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No evidence of expertise-related changes in muscle synergies during rowing

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ABSTRACT

The purpose of the present study was to determine whether expertise in rowing is driven by a specific structure in muscular coordination. We compared seven experienced rowers and eight untrained (i.e., inexperienced) subjects during rowing on an ergometer. Both surface electromyography activity and mechanical patterns (forces exerted at the handle and the foot-stretcher) were recorded during a high intensity rowing exercise. A non-negative matrix factorization was applied to 23 electromyographic patterns to differentiate muscle synergies. Results showed that expertise was not associated with different dimensionality in the electromyographic data and that three muscle synergies were sufficient to explain the majority of the variance accounted for (i.e., >90% of the total variance) in the two populations. The synergies extracted were similar in the two populations, with identical functional roles. While the temporal organization of the propulsive synergies was very similar, slight differences were found in the composition of the muscle synergies (muscle synergy vectors) between the two populations. The results suggests that rowing expertise would not require the development of novel muscle synergies but would imply intrinsic synergies already used in different behaviors. Performance in rowing is more probably linked to adjustments in the mechanical output of the muscle synergies rather than to differences in the shape and timing of their activations.

1. Introduction

Muscle coordination is defined as "a distribution of activation or force among individual muscles to produce a given combination of joint moment" (Prilutsky et al., 1996). The emergence of specific muscle coordination is difficult to understand due to the high dimensionality of the muscular system. This problem of redundancy is referred to as the Bernstein's degrees of freedom problem (Bernstein, 1967). Muscle synergies have been defined as systematic co-variations of activation among various muscles (Torres-Oviedo and Ting, 2007; Bizzi et al., 2008; Tresch and Jarc, 2009) and thus, can be considered as degrees of freedom that are controlled as individual units (Chiel et al., 2009). These synergies can be identified from electromyographic (EMG) patterns recorded from numerous muscles via an algorithm that has two components (Tresch et al., 2006; Hug et al., 2011; Hug, 2011): a fixed component (referred to as "muscle synergy vectors" in this report), which represents the relative weighting of each muscle within each synergy; and, a time-varying component (referred to as "synergy activation coefficient" in this report) which represents the relative activation of the muscle synergy. Results from numerous studies extracting these 'synchronous synergies' have indicated their robustness across different biomechanical constraints (Hug et al., 2011; Torres-Oviedo et al., 2006; Ajiboye and Weir, 2009; Torres-Oviedo and Ting, 2010a,b), and across subjects (Hug et al., 2010). These studies provide compelling evidences that the muscle coordination is constructed by stable and functional muscle synergies, reducing the number of output patterns that the nervous system must specify for a large number of muscles. Therefore, it would simplify the control of complex movements and skill acquisition (Poggio and Bizzi, 2004).

There is substantial evidence showing that training can induce modifications of muscular coordination (for review, see Carson, 2006). Since changes have been observed at both the cortical and spinal levels (Jensen et al., 2005; Adkins et al., 2006; McNamara et al., 2007; Nielsen and Cohen, 2008), where synergies are expected to be encoded (Holdefer and Miller, 2002; Poppele and Bosco, 2003; Cheung et al., 2009), one would presume that muscle synergies would be modified by training. However, a few studies have focused on the effects of training on the muscle synergies. Kargo and Nitz (2003) have shown in animals that early adaptations in a reach-to-grasp task occur by the modulation of both the synergy activation coefficients, and muscle synergy vectors. In humans, by analyzing the evolution of the covariance structure of various muscles in a postural task after five days of training,

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Asaka et al. (2008) showed alterations of the synergy vectors. These results support the view that synergies are variable and adaptable with practice.

Nevertheless, the extent of training-induced changes in muscle synergies during a cycle task involving numerous muscles in humans is not known. Thus, we designed the present study to test how muscle coordination would be influenced by a high volume of training. We studied the task of rowing which involves numerous muscles and requires the skilled coordination of the upper and lower limb (Smith and Spinks, 1995; Soper and Hume, 2004). Contrary to other tasks usually studied in the literature, such as pedaling, running or walking, one can easily find fully inexperienced subjects who have never before performed rowing. Thus, it seemed to be an ideal task to compare untrained to experienced subjects. We hypothesized that expertise in rowing would result in specific muscle synergies that could be discriminated between trained and untrained subjects. To test this hypothesis, we recorded surface EMG activity in 23 muscles during a rowing exercise performed on an ergometer in both untrained subjects and experienced rowers. We used a non-negative matrix factorization algorithm to identify the muscle synergies.

2. Materials and methods

2.1. Subjects

Eight male untrained subjects (UNT, age 24 ± 5 years, height 179 ± 9 cm, body mass 70 ± 6 kg), and seven male experienced rowers (EXP, age 25 ± 3 years, height 187 ± 4 cm, body mass 81 ± 11 kg) volunteered to participate in this study. UNT had no prior experience with rowing (neither in ergometer nor on water). EXP had 10.4 ± 4.2 years of competitive Olympic rowing experience. EXP trained for approximately 11.6 ± 3.2 h per week at the time of the study, and had performed an all-out 2000 m rowing test in 390 ± 15 s in the same year of this experiment. All subjects were informed of the possible risk and discomfort associated with the experimental procedures prior to giving their written consent to participate. The experimental design of the study was approved by the local Ethical Committee and was carried out in accordance with the Declaration of Helsinki.

2.2. Procedure

The tests were divided in two identical sessions to allow for the measurement of the 23 muscles. One week before the first session, UNT performed an all-out 2000 m rowing test on an ergometer to assess their mean power (MP) over this distance. For EXP, the MP was taken from training data (i.e., time to perform a 2000 m rowing) before the official experiments. The estimate of the MP in Watts was determined according to the following equation:

$$MP = 2.8\left(\frac{2000}{t_{2000}}\right)^3 \quad (1)$$

where t_{2000} is the time to perform the 2000 m (in seconds). This formula is based on the power required to keep a boat moving at a constant velocity, 2.8 being a typical drag coefficient for a racing shell (Gordon, 2003).

Subjects were first asked to perform a standardized warm-up consisting of 5-min of rowing at a self-paced intensity following 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 per minute. Afterwards, subjects performed a constant-load test executed at their mean power until exhaustion. They were asked to keep a constant stroke frequency fixed between 28 and 32 strokes per minute. For the purposes of this study, only the first minute (between 30 and 60 s) was taken into consideration for subsequent analysis of EMG/mechanical patterns and for muscle synergies extraction. That reduced the chance of fatigue influencing EMG and mechanical patterns.

In order to test the reproducibility of the EMG patterns and muscle synergies, five out of the eight untrained subjects were studied twice, with an interval of several weeks. For this purpose, they only performed a 2-min constant-load test performed at 90% of the MP.

