Shared muscle synergies in human walking and cycling

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1Electronics Department, University of Minho, Azurém, Guimarães, Portugal; 2Bioengineering Group, Spanish National Research Council (CSIC), Arganda del Rey, Madrid, Spain; 3Sensorimotor Function Group—National Paraplegia Hospital SESCAM, Toledo, Spain; and 4Nursing and Physical Therapy School, Castilla la Mancha University, Toledo, Spain

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Barroso FO, Torricelli D, Moreno JC, Taylor J, Gomez-Soriano J, Bravo-Esteban E, Piazza S, Santos C, Pons JL. Shared muscle synergies in human walking and cycling. J Neurophysiol 112: 1984–1998, 2014. First published July 23, 2014; doi:10.1152/jn.00220.2014.—The motor system may rely on a modular organization (muscle synergies activated in time) to execute different tasks. We investigated the common control features of walking and cycling in healthy humans from the perspective of muscle synergies. Three hypotheses were tested: 1) muscle synergies extracted from walking trials are similar to those extracted during cycling; 2) muscle synergies extracted from one of these motor tasks can be used to mathematically reconstruct the electromyographic (EMG) patterns of the other task; 3) muscle synergies of cycling can result from merging synergies of walking. A secondary objective was to identify the speed (and cadence) at which higher similarities emerged. EMG activity from eight muscles of the dominant leg was recorded in eight healthy subjects during walking and cycling at four matched cadences. A factorization technique [nonnegative matrix factorization (NNMF)] was applied to extract individual muscle synergy vectors and the respective activation coefficients behind the global muscular activity of each condition. Results corroborated hypotheses 2 and 3, showing that 1) four synergies from walking and cycling can successfully explain most of the EMG variability of cycling and walking, respectively, and 2) two of four synergies from walking appear to merge together to reconstruct one individual synergy of cycling, with best reconstruction values found for higher speeds. Direct comparison of the muscle synergy vectors of walking and the muscle synergy vectors of cycling (hypothesis 1) produced moderated values of similarity. This study provides supporting evidence for the hypothesis that cycling and walking share common neuromuscular mechanisms.

The hypothesis that biomechanical tasks reflect synergistic control of muscles is supported by experimental results in animals and humans (Barroso et al. 2013; Cheung et al. 2012; d’Avella and Bizzi 2005; De Marchis et al. 2013; Dominici et al. 2011; Gizzi et al. 2012; Hug 2011; Ivanenko et al. 2005; Moreno et al. 2013; Routson et al. 2013; Ting and Macpherson 2005) and by simulations (Allen and Neptune 2012; Neptune et al. 2009; Raasch and Zajac 1999). Despite the evident difficulty of proving or challenging the muscle synergies hypothesis (Kutch and Valero-Cuevas 2012) and the suggestion of some authors that muscular coactivation is a result of biomechanical constraints (Kutch et al. 2008; Valero-Cuevas et al. 2009), there is convincing evidence that muscle synergies are neurophysiological entities orchestrated by both supraspinal and afferent pathways to facilitate motor control (Barroso et al. 2013; Berger et al. 2013; Bizzi and Cheung 2013; Cheung et al. 2012; Chvatal and Ting 2013; Clark et al. 2010; Moreno et al. 2013; Routson et al. 2013; Torres-Oviedo and Ting 2007). Studies performed in animal models with monkeys (Overduin et al. 2012), cats (Yakovenko et al. 2011), and frogs (Hart and Giszter 2010) support the idea that activation coefficients are expressions of neural activities. Bizzi et al. (1991) found that the costimulation of two different loci in frogs produced a force field very similar to the summation of the force fields resulting from independent stimulus of each locus. Tresch and Jarc (2009) suggested that additional evidence of a neural-based synergistic control of movement can be presented by extracting similar synergies in different kinematic and biomechanical motor tasks.

There is also evidence that the same muscle synergies are shared across different biomechanical conditions, such as speed (Cappellini et al. 2006) and loads (Ivanenko et al. 2004) in human walking and multidirectional postural responses in humans and cats (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007). Whether muscle synergies are directly related to specific kinematic or kinetic goals (Ivanenko et al. 2003) or are shared between different motor tasks is still under investigation.

In this work, we quantitatively explored the hypothesis that human walking and cycling share similar muscle synergies. The rationale behind comparing walking with cycling is the specific neural-mechanical components that are thought to be shared between the tasks. For instance, Hug et al. (2010) pointed out that two of the three synergies extracted during cycling in trained cyclists were similar to two of the four synergies presented by Neptune et al. (2009) in a simulation study of the motor control in human walking. Previous studies also suggested that different forms of rhythmic movements...
may share common neuromuscular mechanisms. For instance, Chvatal and Ting (2013) showed that a common set of muscle synergies mediate reactive balance and walking. Zehr et al. (2007) compared patterns of electromyographic (EMG) and cutaneous reflex modulation during pedaling, stepping, and walking, and results supported the existence of common central control mechanisms. Pacheco et al. (2011) showed that rehabilitation treatments based on pedaling movements have potential positive outcomes on walking. Sadowsky et al. (2013) reported that a long-term treatment based on cycling combined with functional electrical stimulation (FES) in lower limbs improved neurological and functional performance of chronic spinal cord injury (SCI) patients. Therefore, it is reasonable to hypothesize that pedaling should at least share some similar neural mechanisms involved in the coordination of walking [i.e., reflexes responsible for stabilization of locomotion as well as a modular control to reduce the dimensionality problem (Pons et al. 2013)]. In a previous preliminary study, we directly compared modular control of cycling and walking at one matched speed (Barroso et al. 2013), showing that these two motor tasks may in fact share similar muscle synergies. The same evidence was observed by De Marchis et al. (2013). Nevertheless, the processes underlying this similarity are still unknown.

For human walking, it has been reported that four or five synergies are sufficient to explain most of the EMG variability of several lower limb muscles (Clark et al. 2010; Dominici et al. 2011; Ivanenko et al. 2004). In pedaling, most of the muscular activation can be explained by the combination of three muscle synergies in the case of trained cyclists (Hug et al. 2010, 2011) or four muscle synergies in nonprofessional subjects (Barroso et al. 2013; De Marchis et al. 2012).

