Consistency of muscle synergies during pedaling across different mechanical constraints

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Hug F, Turpin NA, Couturier A, Dorel S. Consistency of muscle synergies during pedaling across different mechanical constraints. J Neurophysiol 106: 91–103, 2011. First published April 13, 2011; doi:10.1152/jn.01096.2010.—The purpose of the present study was to determine whether muscle synergies are constrained by changes in the mechanics of pedaling. The decomposition algorithm used to identify muscle synergies was based on two components: “muscle synergy vectors,” which represent the relative weighting of each muscle within each synergy, and “synergy activation coefficients,” which represent the relative contribution of muscle synergy to the overall muscle activity pattern. We hypothesized that muscle synergy vectors would remain fixed but that synergy activation coefficients could vary, resulting in observed variations in individual electromyographic (EMG) patterns. Eleven cyclists were tested during a submaximal pedaling exercise and five all-out sprints. The effects of torque, maximal torque-velocity combination, and posture were studied. First, muscle synergies were extracted from each pedaling exercise independently using non-negative matrix factorization. Then, to cross-validate the results, muscle synergies were extracted from the entire data pooled across all conditions, and muscle synergy vectors extracted from the submaximal exercise were used to reconstruct EMG patterns of the five all-out sprints. Whatever the mechanical constraints, three muscle synergies accounted for the majority of variability [mean variance accounted for (VAF) = 93.3 ± 1.6%, VAF_muscle > 82.5%] in the EMG signals of 11 lower limb muscles. In addition, there was a robust consistency in the muscle synergy vectors. This high similarity in the composition of the three extracted synergies was accompanied by slight adaptations in their activation coefficients in response to extreme changes in torque and posture. Thus, our results support the hypothesis that these muscle synergies reflect a neural control strategy, with only a few timing adjustments in their activation regarding the mechanical constraints.

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The redundancy of the musculoskeletal system (Bernstein 1967) implies vast degrees of freedom. This provides great flexibility but makes the control of these degrees of freedom extremely complex. Consequently, the question of how the central nervous system coordinates activity among numerous muscles is central to understanding motor control. Low-dimensional modules formed by muscles activated in synchrony, named muscle synergies, have been proposed as building blocks that could simplify the construction of motor behaviors (d’Avella and Bizzi 2005; Ivanenko et al. 2003; Ting and Chvatal 2010; Ting and McKay 2007; Torres-Oviedo and Ting 2007). The decomposition algorithm used to identify muscle synergies is based on two components: 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 muscle synergies (Torres-Oviedo and Ting 2007). For example, it has been demonstrated that five muscle synergies account for the majority of the variability in surface electromyographic (EMG) signals of 32 muscles during human locomotion such as walking (Ivanenko et al. 2006) and running (Cappellini et al. 2006). Additionally, they are associated with kinematic and kinetic events of the gait cycle (Neptune et al. 2009).

Although numerous studies have suggested that the central nervous system produces movement through the flexible combination of muscle synergies (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007; Tresco et al. 1999), others have suggested that muscle synergies better reflect task constraints rather than reflecting a neural control strategy (Kutch et al. 2008; Valero-Cuevas et al. 2009). As evidence that the central nervous system uses similar muscle synergy combinations for the construction of different types of locomotion, d’Avella and Bizzi (2005) reported that combinations of a small number of synergies accounted for a large fraction of the variation in the EMG patterns observed during jumping, swimming, and walking in frogs. However, due to different muscle architectures and fiber type composition (and thus to different mechanical advantages) among muscles participating in the same muscle synergy, one would expect specific adaptations of each individual muscle in response to change in mechanical constraints (e.g., posture, load, and/or movement velocity). This would lead to changes in already active muscle synergies and/or new synergies, suggesting that they emerge from the mechanics of the task rather than reflecting a neural control strategy. Interestingly, Wakeling and Horn (2009) recently showed variation in the EMG patterns across muscles that belong to the same muscle synergies (extracted via principal component analysis) in response to changes in load and/or movement velocity during pedaling. Nevertheless, this study extracted a fixed number of muscle synergies (i.e., six) and thus did not focus on the putative change in the number of muscle synergies in response to altered mechanical constraints. While changes in torque and cadence mainly imply modifications in the kinetics of pedaling (Takaishi et al. 1998), changes induced by different postures (e.g., standing vs. seated) also induced kinematic modifications (Li and Caldwell 1998). As suggested by Tresco and Jarc (2009), the use of similar muscle synergies associated with different kinematic and kinetic patterns would provide
additional evidence that the central nervous system produces movement through the flexible combination of muscle synergies.

Taking these elements in mind, the purpose of the present study was to determine whether muscle synergies are constrained by the mechanics of movement during pedaling. First, we tested the effect of “torque” between two pedaling conditions performed at the same pedaling rate but at two extremely different torque levels (i.e., submaximal exercise vs. all-out sprint). Since our goal was to induce different mechanical constraints rather that to isolate the effect of “load” and “movement velocity,” we chose to study all-out sprint because it is an interesting model previously unstudied in the literature. In fact, despite the same maximal involvement of the subjects, manipulating the pedaling rate provides the possibility to place the subjects in different torque-velocity scenarios and hence power-velocity constraints (Dorel et al. 2010). In this way, two extreme conditions were compared, i.e., a maximal sprint at a very high torque and hence a low pedaling rate and a maximal sprint at a high pedaling rate and a low torque. Since the changes in torque and power-velocity combinations mainly induced a change in the kinetics of pedaling, we finally compared two different postures (i.e., seated vs. standing) to add changes in the kinematics of pedaling and in transfers between limbs. For the purpose of this study, we used a non-negative matrix factorization algorithm to identify muscle synergies during pedaling under different mechanical constraints. We focused on the analysis of the number of muscle synergies [providing information on the complexity of motor control (Clark et al. 2010)], muscle synergy vectors, and synergy activation coefficients. We hypothesized that muscle synergies would remain fixed but that the activation of these synergies could vary, resulting in the observed variations in individual EMG patterns.

