showed that the decrease in HT during the fatiguing protocol was greater in CO than in ED and ST. The time to task failure was higher in ED than in CO during the last fatiguing

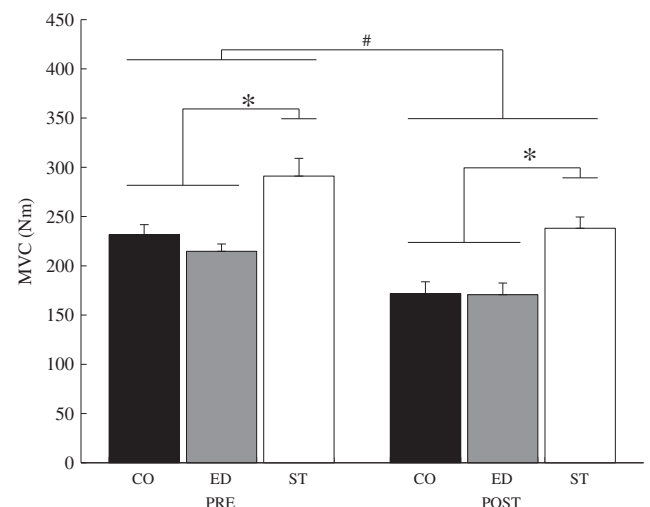


Fig. 3. Mean (\pm SE) maximum knee joint torque (MVC) in control (CO), endurance-trained (ED) and strength-trained (ST) participants before (PRE) and after (POST) fatigue. ‘#’ indicates a significant Fatigue effect, ‘*’ indicates a significant difference compared with ST.

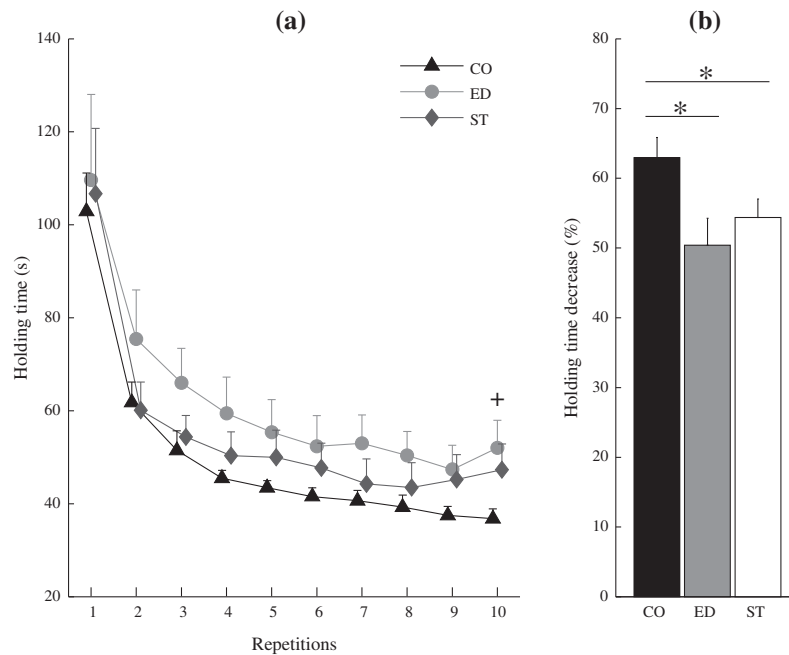


Fig. 4. (a) Mean (\pm SE) holding time (HT) during fatiguing contractions performed by control (CO, \blacktriangle), endurance-trained (ED, \bullet) and strength-trained (ST, \blacklozenge) participants. The '+' symbol indicates significant difference between ED and CO. (b) Proportion of HT decrease between the first and the last contraction in CO, ED and ST. The '*' symbol indicates significant difference with CO.

contraction, without significant difference with ST. These results witnessed a progressive development of muscle fatigue, and support the conclusion that endurance training enhances the ability to withstand fatigue (Glowacki et al., 2004; Pääsuke et al., 1999). Besides, the lack of observed difference in HT among trained groups may be partly explained by the nature of the training program followed by ST, which did not comprise solely strength training during the rugby league season. Previous studies concluded that task failure for a submaximal isometric contraction could be attributed to the alteration of spinal and/or supraspinal central nervous mechanisms (Barry and Enoka, 2007), and specifically to

the inability to sustain the initial descending drive and/or to spinal inhibitions via muscle afferents (Place et al., 2006). In light of such findings, the differences observed in HT may be related to the different adaptations occurring to endurance and strength training in central neural pathways.