2.3. Materials and data collection

Subjects exercised on a rowing ergometer (Rowperfect, Australia) with a fixed stretcher mechanism. As described previously (Colloud et al., 2006), it was instrumented to measure the force produced at the handle with a strain gauge force transducer (SM-1000N; Interface™, measurement range: 1000 N, tolerance of overload: 500 N, linearity: 0.03%; hysteresis: 0.02%) that was placed in series with the chain and the handle using a ball and socket joint (free to rotate in three degrees of freedom). In addition, a position sensor (PT1 Scaime™, France) was installed on the chain. These two mechanical sensors were previously calibrated, and permitted measurement of the power developed by the subject. The right stretcher was equipped with four bi-directional (antero-posterior 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 forms an angle of 45 degrees with the horizontal. The antero-posterior and vertical stretcher forces were calculated using the data provided by the stretcher transducers. All of these mechanical signals were sampled at 125 Hz by an acquisition device (DT 9804, Data Translation™, USA) and digitally stored using an acquisition software (Data-Foundry version 5.1, Data Translation™, USA). A visual feedback of the MP and stroke frequency was displayed on a monitor placed in front of the subjects throughout the experimental protocol. The power displayed to the participant represents the average of power over an entire cycle (Boyas et al., 2006).

Surface EMG was recorded from 23 muscles on the right side of the body. They were recorded in two separate sessions interspaced by four days to one week (see Table 1 for details about the recorded muscles). Five out of the 23 muscles were recorded during both of the two sessions in order to check the consistency of muscle coordination between the two sessions. For each muscle, a dry-surface electrode (Delsys DE 2.1, Delsys Inc, Boston, USA; 1 cm interelectrode distance) was attached to the skin. Prior to 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 SENIAM (Surface EMG for Non-Invasive Assessment of Muscles) (Hermens et al., 2000) for all of the muscles, except for the muscles *latissimus dorsi* (LD), *brachioradialis* (Brad), and *flexor digitorum* (FD) which are not referenced by SENIAM. For LD, the electrode was placed as recommended by de Sèze and Cazalets (2008) i.e., over the muscular curve at T12 and along a line connecting the most posterior point of the posterior axillary fold and the S2 spinous process. For Brad, the electrode was positioned as done by Muceli et al. (2010) i.e., 1/6 of the distance from the midpoint between the cubit fossa to the lateral epicondyle to the styloid process of the ulna. For FD, the electrode was positioned at 1/5 of the distance from the medial humeral epicondyle to the styloid process of the ulna (Zipp, 1982). The wires connected to the electrodes were well secured with adhesive tape to avoid movement-induced artifacts. EMG signals were amplified (×1000; common mode rejection ratio; CMRR = 92 dB; input impedance >10^{15} Ω) and digitized

Table 1
Muscles recorded for each session.

Muscles	Session 1	Session 2
Tibialis anterior (TA)	x	
Gastrocnemius lateralis (GL)	x	
Gastrocnemius medialis (GM)	x	
Soleus (Sol)	x	
Vastus lateralis (VL)	x	
Vastus medialis (VM)	x	
Rectus femoris (RF)	x	
Gluteus maximus (Gmax)	x	
Biceps femoris (BF)	X	
Semitendinosus (ST)	x	
Erector spinae (ES)	x	x
Longissimus (long)		x
Illiocostallis (Ilio)		x
Latissimus dorsi (LD)	x	x
Trapezius lower (TraL)		x
Trapezius medius (TraM)	x	x
Trapezius upper (TraU)		x
Deltoideus posterior (Delt)		x
Biceps brachii (BB)	x	x
Brachioradialis (Brad)	x	x
Flexor digitorum superficialis (FD)		x
Triceps brachii (long head – TriL)		x
Triceps brachii (short head – TriS)		x

For the five muscles recorded twice, we retained the session for which the muscle depicted the best signal (i.e., best signal-to-noise ratio) for both the individual muscle patterns calculation and the muscle synergies extraction.

(bandwidth of 6–400 Hz) at a sampling rate of 1 kHz (Bagnoli 16, Delsys Inc., Boston, USA).

2.4. Muscle synergies extraction

EMG signals were filtered with a bandpass filter (4th order Butterworth) between 20 and 400 Hz (filtfilt function of Matlab, the Mathworks, version R2007b, USA). A band-stop filter (between 48 and 52 Hz) was used to remove the 50 Hz noise. Linear envelopes of each muscle were obtained by low-pass filtering the fully rectified EMG signals with an 8 Hz low-pass filter (zero lag) as recommended by Shiavi et al. (1998). Each rowing cycle (period between two successive catches, Fig. 1) was interpolated to 200 time points. A set of 15 consecutive cycles was averaged to obtain a representative pattern for each muscle, and then was normalized by its maximum value. Then, as previously described (Hug et al., 2010), 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:

$$\mathbf{E} = \mathbf{WC} + \mathbf{e} \tag{2}$$

$$\min_{\substack{W\geq 0\\ C\geq 0}} \|\mathbf{E} - \mathbf{WC}\|_{\mathrm{FRO}}$$

where **E** is a *p*-by-*n* initial matrix (*p* = number of muscles and *n* = number of time points), **W** is a *p*-by-*s* matrix (*s* = number of synergies), **C** is an *s*-by-*n* matrix and *e* is a *p*-by-*n* matrix. $\|\bullet\|_{FRO}$ establishes the Frobenius norm, **W** represents the muscle synergy vectors matrix, **C** is the synergy activation coefficients matrix and **e** is the residual error matrix. The algorithm is based on iterative updates of an initial random guess of **W** and **C** that converge to a local optimal matrix factorization [see (Lee and Seung, 2001) for more details]. To avoid local minima, the algorithm was repeated 10 times for each subject. The lowest cost solution was retained (i.e., minimizing the squared errors between original and reconstructed EMG patterns). The initial matrix **E** consisted of a cycle for each of the 23 muscles (the two sessions were pooled). **E** was thus a 23 rows by 200 columns matrix. Each line of **E** and **C** was normalized by its maximum value. For each subject we iterated the analysis by varying the number of synergies between 1 and 23, and then selected the least number of synergies that accounted for >90% of the Variance Accounted For (VAF) (Torres-Oviedo et al., 2006; Hug et al., 2010, 2011). We ascertained that additional synergy did not increase VAF by >5% (Clark et al., 2010).

For the purpose of highlighting the functional role of the synergies extracted, we also applied matrix factorization to an augmented matrix including both mechanical and EMG data, with a procedure previously described (Torres-Oviedo et al., 2006). The positive and negative components of the mechanical variables have been separated to create new variables, which were all positive. For instance, the horizontal component of the foot-stretcher force (Fx) was divided into Fx− and Fx+. Fx− was taken as positive by using its absolute value. The augmented matrix was: [EMG|Fx − Fx + Fy − Fy + Fh]. Each mechanical variable was a 200×1 vectors and EMG was the initial EMG variable used to extract the muscular synergies.