METHODS

Subjects. Because reaching very high pedaling rates (>180 rpm) would be impossible for untrained subjects, highly trained cyclists were recruited so that a wide range of mechanical conditions could be studied. Eleven subjects (4 women and 7 men) volunteered to participate in this study (age: 21.3 ± 2.9 yr, body mass: 62.1 ± 5.5 kg, height: 166.5 ± 5.2 cm, and maximal anaerobic power: 1,043 ± 126 W for women; and age: 22 ± 4 yr, body mass: 85 ± 6.8 kg, height: 177.9 ± 6.1 cm, and maximal anaerobic power: 1,730 ± 196 W for men). Subjects were informed of the possible risks and discomfort associated with the experimental procedures before they gave their written consent to participate. The experimental design of the study was approved by the local Ethical Committee of Saint-Germain-en-Laye (France; acceptance no. 06016) and was carried out in accordance with the Declaration of Helsinki.

Exercise protocol. Subjects exercised on an electronically braked cycle ergometer (Excalibur Sport, Lode) equipped with standard cranks (length: 170 mm). Vertical and horizontal positions of the saddle, handlebar height, and stem length were set to match the usual racing positions of the participants.

During the first session, subjects performed a force-velocity test that revealed their power-velocity characteristics. They first performed a 20-min warm up consisting of 15 min of cycling at 100–150 W followed by two brief sprints (4–5 s in duration, separated by 5 min of rest). Participants were then asked to perform three maximal cycling sprints (5 s in duration with 8 min of total recovery) according to the protocol proposed by Dorel et al. (2010). Three different resistive torques of 0, 0.7–1, and 1.4–1.8 Nm/kg body mass were applied to obtain maximum force and power values on a large range of pedaling rates among the three bouts. After computation, the cumulated data from the three sprints were used to draw force- and power-velocity relationships and hence to determine the maximum power and corresponding specific optimal pedaling rate ($f_{\text{opt}}$) at which maximum power occurred (for details, see Dorel et al. 2010).

After at least 2 wk, subjects performed a second experimental session consisting of a submaximal cycling exercise at a constant pedaling rate and five maximal cycling exercises performed in an isokinetic mode. After a warm up identical to the one performed during the first session, subjects were asked to perform, in randomized order, a submaximal 3-min exercise at 300 W for men and 220 W for women performed at a constant pedaling rate corresponding to 80% of $f_{\text{opt}}$, four 6-s all-out sprint exercises at 60%, 80%, 100%, and 140% of $f_{\text{opt}}$ in a seated position; and one 6-s all-out sprint at 100% of $f_{\text{opt}}$ in a standing position.

The effect of absolute torque (and hence power output) was evaluated by comparing the submaximal exercise and all-out sprint performed at 80% of $f_{\text{opt}}$ (“torque effect”). The effect of maximal torque-velocity combinations was evaluated by comparing the all-out sprints performed at 60% and 140% of $f_{\text{opt}}$ (“torque-velocity effect”). Finally, the effect of posture was evaluated by comparing the sprints performed at 100% of $f_{\text{opt}}$ in a seated and standing position (“posture effect”). Before the subjects settled on the ergometer and began the effort, the flywheel was set at the target velocity. This procedure reduced the acceleration phase at the start of the sprint and made it possible to briefly reach the isokinetic condition of maximal pedaling without fatigue. A complete 8-min recovery period was performed between each bout. The surface EMG of 11 lower limbs muscles and mechanical parameters of the cycle ergometer were recorded continuously during each exercise.

Material and data collection. The torque exerted on the left and right cranks was measured by strain gauges located in the crank arms of the cycle ergometer. The crank angle and angular velocity were measured (by derivative) based on transistor-transistor logic (TTL) rectangular pulses delivered each 2° by the ergometer. An additional TTL pulse was used to detect the top dead center (TDC; i.e., the highest position of the right pedal with crank arm angle at 0°). Surface EMG activity was continuously recorded for the following 11 muscles [providing information on the complexity of motor control (Clark et al. 2010)], muscle synergy vectors, and synergy activation coefficients. We hypothesized that muscle synergies would remain fixed but that the activation of these synergies could vary, resulting in the observed variations in individual EMG patterns.
of its peak value across the cycles, similar to previous studies focusing on muscle synergies (Hug et al. 2010; Ting and Maepherson 2005). As done in previous studies (Cheung et al. 2009b; Ivanenko et al. 2005; Torres-Oviedo et al. 2006), non-negative matrix factorization was performed from a set of consecutive pedaling cycles. The advantage of this technique is to take into account the intercycle variability (Clark et al. 2010). 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 follows:

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

$$\min_{\mathbf{W}, \mathbf{C}} \| \mathbf{E} - \mathbf{WC} \|_{\text{Fro}}$$

where $\mathbf{E}$ is a $p \times n$ initial matrix (where $p$ is the number of muscles and $n$ is the number of time points), $\mathbf{W}$ is a $p \times s$ matrix (where $s$ is the number of synergies), $\mathbf{C}$ is a $s \times n$ matrix, and $\mathbf{e}$ is a $p \times n$ matrix. Frobenius norm, $\mathbf{E}$ represents the initial matrix, $\mathbf{W}$ represents the muscle synergy vector matrix, $\mathbf{C}$ represents the synergy activation coefficient matrix, and $\mathbf{e}$ is the residual error matrix. 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 2001 for more details). To avoid local minima, the algorithm was restarted 20 times for each subject. The lowest cost solution was kept (i.e., minimized squared error between original and reconstructed EMG patterns).

