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RESEARCH ARTICLE

Fatigue-related adaptations in muscle coordination during a cyclic exercise in humans

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SUMMARY

Muscle fatigue is an exercise-induced reduction in the capability of a muscle to generate force. A possible strategy to counteract the effects of fatigue is to modify muscle coordination. We designed this study to quantify the effect of fatigue on muscle coordination during a cyclic exercise involving numerous muscles. Nine human subjects were tested during a constant-load rowing exercise (mean power output: 217.9±32.4 W) performed until task failure. The forces exerted at the handle and the foot-stretcher were measured continuously and were synchronized with surface electromyographic (EMG) signals measured in 23 muscles. In addition to a classical analysis of individual EMG data (EMG profile and EMG activity level), a non-negative matrix factorization algorithm was used to identify the muscle synergies at the start and the end of the test. Among the 23 muscles tested, 16 showed no change in their mean activity level across the rowing cycle, five (biceps femoris, gluteus maximus, semitendinosus, trapezius medius and vastus medialis) showed a significant increase and two (gastrocnemius lateralis and longissimus) showed a significant decrease. We found no change in the number of synergies during the fatiguing test, i.e. three synergies accounted for more than 90% of variance accounted for at the start (92.4±1.5%) and at the end (91.0±1.8%) of the exercise. Very slight modifications at the level of individual EMG profiles, synergy activation coefficients and muscle synergy vectors were observed. These results suggest that fatigue during a cyclic task preferentially induces an adaptation in muscle activity level rather than changes in the modular organization of the muscle coordination.

Key words: electromyography, task failure, rowing, module, muscle synergies.

INTRODUCTION

Muscle fatigue is an exercise-induced reduction in the muscle's capability to generate force (Bigland-Ritchie and Woods, 1984; Gandevia, 2001). The process of fatigue is gradual and includes important physiological changes that occur before and during the mechanical failure (Hoffman et al., 2009). A possible strategy to counteract the effects of fatigue is to modify muscle coordination (Enoka and Stuart, 1992), defined herein as 'a distribution of muscle activation or force among individual muscles to produce a given combination of joint moments' (Prilutsky, 2000). More precisely, fatigue can induce a redistribution of muscle activity level among muscles and/or changes in muscle activity profile (i.e. shape of muscle activity throughout the movement). For instance, several studies have reported alternating levels of muscle activity among synergist muscles during low-level submaximal isometric exercises (Kouzaki and Shinohara, 2006; Kouzaki et al., 2002). Other authors reported changes in muscle coordination during a dynamic task such as pedaling (Billaut et al., 2005; Dorel et al., 2009), hopping (Bonnard et al., 1994) or vertical jump (Rodacki et al., 2002). Although some of these studies reported modest changes (Dorel et al., 2009; Rodacki et al., 2002), others reported more important changes in both muscle activity level and muscle activity profile (Bonnard et al., 1994). However, to the best of our knowledge, very little is known about the adaptation in muscle coordination during a cyclic task involving numerous muscles, such as in rowing (Rodriguez et al., 1990; Soper and Hume, 2004), which offers numerous possibilities for compensation across muscles. The particularity of rowing is that numerous trunk, upper limb and lower limb muscles are directly involved in the power production. Therefore, in contrast to other cyclic tasks such as pedaling or walking, rowing offers the additional solution of using compensatory strategies between upper and lower limbs during fatigue.

Studies focusing on muscle coordination usually report on muscle activity level and muscle activity profiles (also named electromyographic patterns) of individual muscles. From this electromyographic (EMG) profile, information about muscle activation timing and shape of muscle activity can be extracted (for a review, see Hug, 2011). However, when numerous muscles are recorded [up to 32 muscles in some studies, e.g. Cappellini et al. (Cappellini et al., 2006)], the individual muscle activity profiles can be difficult to interpret in terms of motor strategies. Recently, a technique has emerged that is capable of decomposing large EMG datasets into the summed activation of just a few muscle synergies or modules (Ting and McKay, 2007; Tresch et al., 2006). Although some studies suggested that muscle synergies better reflect task constraints rather than neural control strategies (Kutch et al., 2008; Valero-Cuevas et al., 2009), others proposed that the central nervous system produces movement through the flexible combination of muscle synergies (Torres-Oviedo et al., 2006; Torres-Oviedo and Ting, 2007; Tresch et al., 1999; Bizzi et al., 2008; d'Avella et al., 2003). Indeed, they provide an attractive simplified strategy for the control of complex movements because they reduce the number of

output patterns that the nervous system must specify for a large number of muscles (Bizzi et al., 2008). For example, five muscle synergies account for the majority of variability in the surface EMG signals of 32 muscles during walking (Ivanenko et al., 2004; Ivanenko et al., 2006) and running (Cappellini et al., 2006). As stated by Ting, because they reflect the task-variables that are sensed and regulated by the nervous system, the number of muscle synergies and their corresponding neural commands carries more information than the individual muscle profiles (Ting, 2007). It has been recently shown that the interindividual variability of individual EMG patterns (recorded in 10 muscles) observed during pedaling is not linked to the use of different muscle synergies and thus does not represent differences in the locomotor strategy for pedaling (Hug et al., 2010). Therefore, for a complete understanding of muscle coordination, both individual EMG profiles and muscle synergies should be analyzed (Ting and Chvatal, 2010).

The present study was designed to quantify the effect of fatigue on muscle coordination during a cyclic task involving the whole musculature. Surface EMG activity was recorded in 23 muscles in humans during a submaximal constant-load rowing exercise performed until task failure. In addition to a classical analysis of the changes in both muscle activity level and individual EMG profiles, a non-negative matrix factorization algorithm was used to identify the muscle synergies. In agreement with the literature showing the consistency of muscle synergies across different behaviors (Bizzi et al., 2008) and mechanical constraints (Torres-Oviedo and Ting, 2010; Hug et al., 2011), we hypothesized that fatigue would induce adaptations in muscle activity level to maintain a stable power output rather than changes in the modular organization of the muscle coordination.