As pedaling has fewer mechanical degrees of freedom (Rasch and Zajac 1999) with respect to walking (Zajac et al. 2002), it is expected that the number of synergies in cycling may in fact be lower than in walking. In this work, the similarity analysis has been investigated across four different speeds with a threefold methodology. First, we compared muscle synergies extracted independently for each of the tested speeds and motor tasks. Second, we tested the extent to which EMG patterns from one motor task (e.g., cycling) could be reconstructed by using the synergies of the other motor task (e.g., walking). Finally, we investigated whether synergies of cycling could be a result of a merging process of walking synergies. As a secondary objective, we wanted to identify the condition (speed and cadence) at which similarity mostly emerged. This secondary aim is motivated by the idea of using cycling as a new scenario for the diagnosis and neurorehabilitation of walking in neurologically injured people.

**MATERIALS AND METHODS**

**Subjects**

A local committee provided ethical approval for this research. Eight healthy subjects (6 men and 2 women, age 27.3 ± 1.3 yr, height 1.77 ± 0.07 m, weight 75.9 ± 7.4 kg) volunteered to participate in this study. They were informed about all procedures and possible discomforts before giving their informed consent.

**Protocol**

Each subject was instructed to refrain from intense physical activities during the 2 days before testing. For each participant, the experiment was divided into three testing sessions.

In the first session, four walking speeds were determined experimentally with a treadmill (DOMYOS TC-450 Motorised Treadmill, Decathlon, Villeneuve d’Ascq, France). These speeds were maximum walking speed (MWS, set at 0.1 km/h less than the walking-running transition speed), two intermediate speeds at which each subject walked with a cadence of 70% and 80% of the MWS cadence, and a speed that corresponded with a cadence of 42 strides/min (S42). For the 70%:MWS, 80%:MWS, and S42 conditions—the latter included to allow for an absolute comparison across subjects—a metronome was used to help the subject’s synchronization with the desired cadence. In the second session, four walking trials at the speeds previously determined were performed. In the third session, four pedaling trials on an electronically braked cycle ergometer (MOTOmed viva2, Reck, Betzenweiler, Germany) were performed at matched cadences with respect to walking. During pedaling trials, an auditory metronome was used to allow the user to synchronize with the target cycling frequency. To match cycling and walking cadences, the walking cadence (strides per minute) corresponding to each speed was calculated and then applied to the corresponding cycling trial, in terms of cycling frequency [expressed in revolutions per minute (rpm)]. The order of walking and cycling sessions, as well as the order of intrasession trials, was randomized to avoid biased results. Paired Student’s t-tests (P = 0.05) were performed to compare cadences between motor tasks for each different speed. The three sessions were performed during the same day. In the second and third sessions, each subject was first asked to warm up during a period of 5 min at a self-selected speed and then to execute each trial over 30 s, with 30-s rest between trials (Hidler and Wall 2005). The first session took ~5 min, while the second and third sessions lasted ~15 min each. A 15-min rest between sessions was permitted, in order to prevent muscle fatigue.

In the second and third sessions, muscle activity of eight muscles of the dominant leg was recorded through surface electromyography (sEMG). The skin was preliminarily shaved and cleaned with alcohol to minimize skin impedance. Bipolar EMG electrodes (Ag-AgCl, Ambu Neuroline 720, Ambu, Ballerup, Denmark) were placed, according to SENIAM recommendations (Hermens et al. 1999), on the following muscles: glutaeus medius (GMed), rectus femoris (RF), vastus lateralis (VL), biceps femoris (BF), semitendinosus (ST), gastrocnemius medialis (GM), soleus (SOL), and tibialis anterior (TA). A 2-cm interelectrode distance was ensured. The electrodes were posteriorly wrapped with bandages to ensure that the wires did not impede the subject’s movements and also to avoid movement-induced artifacts. A preliminary test to check for cross talk and cable-induced noise was performed, and, when needed, electrodes and cables were repositioned. One footswitch (NORAXON, Scottsdale, AZ) was placed beneath the heel of the dominant leg in order to record heel strike moments during walking. An EMG amplifier (EMG-USB, OT Bioeletrônica, Torino, Italy) with recording bandwidth of 10–750 Hz, overall gain of 1,000 V/V, and acquisition frequency of 2,048 Hz was used to record EMG activity.

The cycling resistance (gear) was set to a constant and comfortable value for all the trials performed by each subject and also for all the speeds, so that they could cycle with some resistance. A potentiometer (Vishay, Malvern, PA) was mounted on the crank to allow for real-time, accurate pedal angle measurement. Data from potentiometer (acquisition frequency of 50 Hz) and footswitch (acquisition frequency of 1,000 Hz) were used for segmentation of pedaling and stride cycles, respectively. As all the subjects were right leg dominant, the pedaling cycle started at the lowest pedal position (BDC) of the right crank and finished after completion of a revolution. The initiation of a stride cycle was set at each heel strike. EMG, encoder, and footswitch data were synchronized by applying a trigger signal. Data
were analyzed off-line with MATLAB R2011a (The MathWorks, Natick, MA) and IBM SPSS Statistics 20 software (IBM).

**EMG Analysis**

Before starting the EMG processing, we carefully inspected EMG recordings of all the muscles, looking in particular for noise artifacts. For each trial, 10 continuous, noncorrupted stride/cycling cycles were selected for analysis. Raw EMG signals were high-pass filtered (3rd-order Butterworth digital, cutoff frequency of 20 Hz, roll-off rate of 12 dB/decade) to attenuate DC offset and motion artifacts (Moreno et al. 2013). The trials contaminated with 50-Hz electromagnetic interference were additionally filtered by a 50-Hz notch filter (order 10). After that, all the filtered signals were de-meaned, rectified, and low-pass filtered at 5 Hz (3rd-order Butterworth digital, roll-off rate of 12 dB/decade), resulting in the EMG envelopes (Clark et al. 2010; Hug et al. 2010; Moreno et al. 2013).