A pedaling cycle was defined as a complete revolution of the right crank arm as it rotated from the highest pedal position (0%, TDC) to the lowest pedal position (50%, bottom dead center (BDC)) and back to TDC to complete a 360° crank cycle. $\mathbf{E}$ consisted of 6–10 consecutive cycles (depending on the number of cycles performed at the same targeted velocity, i.e., without fatigue) for the 11 muscles. Each cycle was interpolated to 100 time points. $\mathbf{E}$ was thus an 11-row and 600- to 1,000-column matrix, $\mathbf{C}$ was normalized by the average of its peak from all cycles (Hug et al. 2010).

In all our subjects, we iterated the analysis by varying the number of synergies between 1 and 11 and then selected the least number of synergies that accounted for >90% of the variance accounted for (VAF) (Torres-Oviedo et al. 2006). Mean total VAF was defined as follows (Torres-Oviedo et al. 2006):

$$\text{VAF} = 1 - \frac{\sum_{i=1}^{p} \sum_{j=1}^{n} (e_{ij})^2}{\sum_{i=1}^{p} \sum_{j=1}^{n} (E_{ij})^2}$$

According to Torres-Oviedo (2007), we calculated VAF for each muscle to ensure that each muscle activity pattern was well accounted for by the extracted muscle synergies [i.e., muscle VAF (VAFmuscle) > 75%]. VAF was defined as the uncentered Pearson correlation coefficient. Each vector of muscle activation was compared with its reconstruction as follows:

$$\text{VAF}_{\text{muscle}} = 1 - \frac{\sum_{i=1}^{m} (e_{im})^2}{\sum_{i=1}^{m} (E_{im})^2}$$

where $i$ goes from 1 to $n$ (where $n$ is the number of time points) and $m$ is the number of muscles ($m$ assumes a value from 1 to $p$, where $p$ is the number of muscles).

Cross-validation of the extracted muscle synergies. As proposed by previous studies (Cheung et al. 2005, 2009; Torres-Oviedo et al. 2006, 2010; Ting and Chvatal 2010; Clark et al. 2010), to verify the robustness of the extracted muscle synergies, we used a cross-validation procedure. First, we extracted muscle synergies from the entire data pooled across all conditions. To have the same amount of data for each condition, only six pedaling cycles were taken into consideration for each pedaling condition. Thus, we compared these muscle synergies with those extracted independently from each condition. Second, we checked that the muscle synergies (in terms of muscle synergy vectors) extracted from the submaximal condition (i.e., control condition herein) accounted for individual EMG patterns in all other pedaling conditions, as determined by VAFmuscle > 75% (Torres-Oviedo et al. 2007). To do this, the muscle synergy matrix extracted from the submaximal condition ($\mathbf{W}_{\text{submax}}$) was held fixed in the algorithm and the activation coefficient matrix ($\mathbf{C}_{\text{condition}}$) was free to vary. $\mathbf{C}_{\text{condition}}$ was initialized with random values and iteratively updated until convergence. The EMG data matrix ($\mathbf{E}_{\text{condition}}$) of the other pedaling conditions was provided to the algorithm with the following update rule (Lee and Seung 2001):

$$\mathbf{C}_{\text{condition}} \leftarrow \mathbf{C}_{\text{condition}} - \mathbf{W}_{\text{submax}} \mathbf{E}_{\text{condition}}$$

If they did not explain a sufficient percentage of variability, then “specific muscle synergies” were extracted from the remaining variability of the data.

Statistical analysis. Data distributions consistently passed the Shapiro-Wilk normality test (Statistica version 6, Statsoft, Maison-Alfort, France). Therefore, values are reported as means ± SD. Modification of the individual EMG patterns, mechanical patterns, and synergy activation coefficients were assessed using two criteria: the lag time and $r_{\text{max}}$ coefficient (Hug 2011). The lag times assess differences in the timing of the activations (i.e., the magnitude of the time shift between EMG patterns or between synergy activation coefficients) 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). $r_{\text{max}}$ 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, synergy activation coefficients, and mechanical patterns). Pearson’s correlation coefficient ($r$) was used as a similarity criterion for the muscle synergy vectors. As performed in previous studies (Hug et al. 2010; Turpin et al. 2011), $r_{\text{max}}$ and $r$ statistics were based on Z-transformed values. One-way ANOVA with repeated measures was performed to test the effect of each mechanical constraint on pedaling rate, power output, and VAF. Orthogonal contrasts were used as the post hoc test. $P$ values below 0.05 were considered statistically significant.