MATERIALS AND METHODS

Subjects

Nine male untrained subjects (age: 24.2±6.3 years; height: 177.6±5.8 cm; body mass: 68.7±5.9 kg; means ± s.d.) volunteered to participate in this study. They had no prior experience of rowing (either using an ergometer or on water). They were all informed of the possible risk and discomfort associated with the experimental procedures before giving their written consent to participate. The experimental design of the study was approved by the local ethical committee and was conducted in accordance with the Declaration of Helsinki.

Procedure

The tests were divided into two identical sessions to allow for the measurement of 23 muscles. One week before the first session, the subjects performed an all-out 2000 m rowing test on an ergometer to assess their mean power (MP) over this distance.

Subjects were first asked to perform a standardized warm-up consisting of 5 min of rowing at a self-paced intensity followed by three 2-min constant load tests performed at 60, 90 and 120% of the MP, with the cadence fixed between 28 and 32 strokes min^{-1}. Afterwards, subjects performed a constant-load test executed at their MP until exhaustion. They were asked to keep a constant stroke frequency fixed between 28 and 32 strokes min^{-1}. A visual feedback of both the power output and stroke frequency was displayed on a monitor placed in front of them. The test continued until task failure (T_{lim}), i.e. either the subject voluntarily chose to stop the exercise or until a decrease of 10% of the requested power output was repeatedly observed for more than 10 s. Strong encouragements were given to the subjects to ascertain that they were fully exhausted.

Subjects exercised on a rowing ergometer (Rowperfect, Sydney, NSW, Australia) with a fixed stretcher mechanism. As described previously (Colloud et al., 2006), the ergometer was instrumented to measure the force produced at the handle ($\mathbf{F}_h$) with a strain gauge force transducer (SM-1000N; Interface™, Scottsdale, AZ, USA), which was placed in series with the chain and the handle using a ball and socket joint (free to rotate in three degrees of freedom). Additionally, a position sensor (PT1 Scaime™, Annemasse, France) was installed on the chain. The right stretcher was equipped with four in-house-built bi-directional (anteroposterior and vertical axes) strain-gauge transducers (measurement range: 1500 N; tolerance of overload: 750 N; linearity: 0.15%; hysteresis: 0.02%) to record the stretcher force of the subjects (Colloud et al., 2006). The stretcher formed a 45 deg angle with horizontal. The anteroposterior ($\mathbf{F}_x$) and vertical ($\mathbf{F}_y$) stretcher forces were calculated using the data provided by the stretcher transducers. All mechanical signals were sampled at 125 Hz with an acquisition device (DT 9804, Data Translation™, Malboro, MA, USA) and digitally stored using acquisition software (Data-Foundry version 5.1, Data Translation). A visual feedback of the power output and stroke frequency was displayed on a monitor placed in front of the subjects throughout the experimental protocol. The power displayed to the participants corresponded to the average power output over an entire cycle as depicted by Boyas et al. (Boyas et al., 2006).

Surface EMG was recorded from 23 muscles on the right side of the body in two separate sessions interspaced by 4 days to 1 week. The reproducibility of these 23 EMG profiles and muscle synergies was checked in another study (Turpin et al., 2011). The averaged Pearson's correlation coefficient (r) and the correlation coefficient at the maximum of the cross-correlation function (r_{max}) values over the three muscle synergies were 0.85±0.11 and 0.96±0.03 for the synergy vectors and the synergies activation coefficients, respectively. The recorded muscles in the first session were: biceps brachii (BB), biceps femoris (BF), brachioradialis (Br), erector spinae multifidus (ES), gastrocnemius lateralis (GL), gastrocnemius medialis (GM), gluteus maximus (GMax), latissimus dorsi (LD), rectus femoris (RF), semitendinosus (ST), soleus (Sol), tibialis anterior (TA), trapezius medius (TraM), vastus lateralis (VL) and vastus medialis (VM). In the second session, the following muscles were recorded: biceps brachii (BB), brachioradialis (Br), deltoideus posterior (Delt), flexor digitorum superficialis (FD), illiocostallis (Ilio), latissimus dorsi (LD), longissimus (Long), multifidus (ES), trapezius lower (TraL), trapezius medius (TraM), trapezius upper (TraU), triceps brachii (long head; TriL), triceps brachii (short head; TriS). For each muscle, a dry-surface electrode (Delsys DE 2.1, Delsys Inc., Boston, MA, USA; 1 cm interelectrode distance) was attached to the skin. Before electrode application, the skin was shaved and cleaned with a mixture of alcohol and ether to minimize impedance. Each electrode was placed longitudinally with respect to the underlying muscle fibers arrangement and all were located according to the recommendations of surface EMG for non-invasive assessment of muscles (SENIAM) (Hermens et al., 2000) for all the muscles, except for the LD (de Sèze and Cazalets, 2008), Br (Muceli et al., 2010) and FD (Zipp, 1982), which are not referenced by SENIAM. The wires connected to the electrodes were well secured with adhesive tape to avoid movement-induced artefacts. EMG signals were amplified (×1000) and digitized (6–400 Hz bandwidth) at a sampling rate of 1 kHz (Bagnoli 16, Delsys Inc.), and stored on a computer.