To facilitate comparison across subjects, motor tasks, and speeds, the EMG from each muscle was normalized by the average of its peaks from the 10 cycles and resampled at each 1% of the stride/cycling cycle. For each cycle, we subtracted the minimum of that cycle in order to obtain a minimum value of zero for all cycles. For each subject, motor task, and speed, normalized EMGs were combined into an $m \times t$ matrix (EMG$_m$), where $m$ indicates the number of muscles (8 in this case) and $t$ is the time base [t = no. of strides (10) \times 100 samples].

Differences across EMG patterns were assessed with the $r_{max}$ coefficient (Hug 2011; Hug et al. 2011), which is the maximum of the cross-correlation between two signals. The cross-correlation is calculated by the MATLAB xcorr function for centered data (option = “coeff”) and the output values as the maximum of the cross-correlation function, which gives an indication of the similarity of shape of the EMG envelopes.

**Muscle Synergy Analysis**

To extract the muscle synergy vectors and the correspondent activation coefficients, the nonnegative matrix factorization (NNMF) algorithm (Lee and Seung 1999) was applied over the 10 consecutive walking/pedaling cycles of the EMG envelopes (Barroso et al. 2013) for each subject and speed. This algorithm assumes that EMG envelopes from each muscle can be described as a linear combination of a set of muscle synergy vectors (time-invariant profiles) activated by time-variant activation coefficients. This assumption can be described as follows:

$$\text{EMG}_0 = WH + e = \text{EMG}_t + e \quad (1)$$

where $W$ is a $m \times n$ matrix (n is the number of synergies) that specifies the spatial profiles of activation (relative weight of each muscle within each synergy); $H$ is a $n \times t$ matrix that specifies time-varying coefficients of activation (the relative contribution of each synergy for each muscular pattern); EMG$_t$, namely, the reconstructed EMG, is an $m \times t$ matrix resulting from the multiplication of $W$ and $H$; and $e$ is the residual error, i.e., the difference between EMG$_0$ and EMG$_t$, typically related to noise (Dominici et al. 2011). At each iteration, the algorithm updates matrices $W$ and $H$ in order to minimize the residual Frobenius norm between EMG$_0$ and EMG$_t$, assuming a Gaussian distribution of error (Lee and Seung 1999). The number of synergies being an input of the NNMF algorithm, the algorithm was run from two to seven synergies.

To allow comparisons among subjects, speeds, and motor tasks, muscle synergy vectors (columns of matrix $W$) were normalized by the maximum of each column, as done by Hug et al. (2010), and the corresponding activation coefficients (lines of matrix $H$) were scaled by the same quantity (De Marchis et al. 2012).

As NNMF can get stuck in local minima, depending on the random initialization of $W$ and $H$, we applied the algorithm 40 times and selected the run with the lowest reconstruction error. A minimum number of muscle synergies need to be considered reasonable so that the variability between EMG$_0$ and EMG$_t$ can be rated as good. Therefore, the similarity between EMG$_0$ and EMG$_t$ was calculated by the variability accounted for (VAF) coefficient, as represented in Eq. 2:

$$VAF_{total} = 1 - \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} (\text{EMG}_0(i,j) - \text{EMG}_t(i,j))^2}{\sum_{i=1}^{m} \sum_{j=1}^{n} (\text{EMG}_0(i,j))^2} \quad (2)$$

VAF was also computed for each muscle individually (VAF$_{musc}e$). Minimum values of 90% of VAF$_{musc}$ (Hug et al. 2010) and 75% for VAF$_{musc}$ were used to consider the quality of reconstruction acceptable (Hug 2011).

For each speed and motor task, a representative set of matrices $W_0$ and $H_0$ was obtained by pooling the EMG envelopes from all the subjects and then applying the NNMF algorithm. $W_0$ and $H_0$ are different from an averaged profile of activation across subjects, because it takes into account the intra- and intersubject variability. $W_0$ at MWS was also used as a template to order the synergies extracted independently from each subject, by comparing each individual column of matrix $W$ (muscle synergy vectors) with the columns of the reference matrix $W_0$, by means of the normalized scalar product (Gizzi et al. 2011), with the less similar being the last ordered.

We divided data analysis into three sections: section I, analysis of walking; section II, analysis of cycling; and section III, comparison between walking and cycling. Sections I and II aimed to compare our results with the literature on walking and cycling, respectively. Section III aimed to test the hypotheses of this work. To this aim, we performed a threefold analysis. The first analysis was done by correlating muscle synergy vectors of walking with those of cycling, using the normalized scalar product as a metric for similarity. Normalized scalar products = 0.75 were taken as similarity threshold (Cheung et al. 2012). Second, we tested the hypothesis that EMGs of cycling could be reconstructed with the synergies ($W$) extracted from walking, and vice versa, for each speed and subject. VAF values were calculated to evaluate the quality of this reconstruction. Third, we tested the hypothesis that global cycling synergies—obtained by pooled EMG data—could be obtained by merging different walking synergies. We adapted the algorithm described by Cheung et al. (2012) to calculate which synergies extracted at cycling could be reconstructed by linear combinations of synergies extracted at walking, as explained in Eq. 3:

$$w_j = \sum_{k=1}^{n_{walking}} m_{jk} W_0 \quad (3)$$

where $w_j$ is the $j$th muscle synergy vector (column of matrix $W_0$) from cycling, $w_i$ is the $i$th muscle synergy vector from walking, $n_{walking}$ is the number of synergies at walking (4 in this case), $n_{cycling}$ is the number of synergies at cycling (3 in this case), and $m_{ij}$ is a nonnegative coefficient denoting the degree of contribution of the $i$th synergy from walking to the structure of the $j$th synergy from cycling. This algorithm was applied through nonnegative least squares implemented with the IpSonnneg option in MATLAB. A walking synergy was considered to significantly contribute to the corresponding cycling synergy if the merging coefficient ($m_{ij}$) was higher than 0.3. According to this method, and for matched speeds, each synergy extracted at walking (with pooled data) could contribute to the reconstruction of one or more synergies at cycling. After selection of the walking synergies that could contribute for the reconstruction of cycling synergies, similarity between reconstructed $w_j$ and the initially extracted synergy of cycling was assessed by using the normalized scalar product between corresponding columns.