RESULTS

Mechanical data. Figure 1 shows the mechanical data for each of the pedaling conditions. Significant differences in crank torque were logically found between the submaximal pedaling exercise and the sprint performed at 80% of $f_{\text{opt}}$ ($P < 0.001$) and between the sprints performed at 60% and 140% of $f_{\text{opt}}$. Also, a lower but significant ($P = 0.03$) difference was found between the two postures.

The shape of the effective torque normalized to peak torque obtained for each pedaling exercise is shown in Fig. 2. $r_{\text{max}}$ was used as an indicator of the waveform consistency across conditions. Mean $r_{\text{max}}$ values were 0.95 ± 0.02 between the submaximal exercise and the all-out sprint, 0.95 ± 0.03 between the two sprints performed at 60% and 140% of $f_{\text{opt}}$, and 0.98 ± 0.01 between the seated and standing positions. Despite these high similarities in the waveforms, we found a significant shift backward of the effective torque profile for the all-out sprint condition (−2.3 ± 1.3%, $P < 0.001$) compared with the sub-
maximal condition. In contrast, the mechanical pattern shifted forward for the sprint performed at 140% of \( f_{\text{opt}} \) compared with 60% of \( f_{\text{opt}} \) (6.3 ± 3.8%, \( P < 0.001 \)). Also, a significant shift forward was found for the standing posture compared with the seated posture (2.4 ± 1.2%, \( P < 0.001 \)).

**Individual EMG patterns.** For each condition, the EMG patterns for the 11 muscles investigated are shown in Fig. 3. Overall, EMG patterns were similar to those already reported in the literature (for a review, see Hug and Dorel 2009). The intercondition index of similarity (i.e., \( r_{\text{max}} \)) averaged across all muscles was 0.82 ± 0.09, 0.89 ± 0.09, and 0.92 ± 0.04 for torque, torque-velocity, and posture effects, respectively. That indicates that there was overall good similarity in the shape of the EMG patterns between the two maximal torque-velocity combinations and between the two postures. However, a relative lower similarity was found between the submaximal pedaling condition and the all-out sprint. This was partly due to a lower similarity for TF (0.77 ± 0.15) between these two conditions (Table 1, indexes of similarity, and Fig. 3). In fact, taking into account each muscle individually, it appears that some muscles were more affected (i.e., lower \( r_{\text{max}} \)) whatever the constraint, e.g., TA, TF, and SM (Table 1, indexes of similarity).

Table 1 also shows the lag times of the EMG patterns for each comparison. A significant shift backward in the EMG patterns was observed for the four leg muscles in sprint compared with the submaximal condition. In contrast, a significant shift forward was found for 9 of the 11 muscles in the standing posture compared with the seated posture. For the torque-velocity effect, while some leg muscles (GL and GM) were recruited later as the cadence increased, thigh muscles were recruited earlier (Table 1, lag times).

**Extracted muscle synergies from each condition independently.** Figure 4A shows the cumulative percentages of variance explained by each synergy for each condition. Using the criteria previously described (i.e., VAF > 90%), three synergies were identified for all conditions. Nevertheless, three muscle synergies accounted for a significantly lower VAF for the submaximal exercise (90.7 ± 1.4% of the total VAF) than for the all-out sprints (ranging from 93.2 ± 1.4% to 95.8 ± 0.8% of the total VAF for the sprint performed at 80% and 60% of \( f_{\text{opt}} \), respectively). Based on the results of Tresch et al. (2006) showing the influence of the signal-to-noise ratio on VAF values, a lower VAF value during the submaximal exercise might be explained by a lower signal-to-noise ratio of the EMG signals (i.e., a lower phasic EMG activity and an unchanged baseline level).

Figure 4B shows VAF for each muscle and for each condition for the three extracted muscle synergies. VAF\(_{\text{muscle}}\) values were generally more affected by changes in the mechanics of pedaling in muscles that transmit force (e.g., SOL and TA) than in power producer muscles (e.g., VL and VM). However, three muscle synergies accounted for VAF\(_{\text{muscle}}\) > 75% for all muscles (range from 82.5 ± 4.2% to 97.9 ± 1.0% of total VAF for SOL during the submaximal exercise and GL during the all-out sprint performed at 60% of \( f_{\text{opt}} \), respectively; Fig. 4B). Therefore, three muscle synergies can reproduce initial EMG patterns for all pedaling conditions.

By analyzing both the muscle synergy vectors (Fig. 5) and synergy activation coefficients (Fig. 6) during the submaximal exercise, very similar properties to those reported by Hug et al. (2010) were identified for each muscle synergy, as described below for **synergies 1–3**.

**Synergy 1** mainly consists of extensor activity from GMax, the two monoarticular muscles of the quadriceps group (VL and VM), and also, to a lesser extent, RF, SOL, and TF (Fig. 5A). It is active during the downstroke phase of the pedaling cycle (Fig. 6A) with peak activity occurring during the first part of this phase. Note that TF is inserted on the iliotibial tract.
(which crosses the knee) and thus cannot be strictly classified as a monoarticular hip flexor muscle. This could explain its non-negligible implication in this synergy with the knee extensors in this first part of the downstroke phase. GMax, vastii, and SOL were found to be a necessary synergy to deliver power to the crank (Neptune et al. 2000). More precisely, SOL has to be activated synergistically to allow the transfer to the crank of the limb segment energy generated by the two other muscle groups (i.e., hip and knee extensors). This could therefore explain why GMax (hip extensor) and SOL (ankle plantar flexor) are represented in **synergy 1**, whereas GL and GM (also both plantar flexors) are not.