2.5. Variance calculation

Variance Accounted For (VAF) was defined as Torres-Oviedo et al. (2006):

$$\mathrm{VAF} = 1 - \frac{\sum_{i=1}^{p}\sum_{j=1}^{n}(\mathbf{e}_{i,j})^2}{\sum_{i=1}^{p}\sum_{j=1}^{n}(\mathbf{E}_{i,j})^2} \tag{3}$$

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

2.6. Normalization of the time scale and cycle definition

The rowing cycle corresponds to the period between two successive catches (Fig. 1). The catches are identified by means of the minimum in the position curve of the handle, and the transition time to

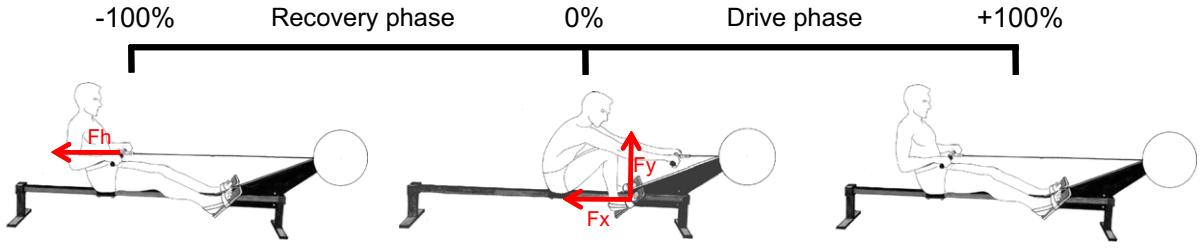

Fig. 1. Definition of the rowing cycle. The rowing cycle corresponds to the period between two successive catches. The rowing cycle has been divided into drive (or propulsive) and recovery phases. The drive phase goes from 0 to 100% and the recovery phase from −100% to 0%, as done in previous studies (Janshen et al., 2009; Pollock et al., 2009). Fx, horizontal component of the foot-stretcher force in Newtons (*N*); Fy, vertical component of the foot-stretcher force (*N*); Fh, handle force (N).

the maximum of this curve (Colloud et al., 2006). The rowing cycle has been divided into drive (or propulsive) and recovery phases (Fig. 1). The drive phase goes from 0 to 100% and the recovery phase from −100% to 0%, as done in previous studies (Janshen et al., 2009; Pollock et al., 2009). Drive and recovery phases have been re-sampled to 100 time-points each. This time scale normalization has been used for the comparison of the EMG patterns, mechanical patterns and synergy activation coefficients ensuring robust comparisons by avoiding the possible bias due to different transition times between subjects (i.e., different duration of the drive and recovery phases among subjects) (Hug, 2011). This normalization procedure was applied after the muscle synergy extraction.

2.7. Intra-group and inter-group similarities

For the purpose of comparing the shape (i.e., waveform) of individual EMG patterns, synergy activation coefficients and muscle synergy vectors, the Pearson's correlation coefficient (r) between EMG patterns was used. As done in previous studies (Ivanenko et al., 2004; Cappellini et al., 2006), statistics on r were based on Z-transformed values. An intra- and an inter-group index of similarity were calculated (Fig. 2). The intra-group index of similarity corresponds to the averaged correlation coefficient between each pair of subjects within the same group. It was used as an indicator of the waveform consistency within each group. The inter-group index of similarity corresponds to the averaged correlation coefficient between each pair of subjects arising from different groups (Fig. 2). It was used as an indicator of the waveform consistency between the two populations as already done in previously published works (Ivanenko et al., 2005; Torres-Oviedo et al., 2006).

Differences in the timing of the activations (i.e., the magnitude of a time shift between EMG patterns or synergy activation coefficients) 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").

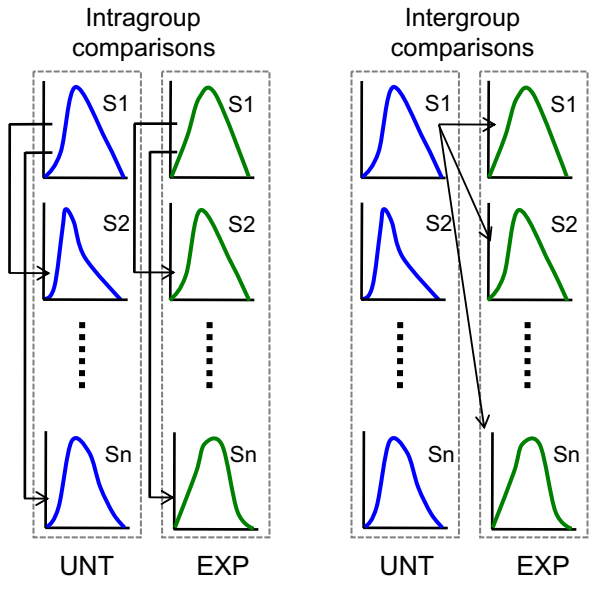

Fig. 2. Determination of the intra- and inter-group similarity indices. The intra-group index is the Pearson coefficient of correlation (r) calculated between each pair of subjects within a group (left side). For each group we therefore had $n \times (n-1)/2$ "r" values. This intra-group similarity index is a measure of the consistency of the patterns (i.e., the shape of EMG patterns and synergy activation coefficients) across subjects. Inter-group comparison (right side) was calculated as the Pearson "r" between each pair of subjects from different groups. We had therefore n^2 inter-group values. S, subject; UNT, untrained subjects; EXP, experienced subjects.

2.8. Statistical analysis

All statistical analyses were performed with Statistica (StatSoft, France). A Student's t-test was used to compare mean power output, stroke rate, and intra-group indices of similarity between the two populations. The evolution of VAF with the number of synergies extracted was compared between the two populations using an analysis of variance for repeated measures. In order to compare individual muscle weightings between groups, a one-way ANOVA has been performed on each of the muscle synergy vectors independently, taking each muscle as an independent variable. Orthogonal contrasts have been used as the post hoc test. A $p \leqslant 0.05$ was considered indicative of statistical significance.

3. Results

3.1. Mechanical data

The rowing exercise was performed at a significantly higher mean power output for EXP compared to UNT (380 ± 45 W vs. 217 ± 30 W, respectively; $p < 0.001$). Since the instructions were respected, no difference was logically found between the two populations concerning the stroke rate (30.2 ± 1.5 vs. 30.1 ± 1.2 strokes min^{-1} for EXP and UNT, respectively; $p = 0.923$).

Fig. 3 depicts the ensemble averaged (±SD) of the mechanical patterns for the two populations. EXP showed significantly higher intra-group similarities (r ranged from 0.95 to 0.98) compared to that for UNT (ranged from 0.85 to 0.96) for all mechanical variables (Table 2). Amplitude of the mechanical variables showed evident differences between the two populations, whereas their shape showed great similarities (Fig. 3). In fact, high values of the inter-groups index of similarity were found (ranged from 0.83 to 0.93; Table 2). All values were >0.8, which demonstrated that the two populations produced a similar pattern for each mechanical variable. However, the distribution of the time lags between each pair of experienced/untrained subjects (Fig. 4) revealed a slight but positive shift (indicating that EXP mechanical patterns are shifted backward compared to the UNT ones) of approximately 4%, visible in Fig. 3.

3.2. Individual EMG patterns

The averaged (±SD) EMG patterns for the 23 muscles investigated are depicted in Fig. 5. We found a low intra-group variability ($r > 0.8$) in the shape of the EMG patterns for most of the muscles, however, heterogeneity was evident for other muscles (Table 3). In fact, seven out of the 23 muscles had intra-group similarities< 0.8 for EXP and 15 out of 23 for UNT. The intra-group similarity was significantly higher for EXP than UNT for 10 out of the 23 muscles (i.e., GL, RF, BF, ST, ES, Long, Ilio, BB, Br and TriL). These differences were associated with low intra-group similarities for UNT (ranged from 0.38 to 0.67). The mean intra-group similarity among all muscles was 0.79 ± 0.15 for EXP and 0.69 ± 0.12 for UNT. UNT showed

Table 2
Intra and inter-group indices of similarity for each mechanical variable.