Although to be interpreted with caution due to morphological and structural adaptations occurring with training (e.g., Farup et al., 2012), the results on MVC and HT suggested that the changes in the neuromuscular performance may be related to specific neural adaptations within motor cortex and spinal cord occurring to each training modality.

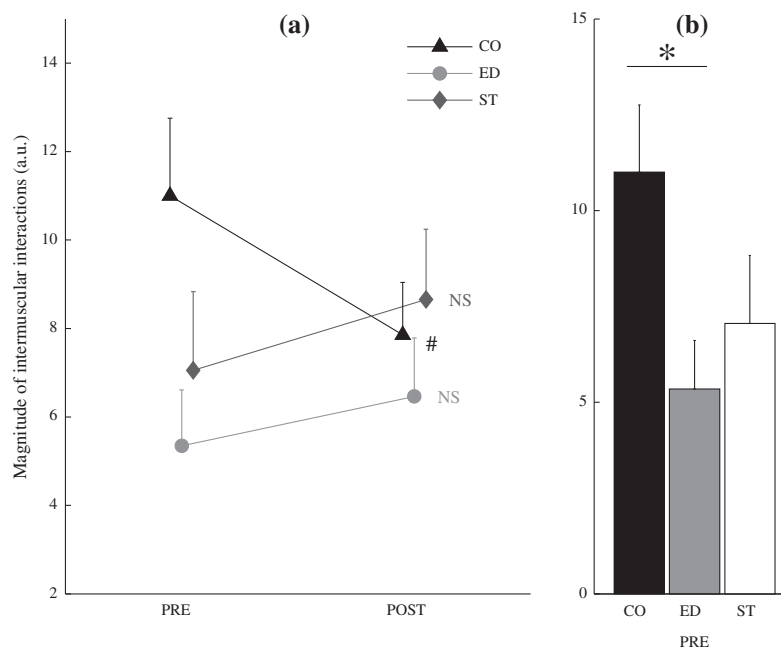


Fig. 5. (a) Mean (\pm SE) magnitude of β intermuscular interactions (IM) before (PRE) and after (POST) fatigue in control (CO, \blacktriangle), endurance-trained (ED, \bullet) and strength-trained (ST, \blacklozenge) participants. '#' indicates significant difference between pre- and post-fatigue for the marked group. (b) Mean (\pm SE) IM in CO, ED and ST before fatigue (PRE). '*' indicates significant difference with CO.

4.2. β intermuscular interactions

Even if we cannot exclude the possibility that a part of β intermuscular interactions may result from crosstalk artifacts inherent to surface EMG recordings, a first important finding was that significant IM were detected for all participants before and after fatigue. Given that β synchronous oscillatory activity of the muscles reflects some coupling among synergistic muscles (Kattla and Lowery, 2010), this finding provides further evidence that supports that intermuscular coupling may be considered as a fundamental mechanism for synergistic activation of agonist muscles.

A second key finding was that IM was higher in CO than in ED, which should be taken together with the strong trend observed toward higher IM in CO than in ST. Interestingly, from a motor control point of view, previous studies highlighted improved control of muscle activation in strength-trained athletes (Amarantini and Bru, 2015), enhanced neural processes underlying muscle contraction (Aagard et al., 2002; Griffin and Cafarelli, 2005; Lucia et al., 2000) and enhanced neural economy (Falvo et al., 2010) following training. In light of these studies, our findings may be interpreted as a form of optimization of intermuscular coupling in trained subjects. In this view, the training-related modulation of β intermuscular interactions may reflect a possible mechanism contributing to the formation of muscle synergies or to the organization of synergist agonist muscles (De Marchis et al., 2015) for improved neuromuscular performance. Based on previous studies reporting that intermuscular coherence could be dependent on the common oscillatory input from the corticospinal pathway (Farmer et al., 2007), the differences in intermuscular coupling between the groups may be related to enhanced corticospinal excitability in endurance- (Adkins et al., 2006 in animal model) and strength-trained individuals (Goodwill et al., 2012).