**Synergy 2** is primarily active during the second part of the downstroke phase and, to a lesser extent, at the beginning of the upstroke phase (Fig. 6A). It consists of activity in the biarticular hamstring group (SM and BF), the biarticular plantar flexors (GL and GM), SOL, and, to a lesser extent, GMax (Fig. 5A). In this phase, the hamstrings and plantar flexors mainly participate in the transfer of additional mechanical energy stored in the limbs to the crank (Raasch and Zajac 1999) and to the optimization of the resultant pedal force orientation (Van Ingen Schenau et al. 1992).

**Synergy 3** is active from the middle of the upstroke phase to the beginning of the downstroke phase (Fig. 6A). It mainly
Indexes of similarity \((r_{\text{max}} \text{ values})\)

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Torque (Submaximal vs. Sprint Exercises)</th>
<th>Torque-Velocity (60% vs. 140% of (f_{\text{opt}}))</th>
<th>Posture (Seated vs. Standing)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TA</td>
<td>0.82 ± 0.12</td>
<td>0.89 ± 0.08</td>
<td>0.91 ± 0.08</td>
</tr>
<tr>
<td>SOL</td>
<td>0.90 ± 0.10</td>
<td>0.94 ± 0.05</td>
<td>0.98 ± 0.01</td>
</tr>
<tr>
<td>GL</td>
<td>0.84 ± 0.07</td>
<td>0.89 ± 0.05</td>
<td>0.94 ± 0.04</td>
</tr>
<tr>
<td>GM</td>
<td>0.84 ± 0.07</td>
<td>0.94 ± 0.04</td>
<td>0.96 ± 0.02</td>
</tr>
<tr>
<td>VL</td>
<td>0.88 ± 0.07</td>
<td>0.86 ± 0.06</td>
<td>0.91 ± 0.04</td>
</tr>
<tr>
<td>VM</td>
<td>0.84 ± 0.13</td>
<td>0.83 ± 0.10</td>
<td>0.92 ± 0.03</td>
</tr>
<tr>
<td>RF</td>
<td>0.89 ± 0.10</td>
<td>0.82 ± 0.12</td>
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<tr>
<td>TF</td>
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<td>0.90 ± 0.07</td>
</tr>
<tr>
<td>BF</td>
<td>0.87 ± 0.11</td>
<td>0.82 ± 0.11</td>
<td>0.95 ± 0.04</td>
</tr>
<tr>
<td>SM</td>
<td>0.86 ± 0.07</td>
<td>0.69 ± 0.12</td>
<td>0.82 ± 0.17</td>
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<tr>
<td>GMax</td>
<td>0.89 ± 0.07</td>
<td>0.89 ± 0.07</td>
<td>0.94 ± 0.05</td>
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Lag times, % of pedaling cycle

<table>
<thead>
<tr>
<th>Muscle</th>
<th>TA</th>
<th>SOL</th>
<th>GL</th>
<th>GM</th>
<th>VL</th>
<th>VM</th>
<th>RF</th>
<th>TF</th>
<th>BF</th>
<th>SM</th>
<th>GMax</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>−7.8 ± 6.9*</td>
<td>−4.9 ± 2.7*</td>
<td>−4.0 ± 2.9*</td>
<td>−5.0 ± 3.9*</td>
<td>−0.7 ± 1.3</td>
<td>−2.2 ± 6.9</td>
<td>8.2 ± 24.7</td>
<td>4.7 ± 17.2</td>
<td>−0.7 ± 4.1</td>
<td>2.0 ± 4.4</td>
<td>−2.5 ± 3.6</td>
</tr>
</tbody>
</table>

Values are means ± SD. \(f_{\text{opt}}\) is the optimal pedaling rate determined during the torque-velocity test. \(r_{\text{max}}\) corresponds to the correlation coefficient at the maximum of the cross-correlation function and gives an indication of the similarity of the waveforms. Lags were calculated as the lag times that maximized the cross-correlation function. A negative bias indicates that the second pattern shifted earlier in the cycle relative to the first pattern. TA, tibialis anterior; SOL, soleus; GL, gastrocnemius lateralis; GM, gastrocnemius medialis; VL, vastus lateralis; VM, vastus medialis; RF, rectus femoris; TF, tensor fascia latae; BF, biceps femoris; SM, semimembranosus; GMax, gluteus maximus. *Lag time significantly different from zero \((p < 0.05)\).

As previously suggested (Neptune et al. 2000), while RF and TF generate energy to the limb segments, TA transmits this energy to the crank.

**Effect of mechanical constraints on the muscle synergies.** As shown in Table 2 (indexes of similarity), the intercondition similarity for muscle synergy vectors was high for the three synergies (i.e., most of the \(r_{\text{max}}\) values were >0.8). The lowest similarity was found between the submaximal exercise and the submaximal exercise compared to the sprint condition lead to a higher time period of activation of the cross-correlation function. A negative bias indicates that the second pattern shifted earlier in the cycle relative to the first pattern. TA, tibialis anterior; SOL, soleus; GL, gastrocnemius lateralis; GM, gastrocnemius medialis; VL, vastus lateralis; VM, vastus medialis; RF, rectus femoris; TF, tensor fascia latae; BF, biceps femoris; SM, semimembranosus; GMax, gluteus maximus. *Lag time significantly different from zero \((p < 0.05)\).