Data processing

EMG signals were filtered with a bandpass filter (fourth order Butterworth) between 20 and 400 Hz (filtfilt function of Matlab, the

Mathworks, version R2007b, Natick, MA, USA). A band-stop filter (48–52 Hz) was used to remove the 50 Hz noise. The mean activity level was calculated as the root mean square using the raw EMG signal over 15 consecutive non-normalized rowing cycles extracted at both the beginning (at ~7±3% of the T_{lim}; referred to as start) and the end (at ~93±12% of the T_{lim}; end) of the fatiguing exercise. For EMG profiles, linear envelopes for each muscle were obtained by low-pass filtering the fully rectified raw EMG signals with a 9 Hz low-pass filter (zero lag). The same 15 consecutive cycles used for the root mean square calculation were extracted at both the start and the end of the exercise. For each period (start and end), the EMG profiles were averaged to obtain a representative profile for each muscle. Then, as previously described (Hug et al., 2010; Hug et al., 2011), a non-negative matrix factorization was performed to extract muscle synergies. For this purpose, we implemented the Lee and Seung algorithm (Lee and Seung, 2001). Matrix factorization minimizes the residual Frobenius norm between the initial matrix and its decomposition, given as:

$$\mathbf{E} = \mathbf{WC} + \mathbf{e}$$

$$\min_{\substack{W\geq 0\\ C\geq 0}} \left\| \mathbf{E} - \mathbf{WC} \right\|_{FRO} , \quad (1)$$

where $\mathbf{E}$ is a p-by-n initial matrix (p is the number of muscles and n is the number of time points), $\mathbf{W}$ is a p-by-s matrix (s is the number of synergies), $\mathbf{C}$ is an s-by-n matrix, and $\mathbf{e}$ is a p-by-n matrix. $\|\bullet\|_{FRO}$ establishes the Frobenius norm, $\mathbf{W}$ represents the muscle synergy vectors matrix, $\mathbf{C}$ is the synergy activation coefficients matrix and $\mathbf{e}$ is the residual error matrix.

Although the muscle synergy vectors represent the relative weighting of each muscle within each synergy, the synergy activation coefficient represents the relative activation of the muscle synergy across the rowing cycle [for more details, see fig. 1 from Hug et al. (Hug et al., 2010)]. The algorithm is based on iterative updates of an initial random guess of $\mathbf{W}$ and $\mathbf{C}$ that converge to a local optimal matrix factorization [see Lee and Seung (Lee and Seung, 2001) for more details]. To minimize the risk of local minima, the algorithm was repeated ten times for each subject. The lowest cost solution was retained (i.e. minimizing the squared errors between original and reconstructed EMG profiles). The initial matrix $\mathbf{E}$ consisted of a cycle for each of the 23 muscles (the two sessions were pooled). $\mathbf{E}$ was thus a 23 row by 200 column matrix. Each line of $\mathbf{E}$ and $\mathbf{C}$ was normalized by its maximum value. Therefore, as done in previous studies (Hug et al., 2010; Hug et al., 2011; Torres-Oviedo et al., 2006), the degree of muscle activity was not taken into consideration for the comparison of muscle synergies. We iterated the analysis by varying the number of synergies between 1 and 23 and selected the least number of synergies that accounted for >90% of the variance accounted for (VAF) (Hug et al., 2010; Hug et al., 2011; Torres-Oviedo et al., 2006). VAF was defined as (Torres-Oviedo et al., 2006):

$$\mathrm{VAF} = 1 - \frac{\sum_{i=1}^{p}\sum_{j=1}^{n}(\mathbf{e}_{i,j})^2}{\sum_{i=1}^{p}\sum_{j=1}^{n}(\mathbf{E}_{i,j})^2} , \quad (2)$$

where i goes from 1 to p (the number of muscles), and j goes from 1 to n (the number of time points).

Cross-validation of the extracted muscle synergies

To verify the robustness of the extracted muscle synergies, we used a cross-validation procedure, as proposed by previous studies (Torres-Oviedo and Ting, 2010; Ting and Chvatal, 2010; Hug et al., 2011). First, we extracted muscle synergies from the entire data pooled across the start and the end of the exercise. Then, we compared these muscle synergies with those extracted independently from the start and the end. Second, we checked that the muscle synergies (in terms of muscle synergy vectors) extracted from the start (i.e. control condition herein) accounted for individual EMG profiles at the end (i.e. fatiguing condition). To do this, the muscle synergy matrix extracted from the start, $\mathbf{W}_{start}$, was held fixed in the algorithm and the activation coefficients matrix, $\mathbf{C}_{end}$, was free to vary. $\mathbf{C}_{end}$ was initialized with random values and iteratively updated until convergence. The EMG data matrix, $\mathbf{C}_{end}$, of the end condition was added to the algorithm with the following update rule (Lee and Seung, 2001):

$$(\mathbf{C}_{end})_{ij} \leftarrow (\mathbf{C}_{end})_{ij} \frac{(\mathbf{W}_{start}^{T}\mathbf{E}_{end})_{ij}}{(\mathbf{W}_{start}^{T}\mathbf{W}_{start}\mathbf{C}_{end})_{ij}} . \quad (3)$$

Normalization of the time scale

The rowing cycle corresponded to the period between two successive catches. The catches were identified by means of the minimum in the position curve of the handle, and the transition time to the maximum of this curve (Colloud et al., 2006). The rowing cycle was then divided into drive (or propulsive) and recovery phases. The drive phase ranged from 0 to 100% and the recovery phase from −100 to 0%, as in previous studies (Pollock et al., 2009). Drive and recovery phases were re-sampled with 100 time-points each. The complete stroke was therefore composed of 200 time-points. As recommended by Hug, this time-scale normalization was used for comparing EMG profiles, mechanical patterns and synergy activation coefficients, ensuring robust comparisons by avoiding a possible bias due to different transition times between subjects (i.e. different duration of the drive and recovery phases among subjects) (Hug, 2011).