The third important finding was that the fatigue-related decline in net torque for all groups was concomitant with a decreased IM for CO, while IM remained stable in ED and ST. Despite apparent discrepancy with previous studies on EMG–EMG coherence in the presence of fatigue, this finding is in fact congruent with increased β intermuscular interactions between submaximal contractions performed at similar absolute force before and after fatiguing contractions (Kattla and Lowery, 2010). Thus, in line with previous studies, our results emphasized the functional importance of intermuscular coupling to sustain a required level of force during fatiguing isometric contractions. Further, the results indicated that fatigue-related modulation of intermuscular coupling seems different depending on whether or not training-related peripheral and central plasticity occurred. In untrained participants, the decrease in β intermuscular interactions could be regarded as altered coupling between synergist agonist muscles to the detriment of the neuromuscular performance. Although it is more difficult to arrive at a definite conclusion for trained participants, we can suggest that the absence of change in intermuscular coupling may be explained by the fact that the neural adaptations to training, such as those that occur at the corticospinal level, contributed to compensate for the deleterious effects of fatigue on intermuscular coupling. Overall, these findings provide evidence that intermuscular coupling would take part in the mechanisms underlying the synchronous activation of synergistic agonist muscles to maintain the performance of the neuromuscular system.

The conclusions drawn in the present study should be considered in regards to the reliability and the limitations of coherence analysis between electrophysiological signals (Farina et al., 2014; van Asseldonk et al., 2014). However, the present study introduces an objective method to render a meaningful interpretation of synchronization processes (Bigot et al., 2011) by properly detecting statistical dependence between time series even when the number of trials is small (Pedrosa et al., 2014).

5. Conclusion

The results of this study revealed higher β intermuscular interactions in CO than in ED and also showed a trend to higher IM in CO when compared to ST during maximal isometric knee extension contractions performed before fatigue. Moreover, the results showed that β intermuscular interactions decreased or remained stable with fatigue depending on whether or not the participants were strength- or endurance-trained. These findings suggested a form of optimization of intermuscular coupling associated with enhanced neuromuscular performance in trained individuals, which may be explained by adaptations induced by training at the corticospinal level. The results also emphasized the importance of intermuscular coupling as a mechanism that could take part in the maintenance of the neuromuscular performance during voluntary contractions. These findings could contribute significantly to fundamental research in motor control and would find application in clinical kinesiology and rehabilitation (e.g., Grosse et al., 2002). Future work should deepen these findings by corticomuscular coherence analysis to provide information about the functional coupling between the cortex and the muscle during voluntary contractions.

Conflict of interest

The authors declare that there are no conflicts of interest.

Acknowledgments

The authors thank Thomas Gov for data acquisition, and Robin Baurès (Brain and Cognition Research Center (CerCo), UMR 5549 CNRS/Paul Sabatier University, Toulouse, France) for expert advice on statistical analysis.

Appendix A

This document is the methodological appendix for the calculation of intermuscular interactions referring to the manuscript entitled: "Fatigue- and training-related changes in 'beta' intermuscular interactions between agonist muscles".

The calculation of intermuscular interactions between EMG signals from VM and RF muscles was done in the time–frequency domain using the *WavCrossSpec* software (Bigot et al., 2011; available for download at: http://www.math.u-bordeaux1.fr/~jbigot/Site/Software_files/WavCrossSpec.zip) based on the *cross wavelet and wavelet coherence toolbox for MATLAB* provided by Grinsted et al. (2004); available for download at: <http://www.glaciology.net/wavelet-coherence>). Noteworthy is that:

- Time–frequency analysis is a suitable tool for coherence analysis of signals such as EMG that can present non-stationary zones (Allen and MacKinnon, 2010).
- Time–frequency analysis has advantages to conventional frequency-domain analysis to account for how the oscillatory patterns change with time (Zhan et al., 2006), even though intermuscular interactions were quantified over a specified time period of interest.

In *WavCrossSpec*, the following parameterization was used to yield accurate identification of oscillatory activity on the $[0.32 \cdot 10^{-2}; 0.23; 79.97]$ Hz frequency range:

- The parameter 'nvoice', which determines the scale resolution of the wavelet, was set at 7.