	Intra-group similarity			Inter-group similarity
	EXP	UNT	p	
Fx	0.95 ± 0.03	0.85 ± 0.13	**0.001**	0.83 ± 0.15
Fy	0.97 ± 0.01	0.93 ± 0.03	**0.000**	0.93 ± 0.03
Fh	0.98 ± 0.02	0.96 ± 0.04	**0.042**	0.90 ± 0.08
Power	0.98 ± 0.02	0.96 ± 0.04	**0.038**	0.89 ± 0.08

Values are expressed as mean ± SD. Significant differences between the two populations are indicated in bold. Fh: handle force; Fx: horizontal component of the foot-stretcher forces and Fy: vertical component of the foot-stretcher forces. EXP, experienced rowers; UNT, untrained subjects.

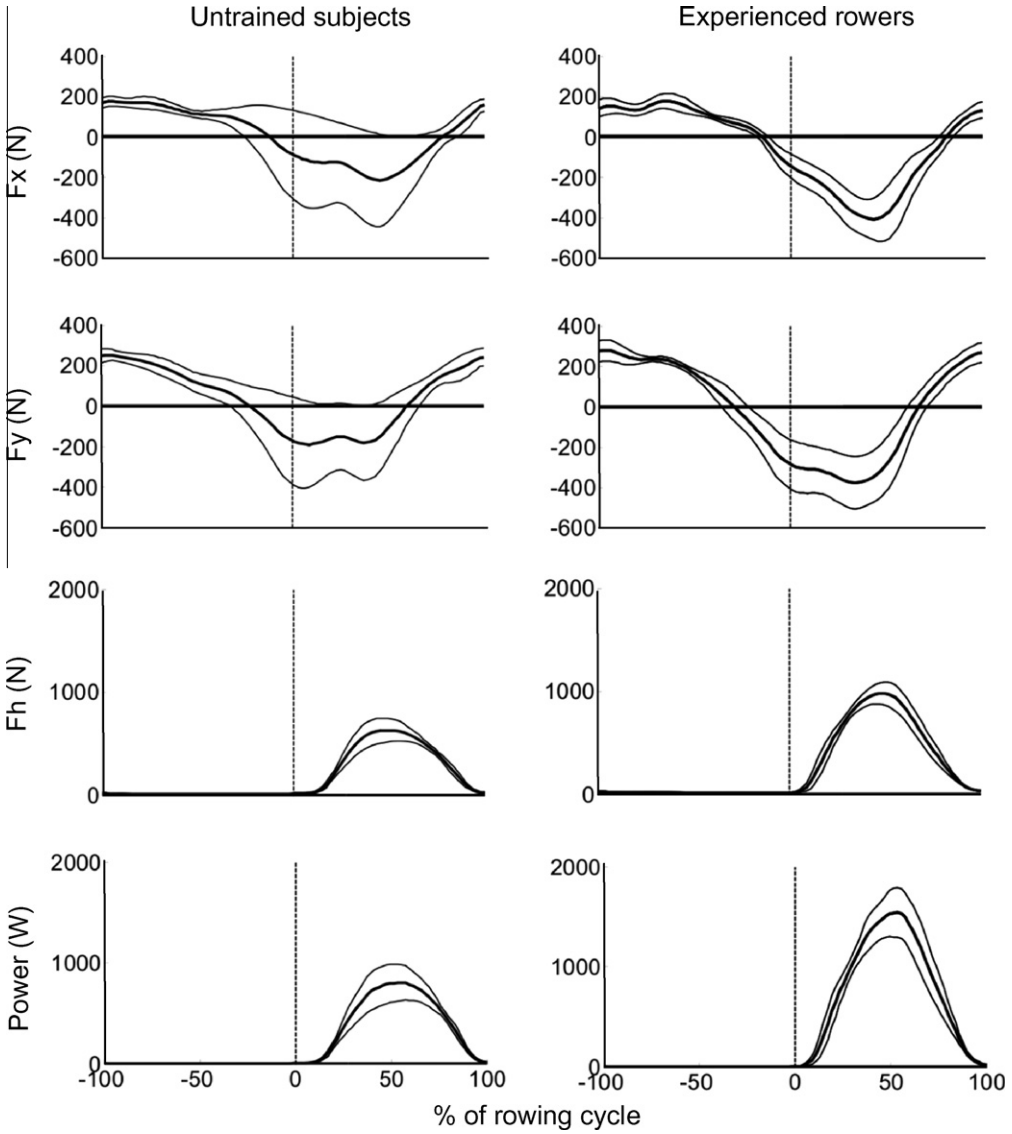

Fig. 3. Ensemble averaged (±SD) mechanical pattern for the two populations. The vertical dashed line indicates the transition between the recovery and drive phases (−100% to 0% represents the recovery phase and 0% to 100% represents the drive phase). Fx, horizontal component of the foot-stretcher force in Newtons (*N*); Fy, vertical component of the foot-stretcher force (*N*); Fh: handle force (N); power, instantaneous power (*W*).

significantly greater intra-group similarity than EXP for TA only ($p < 0.001$).

The inter-group index of similarity averaged across all muscles was 0.68 ± 0.15, indicating that there was not a high similarity in the shape of the EMG patterns between EXP and UNT. However, the shape of some muscles appeared to be very similar ($r > 0.8$) between the populations (e.g., VL, VM and FD), whereas some differences for other muscles (e.g., RF, ST, TrapL and TrapL) were observed (Table 3). To explore the origin of these differences, we have calculated the distribution of the time lags between each pair of experienced/untrained subjects. No evident time lag was found for all of the muscles studied, with a roughly normal distribution of the time lags. These data indicate that the inter-group differences were linked to difference in the shape (i.e., waveform) of EMG patterns rather than to differences in muscle activation timings (i.e., time shift).

3.3. Number of muscle synergies

No significant difference ($p = 0.937$) was found between the two populations concerning the evolution of VAF with respect to the number of muscle synergies showing that both populations possess the same dimensionality in their EMG data. In both groups, using the criteria previously described, three synergies were identified for all subjects that accounted for 92.5 ± 1.4% (ranged from 90.7% to 94.8%) of the total VAF for EXP and 93.1 ± 1.5% (ranged from 90.2% to 95%) of the total VAF for UNT. Thus, three muscle synergies can reproduce initial EMG patterns for all subjects.

Muscle synergy vectors and synergy activation coefficients were very similar across all subjects except for one expert rower who did not express the same third synergy. Consequently, for the similarities index calculation referring to synergy #3, only six experts were included.