Statistical analysis

Values are reported as means ± s.d. All statistical analyses were performed with the Statistica® software (Statistica® v.6, Statsoft, Maison-Alfort, France). Changes in the individual EMG profiles, mechanical profiles and synergy activation coefficients were assessed using two criteria: the lag time and the r_{max} coefficient. The lag times assess differences in the timing of the activations (i.e. the magnitude of the time shift between two profiles) and were calculated as the lag time at the maximum of the cross-correlation function obtained using the Matlab *xcorr* function for centered data (option 'coeff'). One-sample Student's *t*-tests were performed to evaluate the differences in the lag time values from a reference value (i.e. zero). r_{max} corresponds to the correlation coefficient at this maximum of the cross-correlation function and gives an indication on the similarity of the waveforms (i.e. the shape of the EMG, mechanical and synergy activation coefficients' profiles). Pearson's correlation coefficient (r) was used as a similarities criterion for the muscle synergy vectors. We also used the average of the principal angles to assess the similarity between the subspaces spanned by the synergies from the start to the end of the exhaustive test, using the algorithm described by Knyazev and Argentati (Knyazev and Argentati, 1999). ANOVA, with repeated measures, was used to compare subject's differences in time to exhaustion between test 1 and test 2, and to compare the amplitude of mechanical data and the mean EMG activity level between the start and the end of the exercise. Comparison of VAF between the start and the end was performed with an ANOVA with one factor (the number of

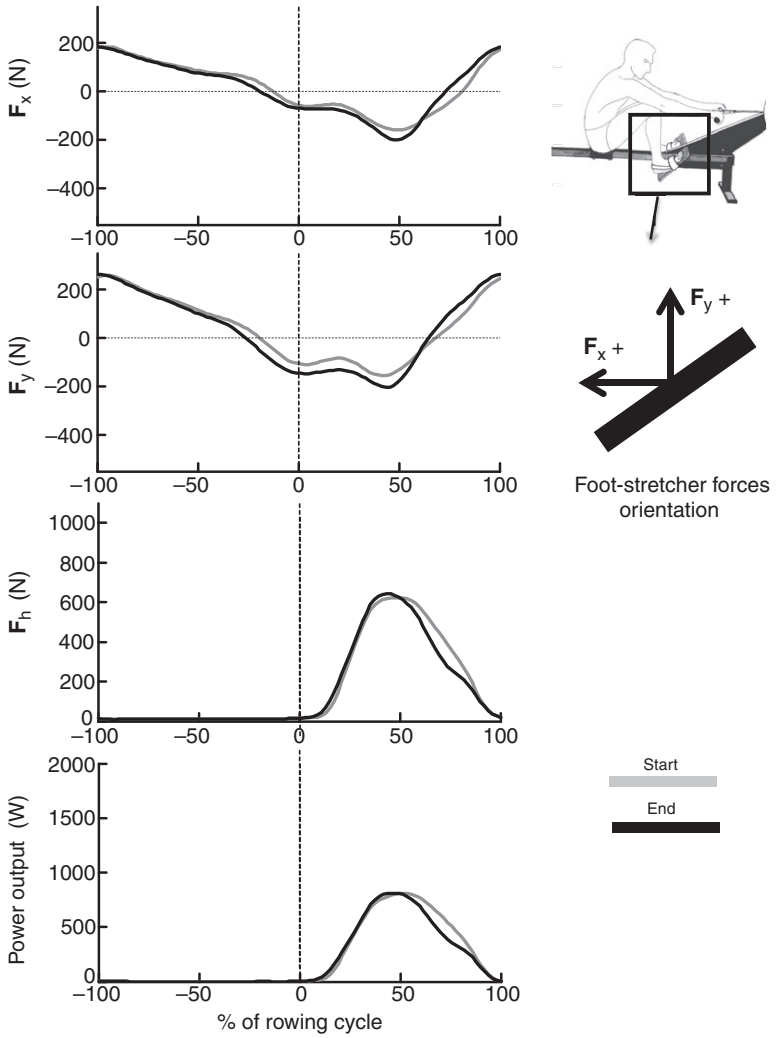

Fig. 1. Ensemble averaged mechanical profiles. The vertical dashed line indicates the recovery-to-drive transition. The recovery phase goes from –100 to 0% and the drive phase (or the propulsive phase) goes from 0 to 100%. The positive $\mathbf{F}_x$ points forward relative to the rower and the positive $\mathbf{F}_y$ points upward. N, newtons.

synergies extracted) and with a repeated measure (start and end). *Post hoc* analyses were performed with the Tukey's method. A *P*-value below 0.05 was considered statistically significant.

RESULTS

The limit time to exhaustion was not significantly different (P=0.96) between test 1 (424.7±119.4 s) and test 2 (423.5±120.4 s).

Mechanical variables

Subjects rowed at a MP output of 217.9±32.4 W, with a stroke frequency of 30.8±2.4 strokes min^{-1}. No significant difference in both power output and stroke frequency was found between the start and the end of the exhaustive test.

The amplitude of $\mathbf{F}_y$ significantly increased from 498.3±109.4 N to 586.9±111.9 N (P=0.005) between the start and the end of the exercise (Fig. 1). In contrast, the amplitude of $\mathbf{F}_x$ (P=0.14), $\mathbf{F}_h$ (P=0.40) and instantaneous power (P=0.83) did not change between the start and the end.

We observed a great similarity in the shape of the mechanical waveforms between the start and the end of the fatiguing exercise (Fig. 1). Mean r_{max} values were 0.94±0.05, 0.97±0.02, 0.99±0.01 and 0.99±0.01 for $\mathbf{F}_x$, $\mathbf{F}_y$, $\mathbf{F}_h$ and the instantaneous power, respectively. Significant time lags were only observed for $\mathbf{F}_h$ (–1.1±1.3% of the drive phase) and the instantaneous power (–1.1±1.3% of the drive phase), indicating an earlier shift of these mechanical profiles at the end of the fatiguing exercise.