- The parameter 'J1', which determines the number of scales used in the wavelet analysis, was set at 50.
- The Morlet mother wavelet parameter 'wavenumber' was set at 10.

In agreement with the conclusions of previous studies (e.g., Neto and Christou, 2010; McClelland et al., 2012), high-pass-filtered EMG signals were not rectified, to properly model time-series data as centered Gaussian processes (Bigot et al., 2011). For each unrectified high-pass-filtered EMG signal of muscle x ($x = \{VM, RF\}$), the wavelet auto-spectrum S_x at frequency ω and time u was defined as:

$$S_x(\omega, u) = \mathbb{E}[W_x(\omega, u)]^2 \quad (1)$$

where W_x is the wavelet transform of x and $\mathbb{E}Z$ denotes the expectation of a random variable Z (refer to Bigot et al. (2011) for detailed equations).

The second step was to calculate the wavelet cross-spectrum between the two time-series of EMG from VM and RF muscles ($S_{VM/RF}(\omega, u)$) with:

$$S_{VM/RF}(\omega, u) = \mathbb{E}(W_{VM}(\omega, u)\overline{W_{RF}(\omega, u)}) \quad (2)$$

and then to calculate the wavelet magnitude-squared coherence between the two time-series of EMG ($R_{VM/RF}^2(\omega, u)$) with:

$$R_{VM/RF}^2(\omega, u) = |S_{VM/RF}(\omega, u)|^2 / (S_{VM}(\omega, u)S_{RF}(\omega, u)) \quad (3)$$