3.4. Functional role of muscle synergies

The three muscle synergies (both synergy activation coefficients and muscle synergy vectors) are depicted in Fig. 6. By applying matrix factorization to an augmented matrix including both mechanical and EMG data, we found that the three muscle synergies well explain the variance of the mechanical data (VAF of each

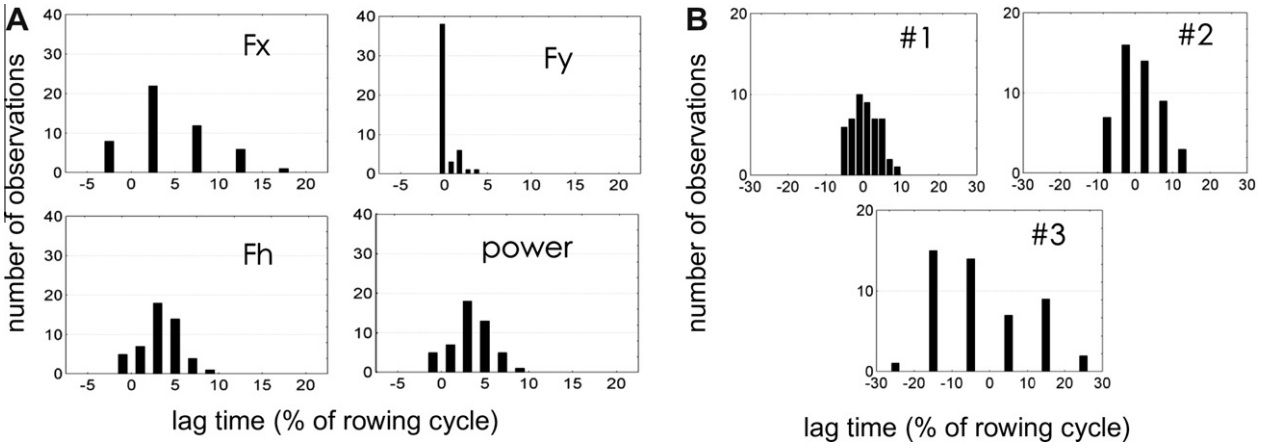

Fig. 4. Lag time distribution between EXP and UNT for the mechanical data (A) and the synergy activation coefficients (B). The time lags were calculated for each pair of experienced/untrained subjects. A positive bias indicates a positive delay of the experienced relative to the untrained subject's waveforms. Fx, horizontal component of the foot-stretcher force; Fy, vertical component of the foot-stretcher force; Fh, handle force; power, instantaneous power. # 1,# 2 and # 3 indicate the number of the muscle synergies.

mechanical data >90% of VAF for each subject). Fig. 7 depicts the weighting coefficients associated with the three muscle synergy vectors for mechanical variables in addition to the VAF for each variable. Muscle synergies were highly similar for both extractions (i.e., EMG only or EMG +mechanical variables; $r > 0.8$) and the functional roles of the synergies described below, inferred from the results of Fig. 7, were the same for the two populations:

Synergy #1: This synergy engages principally the leg and the trunk muscles. It is active before the beginning of the drive, and has its peak of activity before the middle of the drive phase. Overall, this synergy is associated with the beginning of the propulsion phase.

Synergy #2: This synergy engages the action of both the arm and the trunk muscles and is active during the second part of the drive phase.

Synergy #3: This synergy mainly engages TA and TraU. For some subjects (either EXP or UNT), RF and hamstring muscles are also engaged. This synergy is associated with the recovery phase.

3.5. Synergy activation coefficients

The synergies activation coefficients for EXP and UNT are depicted in Fig. 6. Despite a high intra-group similarity of synergy #1 for both groups ($r > 0.86$), EXP showed a significantly higher intra-group similarity than UNT ($p = 0.05$; Table 4). In contrast, UNT had a significantly greater intra-group similarity than EXP for synergy #3 ($p = 0.013$; Table 4). No significant difference was found for synergy #2.

As depicted in Table 4, the inter-group similarity for synergies #1 and #2 was relatively high (0.91 and 0.76, respectively), whereas the synergy #3 showed a lower inter-group similarity (0.51). It suggests that the synergy activation coefficients of synergies #1 and #2 were not different between the two groups, whereas they differed between groups for synergy #3. It is certainly due to the presence of a second burst of activity in EXP during the transition between the recovery and the drive phase (Fig. 6). However, the inter-group similarity is not much lower than the intra-group similarity for this third synergy. It may indicate that the inter-subjects variability would be not specific to the expertise for this synergy.

3.6. Muscle synergy vectors

The intra-group and inter-group indices of similarity of the muscle synergy vectors are depicted in Table 4. There was globally less intra- and inter-group similarity in the synergy vectors than in the synergies activation coefficients. No statistical difference was found between EXP and UNT concerning the intra-group similarity. For both EXP and UNT, the intra-group similarity was acceptable (ranged from 0.64 to 0.75).

The level of similarity between the two populations is in a similar range (ranged from 0.62 to 0.72), suggesting no major effect of the expertise level on the overall muscle synergy vectors. A significantly higher weighting of four upper body muscles has been found (Fig. 6): Delt, Br and TriL ($p = 0.001$, 0.001 and 0.006, respectively) and LD ($p = 0.02$) in synergy #1 for EXP compared to UNT, whereas the weighting of TraL was lower ($p = 0.005$) for EXP compared to UNT in synergy #1. In synergy #2, the weighting of Br was higher ($p = 0.014$) for EXP compared to UNT whereas the weighting of TriL and LD were lower for EXP compared to UNT ($p = 0.016$ and 0.024, respectively). No significant difference in the weighting coefficients was found for synergy #3.

3.7. Reproducibility

The correlation coefficient (between the two tests) averaged across all of the muscles was high, i.e., 0.90 ± 0.09 (ranged from 0.73 to 0.98). We found a near zero temporal shift, i.e., −0.06 ± 2.3% of the rowing cycle between test and re-test. Only two muscles (TraU and ST) showed an averaged r value lower than 0.8, i.e., 0.78 ± 0.18 and 0.73 ± 0.20, respectively. Therefore, the shape of the EMG patterns showed a high similarity (i.e., a good reproducibility) between the two tests.

The synergy activation coefficients showed a higher reproducibility than the muscle synergy vectors. The averaged correlation coefficients over the three muscle synergies were 0.93 ± 0.07 for the synergies activation coefficients and 0.85 ± 0.11 for the synergy vectors. We also found relatively low time lags between the two tests for the synergy activation coefficients (synergy #1: 0.7 ± 1.3%; synergy #2: 0.6 ± 2.5%; synergy #3: 1 ± 3.7% of the rowing cycle). Overall, these values of similarity between the two tests (i.e., test and re-test) were higher than the intra-group similarity (Table 4), even when comparing with the experienced population, indicating that the muscle synergies are robust for a given subject (i.e., reproducible).