Two additional analyses were performed to cross-validate the extracted muscle synergies and their putative robustness across the pedaling conditions. First, when the muscle synergies were extracted from the entire data pooled across all conditions, three synergies were identified for all subjects, which accounted for a mean VAF of 92.3 ± 1.2% of the total VAF (VAF muscle ranged from 88.2 ± 3.6% to 95.8 ± 2.3% for GMax and VL, respectively). Figure 7 shows an individual example demonstrating a very high similarity between the three muscle synergies (especially for the muscle synergy vectors) extracted from the entire data set and those extracted for each condition independently. Both the composition and activation of these three extracted synergies were very similar to those extracted independently from each condition \((r > 0.86 \text{ and } r_{\text{max}} > 0.87)\) for muscle synergy vectors and synergy activation coefficients, respectively; Table 3). This high similarity indicates the non-negative matrix factorization algorithm has more likely identified underlying physiological features of the data (Ting and Chatval 2010) that are consistent across the pedaling task.
Second, as shown in Fig. 8, the muscle synergy vectors extracted for the submaximal condition were sufficient to explain >75% of the variability for each individual muscle in all sprint conditions (VAF_{muscle} ranged from 79.1 ± 9.4% to 95.2 ± 1.9% of total VAF for SM during the all-out sprint performed at 100% of \( f_{opt} \) in the standing position and for GL during the all-out sprint performed at 100% of \( f_{opt} \) in the seated position, respectively). Therefore, we concluded that specific muscle synergies were not needed. Figure 9 shows an individual example of the reconstruction of the individual EMG patterns obtained during the sprint performed at 60% of \( f_{opt} \) from the muscle synergy vectors extracted during the submaximal exercise.

DISCUSSION

The results of the present study show that, whatever the mechanical constraints, three muscle synergies accounted for the majority of variability in the EMG signals of 11 lower limb muscles during pedaling. In addition, there was robust consistency in the global structure of these synergies (i.e., muscle synergy vectors and synergy activation coefficients), especially between the sprints performed at different torque-velocity combinations and with different upper body postures. Thus, based on this considerable similarity in the composition of the three extracted synergies, our results support the hypothesis that these muscle synergies reflect a neural control strategy during a cyclic task, with a slight timing adjustment of their activation regarding the mechanical constraints.

Three muscle synergies well explain surface EMG signals of the lower limb muscles during pedaling. The results of the present study obtained in the submaximal condition are in agreement with a recent work (Hug et al. 2010) that reported that 3 muscle synergies account for the majority of variability in the surface EMG signals of 10 muscles during pedaling. These three synergies are very similar to three of the four muscle synergies proposed by Raasch and Zajac (1999) from a pedaling simulation study. Hug et al. (2010) hypothesized that the fourth muscle synergy (i.e., the muscle group composed of the monoarticular hip and knee flexor muscles acting during the upstroke phase) identified by Raasch and Zajac (1999) was not represented, because they did not record EMG activity in monoarticular hip and knee flexors. In the present work, additional TF muscle activity was recorded, since this muscle can be primarily considered as a hip flexor acting during the upstroke phase. However, neither additional muscle synergy nor modification of already existed synergies was observed compared with the results reported by Hug et al. (2010). In fact, in this condition, TF was included in the third muscle synergy (in addition to TA and RF), which mainly acts at the end of the limb flexion phase and during the limb transition from flexion to extension. Moreover, across all mechanical constraints, the same three muscle synergies were extracted despite some adjustments in their characteristics. Overall, this supports the fact that given the impossibility of measuring other hip and knee flexors noninvasively, three muscle synergies well explain the surface EMG signals of the lower limb muscles during pedaling. Major monoarticular hip and knee flexors should...
be recorded in future studies to confirm (or not) the existence of a fourth muscle synergy.

To the best of our knowledge, only Wakeling and Horn (2009) previously explored the influence of mechanical constraints on muscle synergies during pedaling. However, because they extracted a fixed number of synergies and used a different methodology to extract muscle synergies, it is difficult to make a direct comparison (Ting and Chvatal 2010). In addition, they limited their analysis to submaximal conditions with lower alteration of the mechanical characteristics of the pedaling task (i.e., 60–140 rpm and 6.5–40 Nm) compared with those imposed in the present study (from 60 to 190 rpm and from 20 to 200 Nm with additional changes in the body configuration).

### Functional significance of muscle synergy adjustments across mechanical constraints

Note that, to our knowledge, this study is the first that compares muscle coordination between submaximal and all-out sprint exercises. Despite a few adjustments in the weighting of some muscles, especially in RF and SM in response to an alteration of torque and torque-velocity constraints (Fig. 5), the present results highlight global consistency in the muscle synergy vectors across different mechanical constraints. Consequently, the changes observed at the level of individual muscle patterns (e.g., GL, GM, and SOL; Fig. 3), for which the weighting was only slightly affected, could be better explained by change in the activation profile of activation of the synergies to which they belong.