EMG activity level and EMG profiles

As shown in Table 1, of the 23 muscles tested, 16 showed no change in their mean activity level, five showed a significant increase, i.e. VM (+25.0±19.9%; P=0.02), GMax (+99.1±110.4%; P=0.01), BF (+45.5±33.5%; P=0.002), ST (+42.8±41.0%; P=0.04) and TraM (+25.5±18.5%; P=0.02), and two muscles showed a significant decrease, i.e. GL (–16.5±29.9%; P=0.02) and Long (–22.4±32.5%; P=0.03).

The evolution of the EMG profiles between the start and the end of the exercise is depicted in Fig. 2. The similarity in the shape of the EMG profiles between the start and the end of the exhaustive exercise was high, with a mean r_{max} across all muscles of 0.90±0.11 (ranging from 0.80±0.19 to 0.97±0.02 for Long and VM, respectively; Table 1). Slight but significant time lags were found for three muscles: TA (–1.9±2.4%; P=0.04), LD (–4.2±4.3%; P=0.01) and Br (+5.8±6.6%; P=0.03). This indicates that the EMG profiles shifted earlier for TA and LD and shifted later for Br.

Muscle synergies

For each condition (i.e. start and end), the cumulative percentage of variance explained by each muscle synergy is depicted in Fig. 3. The ANOVA revealed a significant effect of time on the VAF, indicating a lower VAF at the end of the exhaustive test. More precisely, VAF was significantly lower at the end than at the start for 1, 2, 4, 6 and 8 muscle synergies (Fig. 3). Because a decrease in VAF could result from a decrease of the signal-to-noise ratio of

Table 1. Changes in electromyographic (EMG) profile and EMG activity level between the start and the end of the exhaustive exercise

Muscles	r_{max}	Time lag	Changes (% of start)
Tibialis anterior	0.87±0.06	1.9±2.4*	–1.5±19.1
Gastrocnemius lateralis	0.91±0.05	1.1±3.1	–16.5±29.9*
Gastrocnemius medialis	0.87±0.07	2.1±4.6	–14.4±20.2
Soleus	0.92±0.10	0.4±1.9	–2.6±16.6
Vastus lateralis	0.96±0.04	1.2±2.1	14.5±21.0
Vastus medialis	0.97±0.02	0.8±1.6	25.0±19.9*
Rectus femoris	0.84±0.15	2.0±2.7	5.6±32.6
Gluteus maximus	0.96±0.02	–0.3±2.5	99.1±110.4*
Biceps femoris	0.85±0.13	5.8±12.8	45.5±33.5*
Semitendinosus	0.82±0.11	1.7±2.2	42.8±41.0*
Erector spinae	0.86±0.15	–2.7±24.6	0.9±47.8
Longissimus	0.80±0.19	1.6±25.9	–22.3±32.5*
Illiocostallis	0.90±0.11	0.6±10.3	56.4±150.5
Latissimus dorsi	0.96±0.01	4.2±4.3*	15.4±80.3
Trapezius lower	0.88±0.11	–0.9±4.9	54.2±85.6
Trapezius medius	0.96±0.02	–1.2±6.5	25.5±18.5*
Trapezius upper	0.86±0.11	1.7±5.1	34.6±54.8
Deltoideus posterior	0.91±0.14	–0.4±8.4	–1.9±28.5
Biceps brachii	0.92±0.11	–6.4±11.9	13.1±41.4
Brachioradialis	0.92±0.11	–5.8±6.6*	–16.8±23.9
Flexor digitorum superficialis	0.94±0.04	0.6±4.0	17.1±31.3
Triceps brachii (long head)	0.95±0.03	4.4±7.3	30.1±32.9
Triceps brachii (short head)	0.93±0.06	–1.9±3.4	1.1±18.1

Values are means ± s.d.

r_{max} is the correlation coefficient at the maximum of the cross-correlation function and gives an indication of the similarity of the waveforms. A positive time lag indicates that the EMG pattern at the end has been shifted forward in the rowing cycle relative to the start. Changes in the mean EMG activity level between the start and the end are expressed as a percentage of the start value.

*Significant change between the start and the end of the exercise.

EMG data (d'Avella and Tresch, 2006) we calculated the Fano factor for each muscle (Fano factor=variance/mean) and evaluated its change with a repeated measure ANOVA. The Fano factor increased significantly for nine muscles (TA, VL, VM, Gmax, BF, ST, TraL, TraM and TriL) and showed no changes for the other muscles (P>0.05).

All the subjects reached 90% of VAF at three muscle synergies at the start (mean VAF: 92.4±1.5%) and eight of the nine subjects reached this threshold at the end (mean VAF: 91.0±1.8%). The subject who did not reach this threshold had a VAF of 87.0% for three synergies. Because this VAF was close to 90%, we decided for the subsequent analysis to extract three muscle synergies for all the subjects. Note that *post hoc* analysis failed to show any significant difference in VAF for three extracted muscle synergies (Fig. 3).

Fig. 4 depicts the ensemble averaged synergies activation coefficients and the muscle synergy vectors at the start and the end of the exhaustion test. Synergy no. 1 principally engaged the leg and trunk muscles and was associated with the beginning of the drive phase. Synergy no. 2 engaged the action of both the arm and trunk muscles and was associated with the second part of the drive phase. Synergy no. 3 mainly engaged TA, ST and TraU and was associated with the recovery phase. Note that we cannot exclude the possibility that we observed functionally merged synergies rather than individual synergies as previously suggested (Clark et al., 2009). This could explain why we found fewer muscle synergies than during other tasks such as walking [five synergies were reported by Ivanenko et al. (Ivanenko et al., 2004)].