In addition to the analysis of synergies, a simple analysis of temporal activations ($H_0$) was also performed, in order to identify the periods of activation and no activation of each synergy along the gait and pedaling cycle. This analysis was done by defining an onset threshold calculated as the triple SD range of activation for each activation coefficient (Moreno et al. 2013).
RESULTS

Section I. Independent Analysis of Walking

**EMG envelopes.** The average EMG envelopes of each muscle across the eight subjects for all walking speeds are represented in Fig. 1A.

The shapes of the EMG envelopes correlated well across speeds for each individual subject. The lowest correlation value when compared with MWS was obtained for RF at S42 speed (0.79 ± 0.08, range 0.69–0.92), and the higher correlation was obtained for SOL at 80%MWS (0.98 ± 0.01, range 0.96–0.99). From visual inspection of Fig. 1A, it can be

**Fig. 1.** Group-averaged electromyographic (EMG) patterns of the 8 recorded muscles for each of the 4 studied speeds in walking (A) and cycling (B): 10 individual cycles of the 8 subjects (total of 80 cycles), expressed as a function of the cycle. In walking the beginning of the cycle was determined by the heel strike, whereas in cycling it corresponded to the lowest position of the right pedal. For each subject, EMGs from each muscle were previously normalized by the average of its peaks throughout the 10 cycles. GMed, gluteus medius; RF, rectus femoris; VL, vastus lateralis; BF, biceps femoris; ST, semitendinosus; GM, gastrocnemius medialis; SOL, soleus; TA, tibialis anterior; MWS, maximum walking speed; S42, speed at which each subject walked/cycled at 42 strides/revolutions per minute; 70%MWS, speed at which each subject walked/cycled with a cadence of 70% of MWS cadence; 80%MWS, speed at which each subject walked/cycled with a cadence of 80% of MWS cadence; a.u., arbitrary unit.
observed that the peak of activation of some muscles occurs slightly earlier in the gait cycle as the speed increases, e.g., in RF and TA. The lower the speed, the later this peak occurred.

Muscle synergies. Four synergies were sufficient to reconstruct the original EMG envelopes of each subject, for each speed, according to our criteria (VAF\textsubscript{total} > 90% for the total EMG data and VAF\textsubscript{muscle} > 75% for each individual muscle), for all subjects and speeds. A minimum of 90.7% for subject 8 at S42 and a maximum of 96% for subject 3 at MWS were obtained for VAF\textsubscript{total}. Nevertheless, three synergies were also sufficient to fit our criteria in one subject in walking.

The general tendency among subjects was to observe higher VAF\textsubscript{total} values for higher speeds (see Fig. 2A). The inclusion of a fifth synergy did not improve the reconstruction quality considerably.

When analyzing VAF\textsubscript{muscle} with three synergies (see Fig. 3A), some muscles were not so well reconstructed. For instance, ST presented a VAF\textsubscript{muscle} value of 78.3 ± 13.6 at S42 and BF presented a VAF\textsubscript{muscle} value of 77.3 ± 10.7 at 70%MWS. On the other hand, when analyzing VAF\textsubscript{muscle} values with four synergies (see Fig. 3B), all the muscles presented mean VAF\textsubscript{muscle} values higher than 87%, and most of them presented VAF\textsubscript{muscle} values higher than 92%. Like VAF\textsubscript{total}, VAF\textsubscript{muscle} values also increased, in general, with the increase of speed, for three and four synergies, as represented in Fig. 3, A and B, respectively.

A representative set of muscle synergy vectors (columns of matrix W\textsubscript{0}) and the corresponding activation coefficients (lines of matrix H\textsubscript{0}) at the MWS condition of the entire group is represented in Fig. 4, AII and AI, respectively. For all the speeds, matrices W\textsubscript{0} and H\textsubscript{0} (see Fig. 4, AIV and AIII) were extracted by using the NNMF algorithm after concatenating 10 cycles from all eight subjects. The quality of reconstruction of the EMGs when using W\textsubscript{0} and H\textsubscript{0} was quite good with four
synergies. In fact, except for the S42 condition (VAF\textsubscript{total} = 87.7%), it was possible to obtain VAF\textsubscript{total} values higher than 90%. These results improved for higher speeds (90.2% for 70%MWS, 90.7% for 80%MWS, and 90.9% for MWS).

When analyzing matrices W\textsubscript{0} and H\textsubscript{0} from Fig. 4A, the following properties can be identified. Synergy 1 consisted mainly of the activity of GMed (hip abductor and hip flexor) and TA (ankle dorsiflexor) (see Fig. 4AV). For higher speeds, this synergy was also responsible for the activation of VL (mainly a knee extensor). This synergy was mainly activated during early stance. Synergy 2 is represented by the activity of RF (hip flexor, also knee extensor) and, to a minor extent, of VL and TA. This synergy contributed in a lower extent for VL activation with the increase of speed, in opposition to the synergy 1 influence. This synergy 2 presented two peaks of activation: one at midstance phase and the other at initial swing phase. The peak at initial swing phase was lower for lower speeds. Synergy 3 consisted mainly of the activity of GM (knee flexor and ankle plantarflexor) and SOL (ankle plantarflexor) during late stance. Synergy 4 is represented by BF (hip extensor and knee flexor), ST (hip extensor and knee flexor) and, to a minor extent, TA muscles at terminal swing and initial stance. The contribution of this synergy for TA overall activity was higher for decreasing speeds.

Section II: Independent Analysis of Cycling

EMG envelopes. The average EMG envelopes from each muscle across the eight subjects for all cycling speeds are represented in Fig. 1B. The shape of EMG envelopes was very similar across speeds. This is corroborated by the high correlation values across speeds. When compared with MWS, the lowest correlation value was 0.91 ± 0.06 (range 0.80–0.99) for SOL at 70%MWS.