Fig. 5. Muscle synergy vectors extracted from each condition independently. The muscle synergy vectors were averaged (±SD) across subjects for each condition. Individual muscle weightings are shown for each muscle within each synergy (#1, synergy 1; #2, synergy 2; #3, synergy 3). a.u., Arbitrary units. For muscle abbreviations, see Fig. 3.
Although the shapes of each of the three synergy activation coefficients were similar across conditions ($r_{\text{max}} > 0.84$), $r$ values (not reported here; e.g., $0.64 \pm 0.22$ for synergy 3 between submaximal and sprint conditions) were lower than those obtained for muscle synergy vectors, mainly because some lag times appeared for the torque and posture effects (Fig. 6 and Table 2, lag times). In the all-out sprint conditions, adjustments in the timing of the synergy activation coefficients led to a longer period of activity for the two first synergies across the crank cycle compared with the submaximal condition (Fig. 6). These adaptations probably reflect an interesting control strategy to enhance the duty cycle and hence the net mechanical production throughout the cycle by increasing the activity during the TDC transition by synergy 1, the total power produced and transferred to the crank during the downstroke phase as a whole by synergy 2, and the propulsive action in the BDC and upstroke phase by synergy 3. Despite significant changes at the level of individual muscles induced by changes in torque-velocity constraints, the synergy activation coefficients were similar, as shown by the very high $r_{\text{max}}$ values and the absence of a significant time shift. Consistent with the literature (Hug and Dorel 2009; Neptune et al. 1997; Wakeling and Horn 2009), earlier activation of the thigh muscles was found as the pedaling rate increased. This can be viewed as a compensatory strategy used to develop pedal force in the same crank sector despite the constant electromechanical delay (Hug...
and Dorel 2009; Neptune et al. 1997). However, as already reported (Dorel et al. 2010; Samozino et al. 2007), this compensatory strategy was not sufficient to fully prevent the forward shift of the force production at high pedaling rates, as shown in Fig. 2. This could be explained by the fact that no modification (SOL and TA) or a slightly later activation (GL and GM) was observed for leg muscles as the pedaling rate increased. In fact, as previously suggested (Raasch et al. 1997), if the ankle extensors are not activated synchronously with the vastii and GMax, the transfer of the power produced by the knee and hip extensors to the crank is not optimal. The same statement could be made for the dorsiflexor and hip/knee flexors during the upstroke phase. Consequently, in the present study, the opposite temporal changes in recruitment of the leg muscles compared with the thigh muscles might be in opposition with an optimal transfer and thus could be partly responsible of a slight shift forward of the pedal force production. Finally, in the standing condition, the forward shift of the activation for the three muscle synergies ranged from 4.7% to 7.4% of the pedaling cycle (Table 2). This is most likely the result of a shift in the kinematic data of the limb segments among the cycle, i.e., the increase of angular positions of the three articulations as a function of crank position, as reported by Li and Caldwell (1998). The forward shift of the torque profile (Fig. 2) reinforces this hypothesis.

**Neurophysiological interpretations.** As a whole, the analysis of structure of the muscle synergies demonstrated a good robustness of the set of the three extracted synergies. Indeed, both muscle synergy vectors and, to a lesser extent, synergy activation coefficients were only slightly affected by the different mechanical constraints. The consistency of the muscle synergy vectors confirmed some results obtained during different postural tasks (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2010), different behaviors in animals (d’Avella and Bizzi 2005; d’Avella et al. 2003), or different power outputs during a rowing task (Turpin et al. 2011). By comparing muscle synergies between healthy subjects and patients with...
Muscle synergy vectors (rSynergy), synergy activation coefficients (rSynergy activation coefficients) by modulating the duration and timing of muscle synergy vectors can be considered as unaffected. It confirms previous observations suggesting that the composition of muscle synergies (i.e., muscle synergy vectors) is relatively fixed but that their activation (i.e., synergy activation coefficients) can be modified by the specific constraints of the task (Cheung et al. 2009a; Cheung et al. 2009b). In other words, accordingly to previous observations made during postural perturbations (Torres-Oviedo and Ting 2010), our results suggest that the repertoire of pedaling tasks performed in the present study was achieved through the modulation of muscle synergy recruitment but not muscle synergy structure. As proposed by Cheung et al. (2005), sensory afferents may serve to adapt the activation of muscle synergies (i.e., synergy activation coefficients) by modulating the duration and timing so that their functions can be carried out even with mechanical constraints.

The fact that the lag times of two groups of muscles (i.e., gastrocnemii and hamstrings, mainly represented in the same synergy, synergy 2) were differently affected by the torque-velocity constraints could corroborate the uncoupled activity of individual muscles observed within the extracted synergy by Wakeling and Horn (2009). Nevertheless, in our opinion, it is not in contradiction with the hypothesis of the use of flexible combination of muscle synergies by the central nervous system to produce movement. In fact, previous works have shown a clear dissociation of hamstrings and gastrocnemii patterns in

stroke lesions, some authors have also reported a robustness of the muscle synergy vectors (Cheung et al. 2009a; Clark et al. 2010). Thus, our results can constitute additional evidence to confirm the hypothesis that neural drive select, activate, and flexibly combine muscle synergies to produce a wide range of movements (Cheung et al. 2009b). As suggested by another work (Saltiel et al. 2001), these muscle synergies could be specified by networks in the spinal cord and/or brain stem. This type of neural mechanism effectively reduces the musculoskeletal redundancy inherent in the multiligamentous limb (d’Avella and Bizzi 2005).