4. Discussion

We tested the hypothesis that expertise in rowing would be driven by specific muscle synergies. The results showed that training

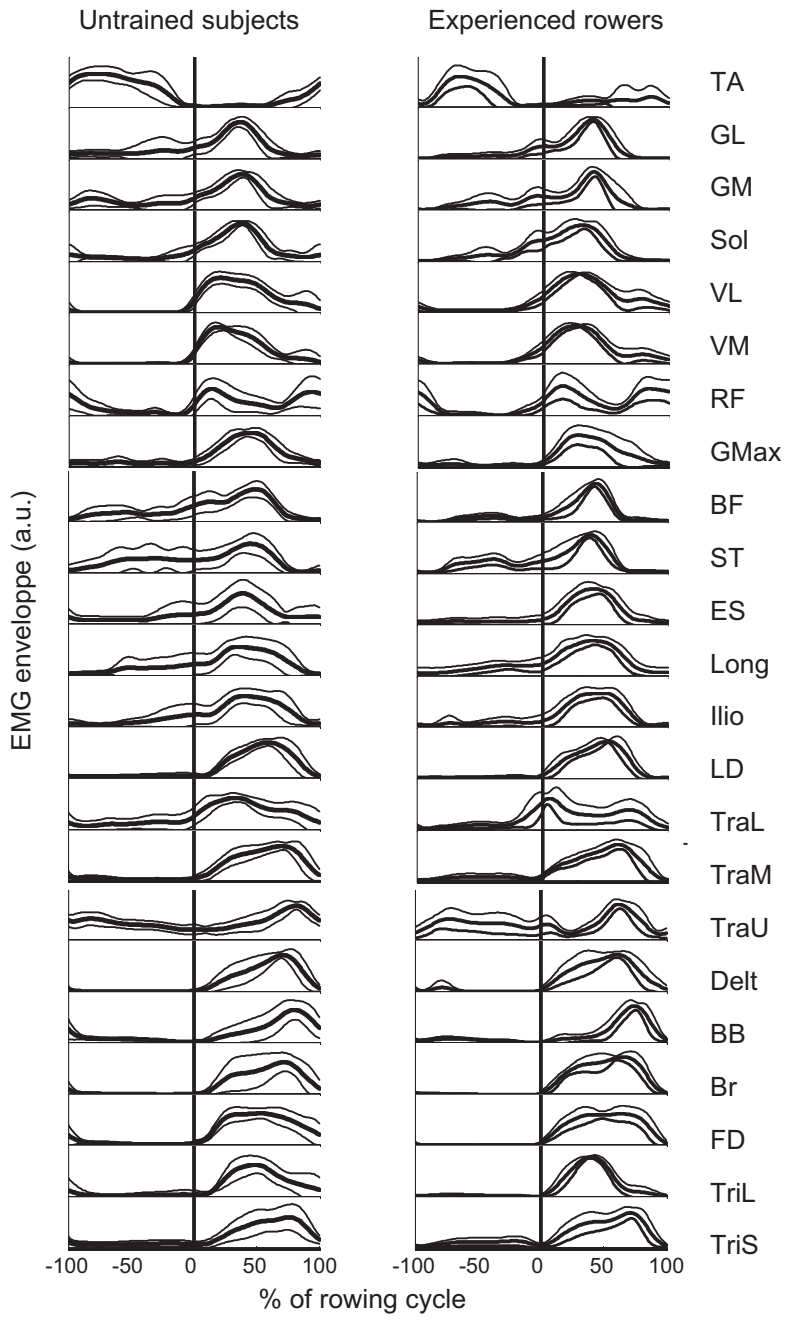

Fig. 5. Ensemble averaged (±SD) EMG patterns of the 23 recorded muscles for the two populations. The vertical dashed line indicates the transition between the recovery and the drive phases (−100% to 0% represents the recovery phase and 0% to 100% represents the drive phase). Muscle abbreviations are described in Table 1.

does not induce different dimensionality of the EMG data, signifying that EXP and UNT use the same number of muscle synergies (i.e., three) to perform the rowing task. Both the synergy activation coefficients and muscle synergy vectors of the two first synergies are similar between EXP and UNT. Higher intra- and inter-group differences were found for the activation of synergy #3 (i.e., synergy activation coefficients), indicating a higher interindividual variability that is not likely linked to expertise.

4.1. Significance of the extracted muscle synergies

The determination of the number of muscle synergies is not a trivial matter and remains an open problem (Tresch et al., 2006). Here and in previous studies (Torres-Oviedo et al., 2006; Clark et al., 2010; Hug et al., 2010), the number of muscle synergies was determined as the least number of synergies that provided 90% of the VAF. In fact, we found that the use of this arbitrary threshold of 90% of VAF led to a better representation of the data for inter-subjects comparison, and ensured in the same time a good reconstruction level (Hug et al., 2010). Other authors use inflexion points (or knee points) in the VAF vs. number of synergies curve (Cheung et al., 2005; Ajiboye and Weir, 2009). This method also implies an arbitrary threshold to decide on the "true" knee point and often leads to more sparse synergy vectors (Ajiboye and Weir, 2009). Overall, there is no agreement on the best method to be used. Thus, the variations in the number of muscle synergies found by the different methods pose the question of the physiological significance of the extracted synergies. In other words, do they represent real

Table 3
Intra- and inter-group indices of similarity depicted for each muscle.

Muscles	Intra-group similarity			Inter-group similarity
	EXP	UNT	*p*	
TA	0.49 ± 0.38	0.78 ± 0.16	**0.000**	0.49 ± 0.29
GL	0.86 ± 0.10	0.67 ± 0.31	**0.016**	0.79 ± 0.22
GM	0.72 ± 0.19	0.71 ± 0.18	0.795	0.67 ± 0.22
Sol	0.83 ± 0.12	0.82 ± 0.15	0.813	0.74 ± 0.17
VL	0.92 ± 0.04	0.84 ± 0.20	0.517	0.87 ± 0.13
VM	0.93 ± 0.03	0.90 ± 0.07	0.592	0.90 ± 0.06
RF	0.65 ± 0.21	0.44 ± 0.35	**0.039**	0.55 ± 0.28
GMax	0.70 ± 0.27	0.85 ± 0.12	0.389	0.73 ± 0.20
BF	0.89 ± 0.10	0.65 ± 0.22	**0.000**	0.66 ± 0.22
ST	0.82 ± 0.09	0.38 ± 0.35	**0.000**	0.55 ± 0.20
ES	0.84 ± 0.16	0.39 ± 0.45	**0.000**	0.62 ± 0.39
Long	0.83 ± 0.08	0.47 ± 0.38	**0.006**	0.65 ± 0.26
Ilio	0.83 ± 0.10	0.66 ± 0.26	**0.032**	0.73 ± 0.21
LD	0.91 ± 0.06	0.88 ± 0.11	0.829	0.77 ± 0.16
TraL	0.55 ± 0.27	0.60 ± 0.26	0.658	0.38 ± 0.32
TraM	0.86 ± 0.12	0.85 ± 0.12	0.902	0.79 ± 0.17
TraU	0.55 ± 0.26	0.64 ± 0.20	0.083	0.25 ± 0.31
Delt	0.84 ± 0.11	0.81 ± 0.19	0.854	0.74 ± 0.22
BB	0.83 ± 0.13	0.63 ± 0.31	**0.006**	0.68 ± 0.27
Br	0.91 ± 0.08	0.62 ± 0.31	**0.001**	0.72 ± 0.31
FD	0.87 ± 0.09	0.83 ± 0.16	0.828	0.85 ± 0.15
TriL	0.94 ± 0.04	0.66 ± 0.40	**0.002**	0.70 ± 0.36
TriS	0.75 ± 0.22	0.69 ± 0.28	0.827	0.73 ± 0.22

Values are expressed as mean ± SD. Significant differences between the two populations are indicated in bold. Muscle abbreviations are described in Table 1. EXP, experienced rowers; UNT, untrained subjects.

units of movement control? Muscle synergies are viewed as functional organization of the motor output (Li, 2006), and therefore the comparison of the synergies and their functional outcome (i.e., the resulting forces) appear to be a logical way to validate the number of synergies extracted. In the present study, we showed that the extracted synergies well explain the variance of the mechanical data (VAF >90%; Fig. 7), confirming the rationale of using three synergies in this case. In addition, we showed that these three muscle synergies are reproducible across time for the five subjects tested twice. However, since the muscle synergy vectors were composed of numerous muscles (upper limbs, lower limbs and or trunk muscles), one would expect that these synergies represent functionally merged synergies rather than intrinsic units of control as already suggested by Clark et al. (2010) during gait in post-stroke subjects.