Muscle synergies. Four synergies were sufficient to describe most of the variance of the EMG envelopes for all the studied subjects and speeds, according to the first inclusion criterion (VAF\textsubscript{total} > 90%), as represented in Fig. 2B. A minimum of 92% for subject 1 at 80%MWS and a maximum of 96% for subject 4 at 70%MWS were obtained for VAF\textsubscript{total}. The individual VAF\textsubscript{muscle} values were higher than 90% (see Fig. 3D) for all muscles and conditions of cycling. In the case of three synergies, VAF\textsubscript{total} oscillated around 90%. Three synergies were sufficient to fit our criteria in six of the eight subjects. A minimum of 87% for subject 1 at 80%MWS and a maximum of 94% for subject 7 at S42 were obtained for VAF\textsubscript{total}. Conversely, the VAF\textsubscript{muscle} was higher than 83% for all muscles, which fit the second inclusion criterion, based on VAF\textsubscript{muscle} > 75% (see Fig. 3C). Interestingly, VAF\textsubscript{total} did not increase with the increase of speed. The inclusion of a fifth synergy did not improve the reconstruction quality considerably (see Fig. 2B).

Representative sets of three and four muscle synergy vectors (columns of matrix W\textsubscript{0}) and the corresponding activation coefficients (lines of matrix H\textsubscript{0}) of the entire group while cycling at MWS are represented in Fig. 4, BII and BI, and Fig. 4, CII and CI, respectively. For all speeds, matrices W\textsubscript{0} and H\textsubscript{0} (see Fig. 4, BIV and BIII and CIV and CIII) were also extracted. This representation allowed us to have a global template of the modular control of cycling for the different speeds and compare it with the literature.

When using three synergies, synergy 1 is represented mainly by the activity of TA and, to a lower extent, by RF, GMed, and SOL (see Fig. 4BIV). The contribution of this synergy to the total activity of RF and GMed decreased drastically with the speed. This synergy was mainly active during the initial upstroke phase of cycling (see Fig. 4BII). Synergy 2 is composed of RF, GMed, VL, and, to a lower extent, SOL, being mainly active during the final upstroke phase and initial downstroke phase of cycling. Synergy 3 is clearly represented by the activity of BF, ST, GM, and SOL. Its contribution to SOL activity decreased with the speed. This synergy was active during the downstroke phase of cycling.

Considering the case of four muscle synergies, as represented in Fig. 4C, it can be observed that two different synergistic profiles were obtained: one for lower speeds (S42 and 70%MWS) and the other for higher speeds (80%MWS and MWS). Comparing the condition of four synergies for higher speeds with the case of three synergies, it can be observed that, respectively, synergy vector 4 corresponds to synergy vector 3, synergy vector 3 has practically the same morphology of synergy vector 2, and synergy vectors 1 and 2 are fractions of synergy vector 1. On the other hand, synergy compositions (columns of W\textsubscript{0}) for S42 and 70%MWS were very different, mainly because synergy 3 was only responsible for the activation of SOL.

The quality of reconstruction of EMG profiles with concatenated data from all the subjects was higher than 84% when using three synergies and higher than 89% when using four synergies.

Section III. Comparison Between Walking and Cycling

Cadence. Similarity in the cadence during walking and cycling trials for all the speeds was preliminarily computed. Results showed that subjects were capable of maintaining a very similar cadence between matched speeds, with no significant differences (P > 0.05 for all speeds). In particular, walking trials were performed at a mean cadence of 42.1 ± 3.0 strides/min for S42, 50.1 ± 3.6 strides/min for 70%MWS, 56.7 ± 4.6 strides/min for 80%MWS, and 67.7 ± 3.3 strides/min for MWS. Cycling trials were performed at a mean cadence of 43.0 ± 2.7 rpm for S42, 46.6 ± 4.8 rpm for 70%MWS, 56.7 ± 5.1 rpm for 80%MWS, and 70.0 ± 4.0 rpm for MWS.

In the following subsections we present the results of the threefold analysis of similarity based on the following approaches: 1) direct comparison of muscle synergy vectors, 2) cross-reconstruction of the EMG of cycling by means of walking synergy vectors and vice versa, and 3) merging walking synergy vectors in order to obtain cycling synergy vectors.

Direct correlation of muscle synergy vectors. The four extracted synergies of walking were compared with the four synergies extracted for cycling, as done in our previous work (Barroso et al. 2013). In this case, we used the normalized scalar product between matched synergy vectors for each subject and speed. The results (see Table 1) showed a mean similarity of 0.738 for the MWS condition, 0.66 for the 80%MWS condition, 0.723 for the 70%MWS condition, and 0.722 for the S42 condition. Nevertheless, at least one of the synergies had, generally, a normalized scalar product lower than 0.75.

Supported by the fact that cycling can be also well represented by three synergies (Hug et al. 2010, 2011), we performed the same methodology described above, but this time correlating the three muscle synergy vectors extracted in
cycling with those extracted in walking that best correlated with them (see Table 2). Synergy 3 of cycling was the one with lower similarity values when compared with walking synergy. Correlation values of synergy 3 also varied considerably across subjects. Nonetheless, correlation values in the case of three synergies were better than those obtained with four synergies, across all conditions. Mean correlation values of 0.777 for the MWS condition, 0.737 for the 80% MWS condition, 0.778 for the 70% MWS condition, and 0.737 for the S42 condition were obtained.

Cross-reconstruction of EMG. For each speed and subject, the NNMF algorithm was applied, using the walking synergy vectors (columns of matrices W) to reconstruct the cycling EMG envelopes, and vice versa, at each corresponding matched speed. An individual example of the reconstruction of the cycling EMG envelopes in the MWS condition is represented in Fig. 5A. The activation coefficients that best fit the walking synergy vectors (represented in Fig. 5C) are depicted in Fig. 5B.