Pedaling is a useful paradigm because task mechanics can be controlled and manipulated. Nevertheless, the circular constraint trajectory of the end point force (i.e., the pedal) could certainly be considered as a reason for the low number of extracted muscle synergies and hence less complexity of motor control organization compared with postural tasks (Torres-Oviedo et al. 2006) or other locomotor tasks, such as running (Cappellini et al. 2006). Nevertheless, the diversity of mechanical constraints that have been imposed herein necessarily induced some important perturbations of the task such as difference in the sensory input signals (muscle tension, velocity of the limbs, etc.) or additional degrees of freedom (in the standing position). Interestingly, it appeared that the timing of the muscle synergies could be modulated, whereas changes in muscle synergy vectors could be considered as unaffected. It confirms previous observations suggesting that the composition of muscle synergies (i.e., muscle synergy vectors) is relatively fixed but that their activation (i.e., synergy activation coefficients) can be modified by the specific constraints of the task (Cheung et al. 2009a; Cheung et al. 2009b). In other words, accordingly to previous observations made during postural perturbations (Torres-Oviedo and Ting 2010), our results suggest that the repertoire of pedaling tasks performed in the present study was achieved through the modulation of muscle synergy recruitment but not muscle synergy structure. As proposed by Cheung et al. (2005), sensory afferents may serve to adapt the activation of muscle synergies (i.e., synergy activation coefficients) by modulating the duration and timing so that their functions can be carried out even with mechanical constraints.

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### Table 3. Comparison between the three muscles synergies extracted from the entire data set and those extracted for each condition independently

<table>
<thead>
<tr>
<th></th>
<th>Submaximal Exercise</th>
<th>Seated Sprints</th>
<th>Standing Sprint</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(80% of fopt)</td>
<td>60% of fopt</td>
<td>80% of fopt</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.87 ± 0.05</td>
<td>0.93 ± 0.06</td>
<td>0.98 ± 0.02</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.93 ± 0.03</td>
<td>0.97 ± 0.02</td>
<td>0.98 ± 0.01</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.87 ± 0.13</td>
<td>0.96 ± 0.04</td>
<td>0.96 ± 0.04</td>
</tr>
<tr>
<td>Muscle synergy vectors (r values)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.86 ± 0.11</td>
<td>0.91 ± 0.10</td>
<td>0.94 ± 0.06</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.97 ± 0.02</td>
<td>0.93 ± 0.09</td>
<td>0.97 ± 0.02</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.91 ± 0.09</td>
<td>0.94 ± 0.06</td>
<td>0.97 ± 0.04</td>
</tr>
</tbody>
</table>

Values are means ± SD.
backward pedaling (Schindler-Ivens et al. 2004; Ting et al. 1999). Thus, one would expect synergy 2 to result from functionally merged synergies rather than from an intrinsic unit of control; such functionally merged synergies have been reported during walking (Clark et al. 2010). However, our cross-validation procedure failed to highlight this phenomenon. In addition, the earlier activity in the hamstrings (BF and SM) and hip flexors (TF and RF) and later activity in the leg muscles (GL, GM, and TA) could reflect a proximodistal trend in the adaptation of individual muscle EMG patterns at high pedaling rates. In this way, it has been argued that the axonal conduction velocity of the motoneuron could explain the coordination problem of distal muscles, especially in large animals (More et al. 2010). In our study, considering a mean conduction velocity of ~45 m/s (Yap and Hirota 1967) and a distance of 0.55 m between BF/SM and GL/GM motor points, the nerve conduction velocity could be responsible for a latency of 12 ms between the EMG manifestation of a common neural command for the distal muscle (GL/GM) compared with the proximal muscle (e.g., BF/SM). The higher the pedal velocity, the higher the difference in terms of the crank position, i.e., ~3.8% of the total crank cycle at 190 rpm. This phenomenon could partially explain that muscles implied in the same synergy (SM, BF, GM, and GL in synergy 2 or RF, TF, and TA in synergy 3) could present different lag times in their EMG pattern. Finally, specifically considering the pedaling task, reaching a very high value of movement velocity seems to constitute the more critical limits of this coordination strategy. Thus, it remains unclear to what extent the sensory input could still assume a modulatory role on the activation of the predetermined muscle synergies in this extreme condition.

Methodological considerations. As done in previous works (Hug et al. 2010; Ting and Macpherson 2005; Torres-Oviedo et al. 2006), EMG activity from each muscle and each of the six pedaling conditions was normalized to the average of its peak value. Therefore, the degree of muscle activity was not taken into consideration for the comparison of individual EMG patterns across conditions or for the comparison of muscle synergies. Thus, it was not possible to directly quantify the power output contributions from each muscle synergy. This choice was motivated by the fact that an ideal normalization method to quantify the degree of muscle activity does not exist (Burden et al. 2010). Also, little is known about the influence of the normalization method on synergy extraction. For instance, it is unclear in which component of the muscle synergies, information about the degree of muscle activity, should be considered (i.e., muscle synergy vectors, synergy activation coefficients, or both)? Moreover, the results of Weisj et al. (1999) suggest that the that timing and amplitude of EMG patterns are controlled independently. Consequently, we considered muscle synergy as a covariation of muscle activation where the output level of this activation was not taken into consideration.

Also, it should be kept in mind that the subjects were trained cyclists. Thus, the results of the present study could have been partially influenced by the fact that they were trained to pedal under these different mechanical constraints. However, as previously mentioned, only these subjects could achieve these torque and torque-velocity constraints.

Conclusions. Overall, our findings are consistent with evidence that, during pedaling, muscle synergy structures are preserved across different mechanical constraints (i.e., torque, maximal torque-velocity combinations, and/or posture). Our results support the hypothesis that muscle synergies reflect a neural control strategy, with only few timing adjustment in their activation regarding the mechanics of movement.

GRANTS
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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

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