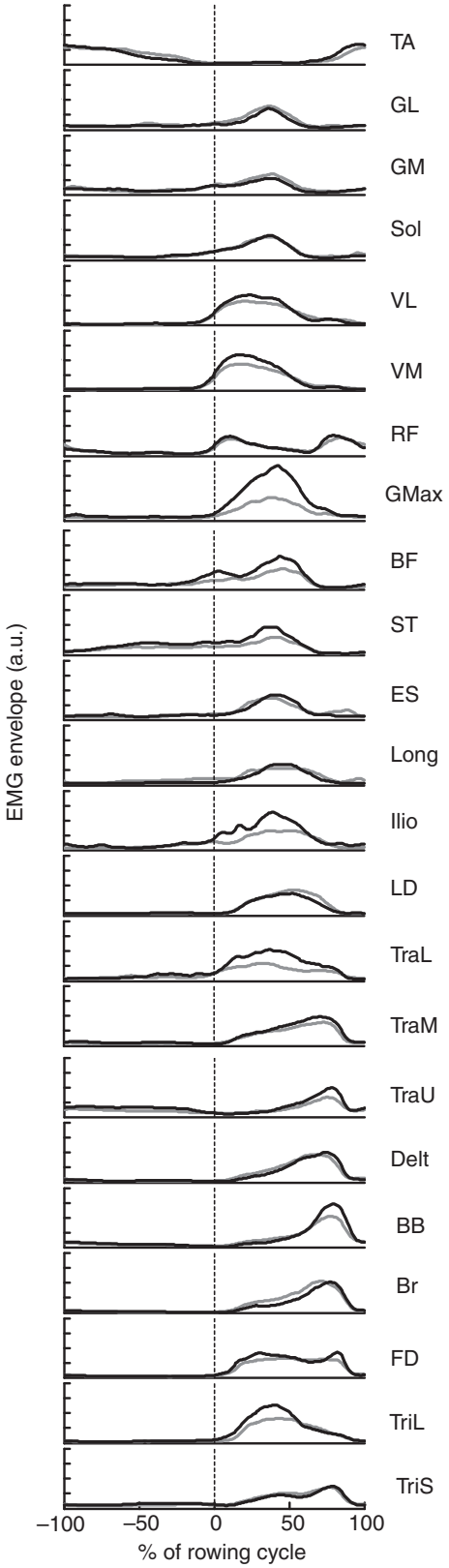

Fig. 2. Ensemble averaged electromyographic (EMG) profiles for the 23 recorded muscles. As in Fig. 1, the gray lines indicate the start and the black line the end of the exhaustion test. Both start and end EMG profiles are normalized by the mean EMG activity of the start, over the entire cycle. See the Materials and methods section for a list of muscle abbreviations. a.u., arbitrary units.

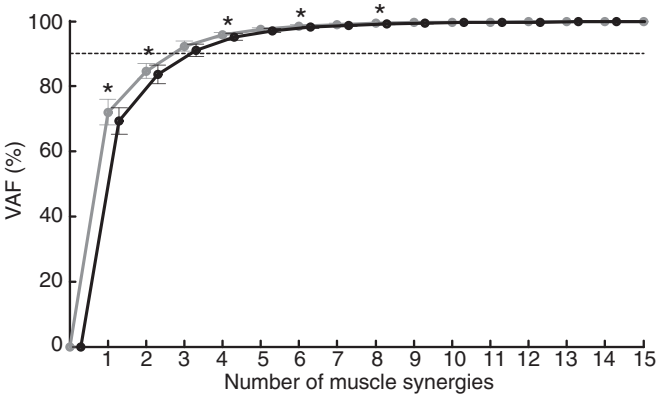

Fig. 3. Mean variance accounted for *versus* the number of extracted synergies. The horizontal line indicates the threshold used in this study, i.e. variance accounted for (VAF) >90%. As in Fig. 1, the gray line is for the start and the black line for the end of the exhaustion test. *Significant differences between the start and the end at a given number of synergies extracted.

Mean r_{max} values for the synergy activation coefficients between the start and the end of the exhaustive exercise were very high: 0.97±0.02, 0.95±0.07 and 0.90±0.05 for synergy no. 1, no. 2 and no. 3, respectively. A slight but significant earlier shift was found for synergy no. 3 (–2.2±2.5% of the recovery phase; P=0.03). Overall, these results indicate that the synergy activation coefficient were very consistent between the start and the end of the exercise.

For the synergy vectors, the mean correlation coefficients were 0.79±0.16, 0.87±0.10 and 0.89±0.06 for synergy no. 1, no. 2 and no. 3, respectively. Note that these r-values cannot be directly compared with the r_{max} values reported for the synergy activation coefficients. The cosine of the average of the principal angles was 0.93±0.03, indicating large similarities between the synergies subspace at three synergies extracted between the start and the end of the exhaustive test.

Cross validation of the similarity of muscle synergies between start and end

As explained in the Materials and methods, two additional analyses were performed to cross-validate the three extracted muscle synergies and their putative robustness during fatigue. First, when the muscle synergies were extracted from the data pooled across the start and the end, three synergies accounted for a mean VAF of 90.1±1.2%. Both the synergy activation coefficients and the muscle synergy vectors were very similar to those extracted independently from start and end (mean r_{max} ranged from 0.94 to 0.98 for synergy activation coefficients and mean r ranged from 0.92 to 0.98 for muscle synergy vectors; Table 2). The averaged cosine of the principal angles 0.95±0.05 and 0.96±0.03 for start+end *versus* start, and start+end *versus* end, respectively. According to Ting and Chvatal, this high similarity indicates that the nonnegative matrix factorization algorithm has more likely identified underlying physiological features that are consistent between the start and the end of the fatiguing exercise. Second, the muscle synergy vectors extracted from the start were sufficient to explain 84.1±2.6% of the variability of the dataset obtained at the end (i.e. with fatigue) (Ting and Chvatal, 2010).