Average VAF<sub> Muscle </sub> values when reconstructing cycling EMG envelopes with the corresponding four synergies from walking are represented in Fig. 4. These values were high for GMed, RF, VL, and TA; on the other hand, low VAF<sub> Muscle </sub> values were found for BF, ST, GM, and SOL. When analyzing VAF<sub> Total </sub> values of this reconstruction but with three synergies (Fig. 6D), a minimum value of 71.9 ± 5.6% for S42 and a maximum value of 77.5 ± 2.4% for MWS were obtained. When using four synergies from cycling, a minimum value of 77.9 ± 4.3% for S42 and a maximum value of 81.5 ± 0.9% for MWS were obtained. Mean VAF<sub> Total </sub> values of this reconstructed data also increased with the increase of speed, with the best reconstruction values achieved for the MWS conditions.

Average VAF<sub> Muscle </sub> values when reconstructing walking EMG envelopes with the corresponding four synergies from cycling are represented in Fig. 6C. These values were high for GMed, RF, VL, and TA; on the other hand, low VAF<sub> Muscle </sub> values were found for BF, ST, GM, and SOL. When analyzing VAF<sub> Total </sub> values of this reconstruction but with three synergies (Fig. 6D), a minimum value of 71.9 ± 5.6% for S42 and a maximum value of 77.5 ± 2.4% for MWS were obtained. When using four synergies from cycling, a minimum value of 77.9 ± 4.3% for S42 and a maximum value of 81.5 ± 0.9% for MWS were obtained. Mean VAF<sub> Total </sub> values of this reconstructed data also increased with the increase of speed, with the best reconstruction values achieved for the MWS conditions.

When comparing the two types of reconstruction, similar values of VAF<sub> Total </sub> were achieved when using three synergies. On the contrary, the reconstruction of cycling envelopes with walking synergies was better than the other reconstruction, when using four synergies.

**Merging of muscle synergy vectors.** Muscle synergy vectors extracted from concatenated data of walking (those represented in Fig. 4AIV) were merged, by linear combination, in order to reconstruct synergy vectors similar to those extracted from concatenated data of cycling (represented in Fig. 4BIV), according to Eq. 3. The schematic of the merging process for MWS condition is represented in Fig. 7. The merging coefficients of the merging process are presented in Table 3.

**Table 1. Normalized scalar product between matched synergies from walking and cycling, according to their similarity values**

<table>
<thead>
<tr>
<th>Subject 1</th>
<th>Subject 2</th>
<th>Subject 3</th>
<th>Subject 4</th>
<th>Subject 5</th>
<th>Subject 6</th>
<th>Subject 7</th>
<th>Subject 8</th>
<th>Mean Values</th>
<th>Mean Values for Each Speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>S42</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.722</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.99</td>
<td>0.61</td>
<td>0.67</td>
<td>0.85</td>
<td>0.85</td>
<td>0.61</td>
<td>0.72</td>
<td>0.66</td>
<td>0.75</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.92</td>
<td>0.88</td>
<td>0.51</td>
<td>0.92</td>
<td>0.47</td>
<td>0.75</td>
<td>0.82</td>
<td>0.69</td>
<td>0.75</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.91</td>
<td>0.75</td>
<td>0.99</td>
<td>0.68</td>
<td>0.79</td>
<td>0.78</td>
<td>0.87</td>
<td>0.96</td>
<td>0.84</td>
</tr>
<tr>
<td>Synergy 4</td>
<td>0.76</td>
<td>0.11</td>
<td>0.48</td>
<td>0.78</td>
<td>0.63</td>
<td>0.52</td>
<td>0.78</td>
<td>0.39</td>
<td>0.56</td>
</tr>
<tr>
<td>70% MWS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.723</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.79</td>
<td>0.47</td>
<td>0.89</td>
<td>0.71</td>
<td>0.89</td>
<td>0.84</td>
<td>0.76</td>
<td>0.67</td>
<td>0.75</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.94</td>
<td>0.36</td>
<td>0.91</td>
<td>0.83</td>
<td>0.81</td>
<td>0.78</td>
<td>0.89</td>
<td>0.79</td>
<td>0.79</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.73</td>
<td>0.64</td>
<td>0.93</td>
<td>0.6</td>
<td>0.76</td>
<td>0.7</td>
<td>0.42</td>
<td>0.56</td>
<td>0.67</td>
</tr>
<tr>
<td>Synergy 4</td>
<td>0.75</td>
<td>0.61</td>
<td>0.65</td>
<td>0.69</td>
<td>0.76</td>
<td>0.43</td>
<td>0.65</td>
<td>0.91</td>
<td>0.68</td>
</tr>
<tr>
<td>80% MWS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.66</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.27</td>
<td>0.66</td>
<td>0.85</td>
<td>0.76</td>
<td>0.85</td>
<td>0.75</td>
<td>0.57</td>
<td>0.69</td>
<td>0.68</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.71</td>
<td>0.83</td>
<td>0.99</td>
<td>0.96</td>
<td>0.95</td>
<td>0.24</td>
<td>0.69</td>
<td>0.83</td>
<td>0.66</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.56</td>
<td>0.12</td>
<td>0.71</td>
<td>0.65</td>
<td>0.91</td>
<td>0.69</td>
<td>0.57</td>
<td>0.23</td>
<td>0.56</td>
</tr>
<tr>
<td>Synergy 4</td>
<td>0.73</td>
<td>0.64</td>
<td>0.93</td>
<td>0.82</td>
<td>0.75</td>
<td>0.53</td>
<td>0.68</td>
<td>0.91</td>
<td>0.75</td>
</tr>
<tr>
<td>MWS</td>
<td></td>
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<td>0.738</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.7</td>
<td>0.84</td>
<td>0.82</td>
<td>0.93</td>
<td>0.68</td>
<td>0.84</td>
<td>0.74</td>
<td>0.87</td>
<td>0.80</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.79</td>
<td>0.84</td>
<td>0.31</td>
<td>0.95</td>
<td>0.52</td>
<td>0.15</td>
<td>0.81</td>
<td>0.97</td>
<td>0.67</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.75</td>
<td>0.85</td>
<td>0.7</td>
<td>0.79</td>
<td>0.85</td>
<td>0.75</td>
<td>0.72</td>
<td>0.36</td>
<td>0.72</td>
</tr>
<tr>
<td>Synergy 4</td>
<td>0.78</td>
<td>0.83</td>
<td>0.84</td>
<td>0.81</td>
<td>0.75</td>
<td>0.64</td>
<td>0.66</td>
<td>0.78</td>
<td>0.76</td>
</tr>
</tbody>
</table>

Similarity was calculated between the 4 extracted synergies for both motor tasks. The similarity threshold was set to 0.75. S42, speed corresponding to a cadence of 42 strides/revolutions per minute; MWS, maximum walking speed.
A walking synergy was considered to significantly contribute to the merging of a cycling synergy if the merging coefficient was >0.3. After selecting the contribution of the selected synergies and merging them, similarity between reconstructed and original synergies of cycling was assessed. The results are presented in Table 4.