References

- Aagard P, Simonsen EB, Andersen JL, Magnusson P, Dyhre-Poulsen P. Neural adaptation to resistance training: changes in evoked V-wave and H-reflex responses. *J Appl Physiol* 2002;92(6):2309–18.
- Adkins DL, Boychuk J, Remple MS, Kleim JA. Motor training induces experience-specific patterns of plasticity across motor cortex and spinal cord. *J Appl Physiol* 2006;101(6):1776–82.
- Allen DP, MacKinnon CD. Time-frequency analysis of movement-related spectral power in EEG during repetitive movements: a comparison of methods. *J Neurosci Meth* 2010;186(1):107–15.
- Amarantini D, Bru B. Training-related changes in the EMG-moment relationship during isometric contractions: further evidence of improved control of muscle activation in strength-trained men? *J Electromyogr Kinesiol* 2015;25(4):697–702.
- Barry BK, Enoka RM. The neurobiology of muscle fatigue: 15 years later. *Integr Comp Biol* 2007;47(4):465–73.
- Bigot J, Longcamp M, Dal Maso F, Amarantini D. A new statistical test based on the wavelet cross-spectrum to detect time-frequency dependence between non-stationary signals: application to the analysis of cortico-muscular interactions. *Neuroimage* 2011;55(4):1504–18.
- Boonstra TW, van Wijk BC, Praamstra P, Daffertshofer A. Corticomuscular and bilateral EMG coherence reflect distinct aspects of neural synchronization. *Neurosci Lett* 2009;463(1):17–21.
- Borcard D. Transformation de données: normalisation, stabilisation des variances [Online]. Département de sciences biologiques, Université de Montréal; 1998.
- Dal Maso F, Longcamp M, Amarantini D. Training-related decrease in antagonist muscles activation is associated with increased motor cortex activation: evidence of central mechanisms for control of antagonist muscles. *Exp Brain Res* 2012;220(3–4):287–95.
- Danna-Dos-Santos A, Poston B, Jesunathadas M, Bobich LR, Hamm TM, Santello M. Influence of fatigue on hand muscle coordination and EMG-EMG coherence during three-digit grasping. *J Neurophysiol* 2010;104(6):3576–87.
- Daumas F. Méthodes de normalisation des données. *Revue de statistique appliquée* 1982;30:23–38.
- De Marchis C, Severini G, Castronovo Margherita, Schmid M, Conforto S. Intermuscular coherence contributions in synergistic muscles during pedaling. *Exp Brain Res* 2015;233(6):1907–19.
- De Muth JE. Basic statistics and pharmaceutical statistical applications, 3rd ed. Baco Raton: CRC Press (Taylor and Francis Group); 2006.
- Falvo MJ, Sirevaag EJ, Rohrbach JW, Earhart GM. Resistance training induces supraspinal adaptations: evidence from movement-related cortical potentials. *Eur J Appl Physiol* 2010;109(5):923–33.
- Farina D, Negro F, Dideriksen JL. The effective neural drive to muscles is the common synaptic input to motor neurons. *J Physiol* 2014;592(16):3427–41.
- Farmer SF, Gibbs J, Halliday DM, Harrison LM, James LM, Mayston MJ, et al. Changes in EMG coherence between long and short thumb abductor muscles during human development. *J Physiol* 2007;579(2):389–402.
- Farup J, Kjølhed T, Sørensen H, Dalgas U, Møller AB, Vestergaard PF, et al. Muscle morphological and strength adaptations to endurance vs. resistance training. *J Strength Cond Res* 2012;26(2):398–407.
- Ferri-Morales A, Alegre LM, Basco A, Aguado X. Test-retest relative and absolute reliability of knee extensor strength measures and minimal detectable change. *Isokinet Exerc Sci* 2014;22(1):17–26.
- Folland JP, Williams AG. The adaptations to strength training: morphological and neurological contributions to increased strength. *Sports Med* 2007;37(2):145–68.
- Glowacki SP, Martin SE, Maurer A, Baek W, Green JS, Crouse SF. Effect of resistance, endurance and concurrent exercise on training outcomes in men. *Med Sci Sports Exerc* 2004;36(12):2119–27.
- Goodwill AM, Pearce AJ, Kidgell DJ. Corticomuscular plasticity following unilateral strength training. *Muscle Nerve* 2012;46(3):384–93.
- Griffin L, Cafarelli E. Resistance training: cortical, spinal, and motor unit adaptations. *Can J Appl Physiol* 2005;30(3):328–40.
- Grinted A, Moore JC, Jevrejeva S. Application of the cross wavelet transform and wavelet coherence to geophysical time series. *Nonlin Processes Geophys* 2004;11(5/6):561–6.
- Grosse P, Cassidy MJ, Brown P. EEG-EMG, MEG-EMG and EMG-EMG frequency analysis: physiological principles and clinical applications. *Clin Neurophysiol* 2002;113(10):1523–31.
- Gwin JT, Ferris DP. Beta- and gamma-range human lower limb corticomuscular coherence. *Front Hum Neurosci* 2012;6:258. eCollection.
- Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G. Development of recommendations for SEMG sensors and sensor placement procedures. *J Electromyogr Kinesiol* 2000;10(5):361–74.
- Howell DC. Statistical methods for psychology, 6th ed. Belmont: Cengage Learning; 2006.
- Kattla S, Lowery MM. Fatigue related changes in electromyographic coherence between synergistic hand muscles. *Exp Brain Res* 2010;202(1):89–99.
- Lattier G, Millet GY, Maffiuletti NA, Babault N, Lepers R. Neuromuscular differences between endurance-trained, power-trained and sedentary subjects. *J Strength Cond Res* 2003;17(3):514–21.
- Lucia A, Hoyos J, Pardo J, Chicharro JL. Metabolic and neuromuscular adaptations to endurance training in professional cyclists: a longitudinal study. *Jpn J Physiol* 2000;50(3):381–8.
- McClelland VM, Cvetkovic Z, Mills KR. Rectification of the EMG is an unnecessary and inappropriate step in the calculation of corticomuscular coherence. *J Neurosci Methods* 2012;205(1):190–201.
- Mikkola J, Rusko H, Izquierdo M, Gorostiaga EM, Häkkinen K. Neuromuscular and cardiovascular adaptations during concurrent strength and endurance training in untrained men. *Int J Sports Med* 2012;33(9):702–10.
- Neto OP, Christou EA. Rectification of the EMG signal impairs the identification of oscillatory input to the muscle. *J Neurophysiol* 2010;103(2):1093–103.
- Pääsuke M, Erilne J, Gapeyeva H. Neuromuscular fatigue during repeated exhaustive submaximal static contractions of knee extensor muscles in endurance-trained, power-trained and untrained men. *Acta Physiol Scand* 1999;166(4):319–26.
- Pedrosa DJ, Quatuor E-L, Reck C, Pauls KAM, Huber CA, Visser-Vandewalle V, et al. Thalamomuscular coherence in essential tremor: hen or egg in the emergence of tremor? *J Neurosci* 2014;34(43):14475–83.
- Place N, Matkowski B, Martin A, Lepers R. Synergists activation pattern of the quadriceps muscle differs when performing sustained isometric contractions with different EMG biofeedback. *Exp Brain Res* 2006;174(4):595–603.
- Prilutsky B, Zatsiorsky VM. Optimization-based models of muscle coordination. *Exerc Sport Sci Rev* 2002;30(1):32–8.
- Semmler JG, Ebert SA, Amaraseena J. Eccentric muscle damage increases intermuscular coherence during a fatiguing isometric contraction. *Acta Physiol* 2013;208(4):362–75.
- Shinohara M, Yoshitake Y. Alterations in synergistic muscle activation impact fluctuations in net force. *Med Sci Sports Exerc* 2009;41(1):191–7.
- van Asseldonk EH, Campens SF, Verwer SJ, van Putten MJ, Stegeman DF. Reliability and agreement of intramuscular coherence in tibialis anterior muscle. *PLoS ONE* 2014;9(2):88428. eCollection.
- Vila-Chà C, Falla D, Farina D. Motor unit behavior during submaximal contractions following six weeks of either endurance or strength training. *J Appl Physiol* 2010;109(5):1455–66.
- Vila-Chà C, Falla D, Correia M Velhote, Farina D. Changes in H reflex and V wave following short-term endurance and strength training. *J Appl Physiol* 2012;112(1):54–63.
- Wings SA, Johnston JA, Santello M. Muscle-pair specific distribution and grip-type modulation of neural common input to extrinsic digit flexors. *J Neurophysiol* 2006;96(3):1258–66.
- Zajac FE, Neptune RR, Kautz SA. Biomechanics and muscle coordination of human walking. Part I: introduction to concepts, power transfer, dynamics and simulations. *Gait Posture* 2002;16(3):215–32.
- Zhan Y, Halliday D, Jiang P, Liu X, Feng J. Detecting time-dependent coherence between non-stationary electrophysiological signals – a combined statistical and time-frequency approach. *J Neurosci Meth* 2006;156(1–2):322–32.
- Zhang Q, Hayashibe M, Papaianidou M, Fraisse P, Fattal C, Guiraud D. Torque prediction using stimulus evoked EMG and its identification for different muscle fatigue states in SCI subjects. In: Conf proc IEEE eng med biol soc 2010; 2010. p. 3523–6.