4.2. Effect of expertise on muscle synergies

Individual EMG patterns reported in the present study are in agreement with EMG patterns reported in literature (Wilson et al., 1988; Rodriguez et al., 1990; Hase et al., 2004). However, these previous studies recorded a limited number of muscles (up to 12 muscles). Thus, to our knowledge, this is the first study that compares numerous individual EMG patterns (i.e., 23) between untrained subjects and experienced rowers.

The observation that UNT and EXP use the relatively similar three muscle synergies is an unexpected result due to the apparent complexity of the task (many degrees of freedom compared to pedaling for example). This could be explained by the fact that rowing expertise would not require the development of novel muscle synergies but would imply intrinsic synergies already used in different behaviors. Previous studies already suggested that muscle synergies are innately specified and quickly adapted for other behaviors (Georgopoulos and Grillner, 1989; Kargo and Nitz, 2003). For instance, synergy #3 appears to be similar (in terms of both muscle synergy vectors and synergy activation coefficients) to a combination of the fourth and fifth muscle synergy extracted by Ivanenko et al. (2005) during normal walking. Also, one would expect that muscle synergies extracted in the present study would be functionally merged synergies as previously suggested by Clark et al. (2010) during walking in pathological subjects. This could explain the lower number extracted muscle synergies compared to number extracted during other locomotor tasks such as walking and

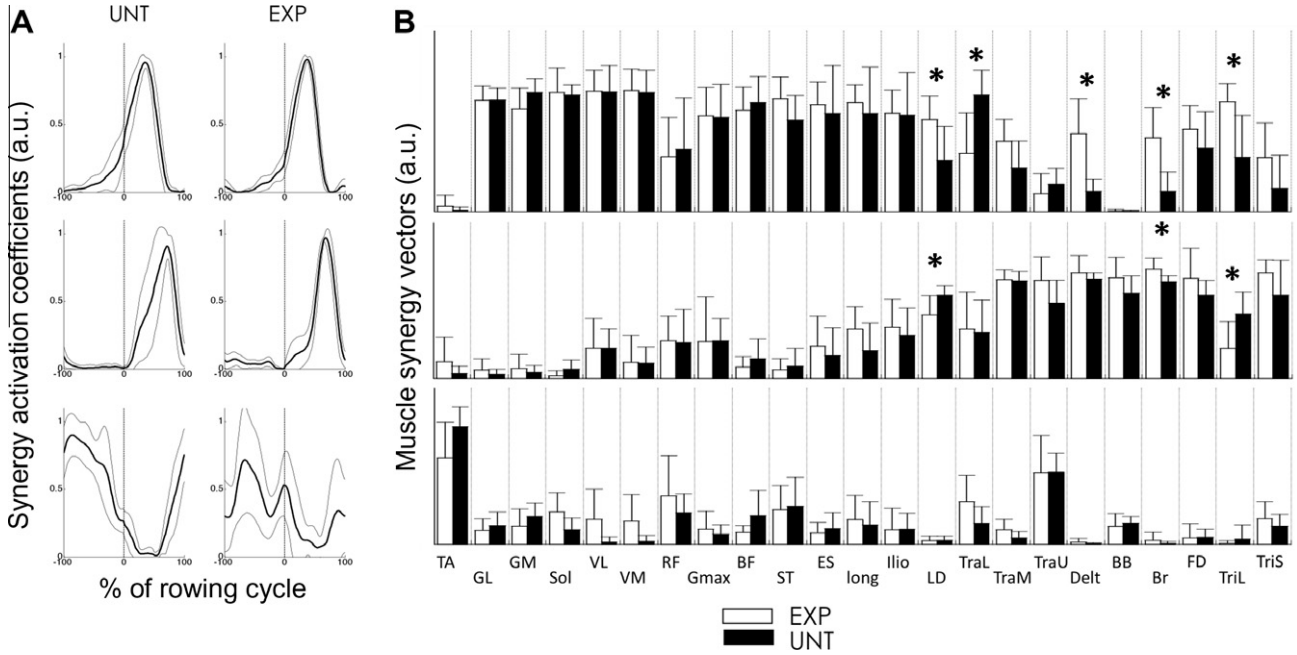

Fig. 6. Synergy activation coefficients (A) and muscle synergy vectors (B) depicted for the two populations. (A) Synergy activation coefficients were averaged (±SD) across the subjects for the three extracted synergies and the two populations. The synergy activation coefficients are expressed as a function of percentage of the rowing cycle (−100% to 0% represents the recovery phase and 0% to 100% represents the drive phase). Between subjects comparisons were possible after normalizing each muscle by its peak value. (B) The muscle synergy vectors were averaged (±SD) across the subjects for the three extracted synergies and the two populations. Individual muscle weightings are depicted for each muscle within each synergy. EXP, experienced rowers; UNT, untrained subjects. *: indicates a significant difference between the two populations ($p < 0.05$).