MWS and 80%MWS were the speeds at which more similarities were found in the merging process. Synergy 3 from cycling was always very well reconstructed with linear combinations from synergies 3 and 4 from walking, for all speeds (see similarity values in Table 4). Also, for MWS and 80%MWS conditions, synergies 1 and 2 from cycling could both be reconstructed by merging synergies 1 and 2 from walking (see Table 3). For S42 and 70%MWS, synergy 2 from cycling could be well reconstructed by merging synergies 1 and 2 from walking. Finally, synergy 1 from cycling at S42 and 70%MWS conditions could not be well reconstructed by merging synergies from walking.

### DISCUSSION

#### Novelty of the Work

The most remarkable finding of this work is that, in healthy subjects, synergies composing modular control of cycling can be explained by a merging process of walking synergies. In our previous study (Barroso et al. 2013), we directly compared modular control of cycling and walking at one selected speed (MWS), giving preliminary evidence that these two motor tasks have similar muscle synergies. In the present work, we reproduced the experiments with different subjects and a bigger sample size, including three more different speeds, and investigated the additional merging hypothesis as well as the cross-reconstruction of EMG patterns.

#### Cadence

As no statistically significant differences ($P > 0.05$ for all speeds) between matched speeds for walking and cycling were verified, the rhythmic activity generated by central pattern generators (CPGs) (Lacquaniti et al. 2012) did not bias the comparison.

#### Electromyographic Patterns in Walking and Cycling

According to a large number of previous studies (Clark et al. 2010; Dominici et al. 2011; Gizzi et al. 2011, 2012; Hug et al. 2011), EMG signals from both legs are very similar in healthy people. For this reason, and since all the subjects were right leg dominant, we analyzed muscles from the right leg.

The EMG envelopes recorded for walking trials were very similar to those in the literature (Clark et al. 2010; Dominici et al. 2011; Gizzi et al. 2012; Hidler and Wall 2005; Ivanenko et al. 2004; Moreno et al. 2013; Nymark et al. 2005; Ricamato and Hidler 2005). The peak of activation of some muscles occurred earlier in the gait cycle as the speed increased, in agreement with other authors (Hof et al. 2002; Ivanenko et al. 2004). This behavior seems to be related to changes in the duration of stance (Ivanenko et al. 2004). As the walking speed increases, the activations are simply played faster, with no change in the relative timing of activation of EMG profiles (Hof et al. 2002).

As to cycling, EMG envelopes were also similar to those presented in the literature (De Marchis et al. 2013; Hug et al. 2010, 2011; Wakeling and Horn 2009), with the exception of some muscles (e.g., RF, BF, and ST) whose activations occurred earlier within the pedaling cycle. This might be due to the slightly different seating position of the subjects in our study; whereas the individuals analyzed in the studies referred to above were seated in an ergometer with the seat above the axis of rotation, we used a conventional chair with a seating position closer in height to the axis of rotation. The correlation between the EMG envelopes at MWS and the other speeds was higher than those observed for walking. Best correlation values were obtained for higher speeds. This can be explained by the evidence (Baum and Li 2003; Marsh and Martin 1995; Wakeling and Horn 2009) that cadence affects EMG profiles of some muscles of the lower limb.

#### Dimensionality of Modular Control

Our results show that a low-dimensional and impulsive control is sufficient to control both motor tasks. Four synergies were sufficient to explain >90% of total variability of EMG...
activity of the eight studied muscles for all subjects and speeds during walking and cycling. For cycling movements, this dimensionality seems to be reduced if compared with walking (see Figs. 2 and 3). Six of the eight subjects just needed three synergies to fit our criteria ($VAF_{total} \geq 90\%$ and $VAF_{muscle} \geq 75\%$) for cycling. On the other side, seven of the eight subjects needed four synergies in walking. Apparently, three synergies are sufficient to represent most of the EMG activity of non-
trained cyclists with the subset of eight muscles analyzed. In our previous work (Barroso et al. 2013), we found four muscle synergies for both walking and cycling at MWS. Nevertheless, we note that, in the case of cycling, two of the four synergies (one related to the main activation of hamstrings and the other mainly responsible for GM and SOL activation) were activated by similar activation coefficients (both in time and in shape).

There are many factors that can influence the number of extracted synergies. One main issue that is rarely referred to is the cutoff frequency of the low-pass filter to obtain EMG envelopes. This value should be adapted to the type of study and frequency of movement (Hug 2011). In this case, we applied the same cutoff frequency for all trials and types of movement. Another aspect is the number of muscles considered, which can affect the number of extracted synergies (Clark et al. 2010; Monaco et al. 2010; Steele et al. 2013). In contrast to what we did in our previous work (Barroso et al. 2013), here we did not analyze EMG activity from gluteus maximus and tensor fasciae latae; we also applied a different processing methodology to obtain EMG envelopes. All these factors may explain the differences in the dimensionality. Finally, little is known about the influence of the normalization procedures on the number of extracted synergies (Hug et al. 2011), as well as on their composition. Nonetheless, as reported by Gizzi et al. (2012), the small differences in dimensionality found in different studies are not in disagreement with the hypothesis that motor coordination can be represented by a small set of muscle synergies, robust to explain differences between subjects and conditions.