DISCUSSION

The aim of the present study was to track the possible changes in muscle coordination during a submaximal constant load cyclic exercise performed until task failure. Although significant changes

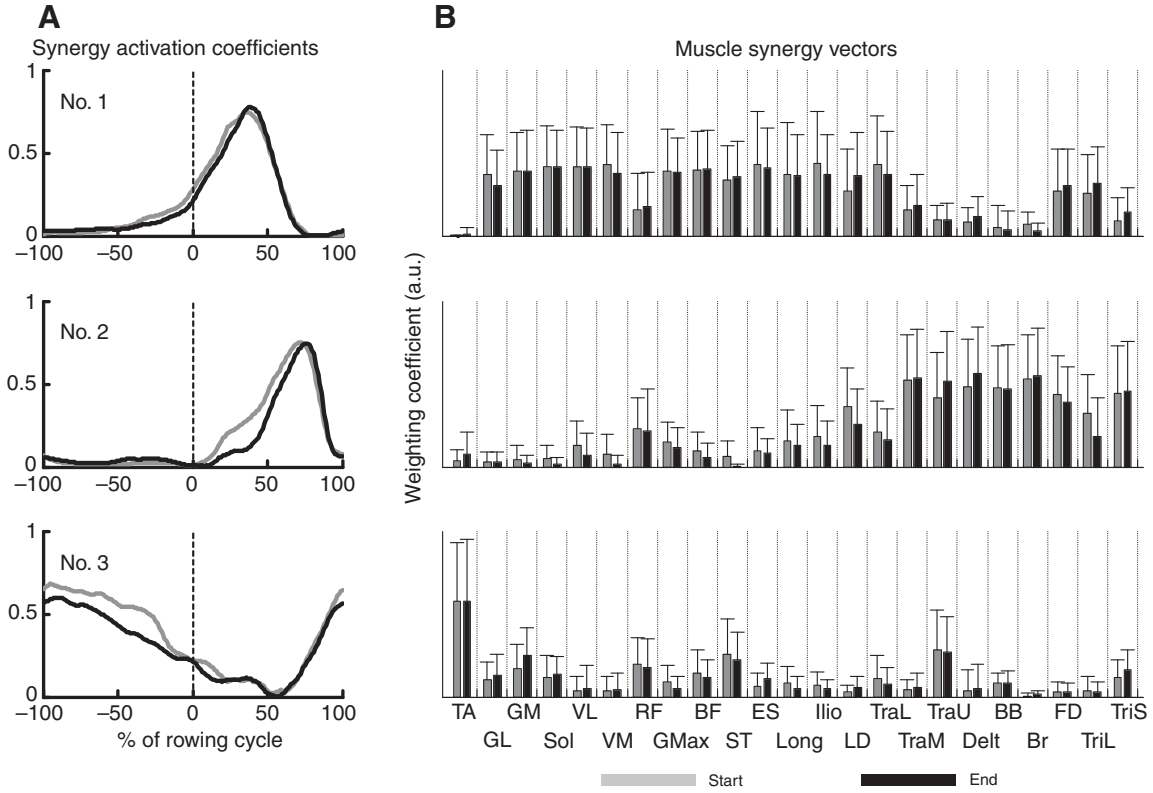

Fig. 4. Ensemble averaged synergies activations coefficients (A) and the corresponding muscle synergy vectors (B). The weighting coefficients of the synergy vectors are reported as means ± s.d. a.u., arbitrary units.

Table 2. Comparison between the muscle synergies extracted from the pooled dataset (start+end) and those extracted independently from start and end

	Synergy activation coefficients		Muscle synergy vectors
	r_{max}	Lag times (%)	r
Start+end *versus* start			
Synergy no. 1	0.98±0.02	2.2±3.9	0.92±0.10
Synergy no. 2	0.98±0.03	1.5±4.2	0.95±0.05
Synergy no. 3	0.98±0.01	–0.1±0.8	0.98±0.02
Start+end *versus* end			
Synergy no. 1	0.98±0.06	0.1±0.4	0.93±0.10
Synergy no. 2	0.97±0.03	–1.3±1.7	0.95±0.05
Synergy no. 3	0.94±0.08	0.5±1.1	0.95±0.02

Values are depicted as means ± s.d.

r, Pearson's correlation coefficient; r_{max}, the correlation coefficient at the maximum of the cross-correlation function and gives an indication of the similarity of the waveforms.

in muscle activity level were reported for seven of the 23 muscles, the results showed that the muscle activity profiles were stable. In addition, the same number (3) and similar muscle synergies were used throughout the fatiguing exercise (i.e. until task failure). This suggests that fatigue preferentially induces an adaptation in muscle activity level rather than a change in the overall modular organization of the muscle coordination (i.e. muscle synergies).

Changes in muscle activity level

To the best of our knowledge, the very few studies that have previously focused on EMG changes during a fatiguing rowing exercise recorded only a few muscles, e.g. three muscles in Caldwell et al., five muscles in Guével et al. and eight muscles in Pollock et al. (Caldwell et al., 2003; Guével et al., 2011; Pollock et al., 2009; Pollock et al., 2011). Thus, this is the first study that reports muscle coordination changes in numerous muscles (23 muscles aimed at representing the whole musculature) during a fatiguing rowing exercise, and more generally during a cyclic exercise.