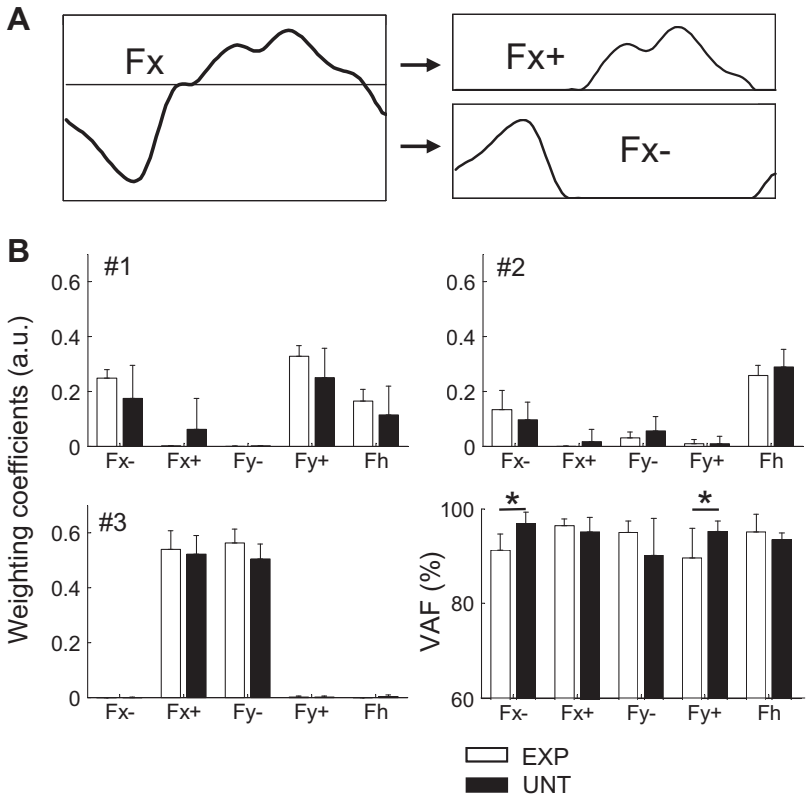

Fig. 7. Muscle synergy vectors for the mechanical variables. An augmented matrix regrouping both EMG and mechanical variables (i.e., [EMG | Fx − Fx + Fy − Fy + Fh]) was used to extract the muscle synergies in all of the subjects. The positive and negative components of the mechanical variables have been separated to create new variables, which were all positive (Panel A). Muscle synergies were highly similar for both extractions (i.e., EMG only or EMG+ mechanical variables; $r > 0.8$; Panel B). The weighting of each mechanical variable is depicted for each of the muscle synergies. The variance accounted for by each mechanical variable is shown at the bottom right of the figure. # 1, # 2 and # 3 refer the number of the muscle synergy. * indicates a significant differences between the two populations ($p < 0.05$). Fx−, Fx+, negative and positive components of the horizontal foot-stretcher force; Fy−, Fy+, negative and positive components of the vertical foot-stretcher force; Fh, handle force. EXP, experienced rowers; UNT, untrained subjects.

Table 4
Intra- and inter-group indices of similarity depicted for each synergy activation coefficients and muscle synergy vectors.

	Intra-group similarity			Inter-group similarity
	EXP	UNT	*p*	
Synergy activation coefficients (C)				
Synergy #1	0.95 ± 0.04	0.86 ± 0.10	**0.005**	0.91 ± 0.07
Synergy #2	0.86 ± 0.08	0.66 ± 0.30	0.075	0.76 ± 0.19
Synergy #3	0.57 ± 0.40	0.83 ± 0.10	**0.013**	0.51 ± 0.31
Muscle synergy vectors (W)				
Synergy #1	0.70 ± 0.05	0.64 ± 0.13	0.110	0.62 ± 0.13
Synergy #2	0.74 ± 0.11	0.70 ± 0.10	0.710	0.72 ± 0.10
Synergy #3	0.65 ± 0.22	0.75 ± 0.09	0.100	0.66 ± 0.19

Values are mean ± SD. Significative differences between the two populations are indicated in bold. EXP, experienced rowers; UNT, untrained subjects.

running (Cappellini et al., 2006). Future studies are needed to examine this connection.

The slight differences observed in the present study between UNT and EXP mainly correspond to changes in the weighting of some muscles into the muscle synergy vectors. More precisely, we observed an increase in the weighting of some upper limb muscles engaged in synergy #1 that implies principally leg and thigh muscles. Similar changes in the composition of muscle synergies in the context of a skill acquisition have been already documented (Jamison and Caldwell, 1993; Shemmell et al., 2005). This increase in the weightings could be interpreted as more synchrony in the activation pattern of these muscles. However, it is difficult to speculate about the mechanisms responsible for these changes. In fact, one would expect that this increase in synchrony in the first synergy could result from better synchrony between merged synergies and/or from an adaptation at the level of the synergies themselves (i.e., plasticity).

4.3. Expertise in rowing

The level of expertise in rowing could be discriminated by indices constructed via the mechanical patterns i.e., handle and foot-stretcher forces profiles (Smith and Spinks, 1995; Soper and Hume, 2004; Hofmijster et al., 2008). For instance, it has been shown that low variability in the handle force profile is associated with a high level of expertise (Smith and Spinks, 1995) and that greater co-variation between handle and foot-stretcher forces are related to higher efficiency (Hofmijster et al., 2008). Our data showed that the handle forces (Fh) and the negative horizontal component of the stretcher force (Fx−) represent the summed mechanical output of the two first synergies (Fig. 7). We observed a positive lag time of these mechanical data between experienced and untrained subjects, but no such delays were found for the synergy activation coefficients (Fig. 4). One would expect that an unbalanced mechanical response (i.e., transformation of activation to muscle force) of the two first muscle synergies would cause this shift of Fx− and Fh patterns toward the most important mechanical response (Fig. 8). In fact, the handle force (Fh, mainly due to synergy #2) represented approximately 3.8 ± 2.9-fold change the foot-stretcher forces (Fx-, mainly due to synergy #1) in UNT whereas it was only 2.2 ±

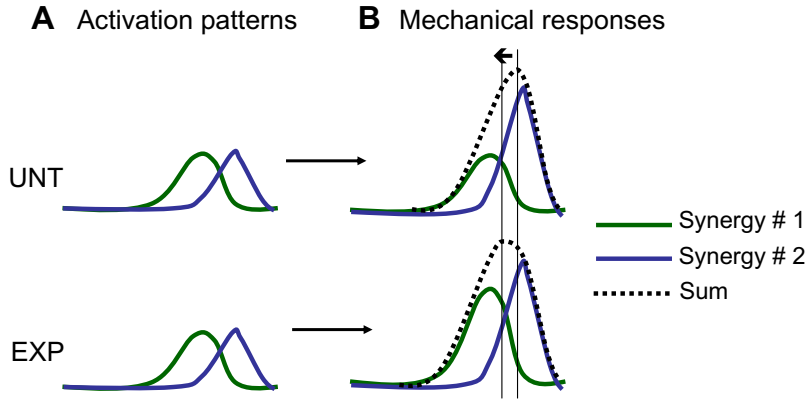

Fig. 8. Possible explanation for the observed time lags of the mechanical patterns between EXP and UNT. Schematic representation of the activation of the two first synergies is depicted in Panel A. We hypothesized that the mechanical response (i.e., transformation of muscle activation into muscle force) of one of the two muscle synergies would differ between untrained subjects and experienced rowers (Panel B). Therefore, the sum of these responses would be shift toward the most important mechanical response.

0.6-fold change in EXP (Fig. 3). In conclusion, one would expect that this particular balance between the mechanical responses of these two first synergies would induce the shift mechanical response for EXP compared to UNT. That suggests that the expertise in rowing mainly involves adjustment in the mechanical response of the muscle synergies rather than in the sequence of synergies' activation (i.e., motor programs as defined by Kargo and Nitz, 2003). Changes in mechanical response of the muscle synergies could be due to: (i) changes in the muscle efficiency (architectural changes such as muscle cross sectional area, pennation angle, etc.), or, (ii) in the activation level of the synergies.

5. Conclusion

A great similarity was observed in the muscle synergies organizing the muscular coordination in rowing between experienced and untrained subjects. These results suggest that rowing expertise would not require the development of novel muscle synergies, but would imply intrinsic synergies already used in different behaviors. Expertise in rowing is more likely to be linked to adjustments in the mechanical output of the muscle synergies rather than to differences in the shape and timing of their activations. We conclude that the same motor strategies are used by experienced rowers and untrained subjects during rowing. Additional experiments are needed to explore the effect of training in a more complex task.

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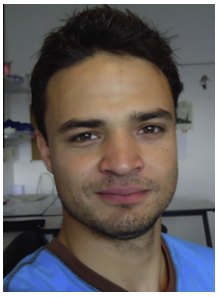

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