Camille Charissou obtained her Master's degree in Biomechanics from the Paul Sabatier University (Toulouse, France) in 2014. She is currently a Ph.D student in the Institute of Movement Sciences (UMR CNRS 7287) at the Aix-Marseille University, France. Her research work focuses on the mechanisms underlying the activation of synergist muscles during human muscle contraction.



Eric Berton obtained his Ph.D. degree in Mechanics in 1992. He is currently Professor in Mechanical Engineering at the University of the Mediterranean, Marseille, France. Eric Berton is head of the Biomechanics of Movement and Modeling Team and is director at the "Movement and Perception Laboratory" (CNRS). His main research interests concern Biomechanics and Movement, Biomechanical Models, and Sport Engineering.



Laurent Vigouroux is a Ph.D. in biomechanics and sport sciences (Joseph Fourier University, Grenoble, France), currently assistant professor at the Institute of Movement Sciences (UMR CNRS 7287) in Marseille, France. His work focuses on understanding the hand and the grip functions in human beings. He currently uses biomechanical analysis and biomechanical modelling to assess descriptive variables of the grasping tasks (articular and muscle forces) which are impossible to measure directly and still currently unknown.



David Amarantini obtained his Ph.D. degree in Biomechanics from the Joseph Fourier University (Grenoble, France) in 2003. He is currently employed as an Assistant Professor in biomechanics at the Paul Sabatier University of Toulouse, France. His main research interests are estimation of muscle forces and joint moments, multi-muscle and multi-degrees of freedom coordination, neuro-biomechanics and biomechanical applications of numerical optimization and signal processing.