During a fatiguing exercise, in case of no change in the kinematics of movement, an increase in EMG activity level associated with the same muscle force production is usually interpreted as a sign of neuromuscular fatigue (Petrofsky, 1979) as a result of (1) an additional recruitment of motor units to compensate for the decrease in the force of contraction that occurs in fatigued muscle fibers (Edwards and Lippold, 1956); (2) an increased in firing frequency and/or synchronization of motor unit recruitment (Gandevia, 2001); and/or (3) slowing of muscle fiber action potential conduction velocity (Linstrom et al., 1970). Consequently, as noted by Hug, in fatigued muscles a constant EMG activity level can be associated with a lower force production (Hug, 2011). Interestingly, in the present study, a slight diminution of $\mathbf{F}_h$ was observed at the end of the exercise during the second part of the drive phase (Fig. 1), during which mainly synergy no. 2 was activated. Nevertheless, the EMG activity level of the upper limb muscles, which are mainly represented in synergy no. 2, did not change. That could indicate that fatigue occurred in some of these upper limb muscles. In order to keep the MP output constant, one would expect that this decrease in force production would have been compensated for by other power-producer muscles, such as the hamstrings and gluteal that are known to be the main muscles of hip extension during the leg drive (Pollock et al., 2009). Our results, which showed a mean increase in EMG activity level of 99.1, 45.5 and 42.8% for GMax, BF and ST, respectively, seem to be in line with this assumption. Also, the significant increase in the amplitude of $\mathbf{F}_y$ during the first part of the drive phase is probably attributable to the increase in the activity level of these hip extensors, which tend to produce a greater proportion of force in the direction of the negative component of $\mathbf{F}_y$. Consequently, the increase activity of these muscles would be a compensatory strategy to counteract the lower production of fatigued muscles (i.e. the upper limb muscles) rather than a manifestation of muscle fatigue. This hypothesis seems to be confirmed by recent results (Pollock et al., 2011) suggesting the absence of fatigue in GMax and BF during a maximal 2000 m rowing exercise, similar to the exercise performed in the present study. Interestingly, such an intermuscular compensatory strategy has already been observed between the hip extensors and the quadriceps muscles during a fatiguing pedaling exercise (Dorel et al., 2009).

Changes in the modular organization of muscle coordination

Support for a modular organization of the motor system (i.e. the use of muscle synergies as units of control by the central nervous system) has recently come from the observation of low dimensionality in the motor commands (d'Avella and Pai, 2010). More precisely, decomposition algorithms have been used to show that most of the variation in the EMG activity patterns is explained by the combination of a small number of synergies, with respect to the numerous muscles involved. The results of the present study are in accordance with this observation. Indeed, they showed that the rowing patterns can be compactly represented because only three synergies could account for the majority of the variance (i.e. VAF>90%; Fig. 3). However, to date there is no direct evidence of the use of muscle synergies as units of control by the central nervous system (d'Avella and Pai, 2010; Tresch and Jarc, 2009).

Additional evidence for the muscle synergies would be the consistency of muscle synergies across various mechanical or physiological constraints (d'Avella and Pai, 2010). In this way, the present analysis of structure of the muscle synergies demonstrated a good robustness. Indeed, both synergy activation coefficients and the muscle synergy vectors were only slightly affected by fatigue. Overall, in addition to the results of the cross-validation procedure, this confirms that the muscle synergies were very robust throughout the fatiguing exercise. This consistency in the muscle synergies confirmed some results obtained from different postural tasks (Torres-Oviedo et al., 2006; Torres-Oviedo and Ting, 2010), different mechanical constraints (Hug et al., 2011) and in various behaviors in animals (d'Avella and Bizzi, 2005; d'Avella et al., 2003). In the rowing task, because of the different fiber type and/or different involvement of the various muscles participating in the same synergy (e.g. SOL and VL in synergy no. 1) one would have expected specific fatigue-induced changes in each of these muscles, leading to modifications in muscle synergies (in their number and/or composition). In this way, the fact that muscle synergies were very robust in a 'fatigue' condition could constitute additional evidence to confirm the hypothesis that the central nervous system produces movement through the flexible combination of groups of muscle synergies (Tresch and Jarc, 2009). In other words, the neural drive would select, activate and flexibly combine muscle synergies to produce a wide range of movements (Cheung et al., 2009a).

Methodological considerations

The determination of the number of muscle synergies is not a trivial matter and remains an open problem (Tresch et al., 2006). To ascertain that no change in the number of synergies occurred with fatigue, we compared the threshold method used here with a recent method used by Cheung et al. (Cheung et al., 2009b). In Cheung

et al.'s method, the VAF *versus* number of synergies curve is constructed from both the original EMG dataset and an unstructured EMG dataset generated by randomly shuffling the original dataset across time and muscles. The number of muscle synergies is then defined as the point beyond which the original slope drops below 75% of the surrogate slope. It corresponds to the number beyond which any further increase in the number of extracted synergies yields a VAF increase smaller than 75% of that expected from chance. This confirmed our results showing no change in the number of muscle synergies with fatigue, reinforcing the observation that, despite fatigue, the structure of the motor output, or its complexity, remained unchanged. However, the number of muscle synergies should be interpreted with caution. This should only be viewed as an index of complexity or compactness of the motor output (Clark et al., 2009), particularly in humans, where there has, as yet, been no direct evidence of the modularity of motor control.

In order to record many muscles, EMG activity was recorded during two different sessions. Thus, we had to perform our synergy analysis on averaged EMG patterns, as previously performed by Ivanenko et al. (Ivanenko et al., 2004). There was therefore no consideration of the cycle-to-cycle variability in these analyses. Using data published in a recent article (Hug et al., 2010), we compared the muscle synergies extracted from a set of 40 consecutive pedaling cycles and those extracted from the averaged patterns across these 40 cycles. Because we found very similar muscle synergies, we think that the extraction of muscle synergies from the averaged EMG pattern did not interfere in our conclusion.

We also checked that the number of averaged cycles did not influence the extracted muscle synergies. More precisely, by comparing the principal angles between the subspaces (see the Materials and methods) at three synergies extracted, we found great similarities across five, 10 and 15 cycles, for both the start and the end of the fatiguing exercise (principal angle >0.96).

Conclusions

The present results show that fatigue during a cyclic task preferentially induces an adaptation in muscle activity level rather than a change in the global temporal and spatial organization of the motor output, as revealed by the muscle synergies. Such independent control of the timing and amplitude of muscle activity has already been suggested by Weijs et al. (Weijs et al., 1999). Overall, it provides additional evidence that the muscle synergies are very stable, and thus they reflect neural control strategies rather than task constraints.

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