According to d’Avella and Bizzi (2005) and Bizzi and Cheung (2013), muscle synergies may act to constrain the possibilities of motor output. As cycling is a motor task with fewer degrees of freedom than walking (Raasch and Zajac 1999; Zajac et al. 2002), it is expected that a higher number or at least the same number of synergies are needed to adequately reconstruct EMG envelopes of walking when compared with cycling.

**Reconstruction Quality**

At walking, VAF$_{total}$ increased with the speed for most of the subjects, which is in accordance with the results presented by Ivanenko et al. (2004). According to Tresch et al. (2006), lower signal-to-noise ratio of EMG envelopes at lower speeds may result in lower VAF$_{total}$ values. On the other hand, VAF$_{total}$ of cycling was constant across speeds, for the same number of synergies.

The quality of reconstruction of EMG data obtained by pooling together all the subjects was also quite good when using four synergies for walking (VAF$_{total} > 88\%$ for all speeds) and three synergies for cycling (VAF$_{total} > 84\%$ for all speeds). These results show that intra- and intersubject variability can be represented by a unique and fixed set of muscle synergies.
Functional Interpretation of Muscle Synergies

Coordination of muscular activation is needed in order to execute biomechanical tasks, because individual muscle action cannot, in general, result in a functional biomechanical function (Zajac et al. 2002). Because of the articulated nature of the body, the activation of a muscle may be reverberated in other muscles and joints that are not connected to that muscle. Synergies may incorporate knowledge of both musculoskeletal dynamics (Berniker et al. 2009) and other biomechanical properties of the limb. The set of all existing synergies should be thought as a compendium of coordinative patterns to execute several movements under different biomechanical conditions (Bizzi and Cheung 2013). Nevertheless, other mechanisms such as feedback-related activities (Kutch and Valero-Cuevas 2012) and monosynaptic stretch reflexes may also contribute to individual muscular activity and muscle coupling.

We analyzed the representative sets of muscle synergy vectors (columns of matrices $W_0$) and the corresponding activation coefficients (lines of matrices $H_0$), extracted by pooling EMG data from all subjects (Fig. 4, A–C, IV and III), and obtained the following functional interpretation.

Table 3. Representation of the merging coefficients

<table>
<thead>
<tr>
<th>Cycling</th>
<th>Synergy 1</th>
<th>Synergy 2</th>
<th>Synergy 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>S42 walking</td>
<td>0.28</td>
<td>0.78</td>
<td>0.00</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.02</td>
<td>0.86</td>
<td>0.03</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.07</td>
<td>0.00</td>
<td>0.82</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.34</td>
<td>0.00</td>
<td>0.66</td>
</tr>
<tr>
<td>70%MWS walking</td>
<td>0.47</td>
<td>0.56</td>
<td>0.00</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.10</td>
<td>0.84</td>
<td>0.00</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.09</td>
<td>0.05</td>
<td>0.77</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.17</td>
<td>0.00</td>
<td>0.97</td>
</tr>
<tr>
<td>80%MWS walking</td>
<td>0.51</td>
<td>0.52</td>
<td>0.02</td>
</tr>
<tr>
<td>Synergy 1</td>
<td>0.50</td>
<td>0.55</td>
<td>0.00</td>
</tr>
<tr>
<td>Synergy 2</td>
<td>0.07</td>
<td>0.11</td>
<td>0.75</td>
</tr>
<tr>
<td>Synergy 3</td>
<td>0.07</td>
<td>0.00</td>
<td>0.88</td>
</tr>
<tr>
<td>Synergy 4</td>
<td>0.00</td>
<td>0.18</td>
<td>0.96</td>
</tr>
</tbody>
</table>

Merging coefficients >0.3 (bold) were considered to contribute to the merging procedure.

Table 4. Similarity between reconstructed synergies, as obtained by merging process, and corresponding cycling synergies

<table>
<thead>
<tr>
<th></th>
<th>Synergy 1</th>
<th>Synergy 2</th>
<th>Synergy 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>S42</td>
<td>0.61</td>
<td>0.98</td>
<td>0.89</td>
</tr>
<tr>
<td>70%MWS</td>
<td>0.62</td>
<td>0.93</td>
<td>0.95</td>
</tr>
<tr>
<td>80%MWS</td>
<td>0.76</td>
<td>0.84</td>
<td>0.98</td>
</tr>
<tr>
<td>MWS</td>
<td>0.85</td>
<td>0.75</td>
<td>0.98</td>
</tr>
</tbody>
</table>

Similarity was assessed by using the normalized scalar product between corresponding columns. Values >0.75 (representing good similarity) appear in bold.

Fig. 7. Cycling synergies explained as a merging (linear combination) of walking synergies for MWS speed. Each of the 4 walking synergies was considered to contribute significantly to the merging of a cycling synergy if its merging coefficient was >0.3 (see Table 3). Each synergy extracted at walking could contribute to the reconstruction of 1 or more synergies at cycling. After selection of the contribution of the selected synergies for the merging model, similarity between reconstructed and original cycling synergies was assessed by using the normalized scalar product between corresponding columns. For instance, at MWS synergies 1 (W1) and 2 (W2) from cycling could be well reconstructed by merging synergies 1 (W1) and 2 (W2) from walking and synergy 3 (W3) from cycling could be well reconstructed by merging synergies 3 (W3) and 4 (W4) of walking. Reconstructed synergies presented high degrees of similarity when compared with original synergies: 0.85 for W1, 0.75 for W2, and 0.98 for W3.
Synergy 2 (hip flexor and knee extensors) contributed to the control of the ankle during initial stance and initial swing (foot liftoff) (Lacquaniti et al. 2012; Moreno et al. 2013; Neptune et al. 2009). Synergy 3 (knee flexors and ankle plantarflexors) mainly contributed to the forward propulsion of the foot during terminal stance phase (Lacquaniti et al. 2012; Moreno et al. 2013; Neptune et al. 2009). Synergy 4 (hip extensors and knee flexors) was a major factor responsible for leg movement during terminal swing (deceleration of the leg in preparation for heel contact) and preparation for initial stance (stabilizing the leg after heel contact) (Lacquaniti et al. 2012; Moreno et al. 2013; Neptune et al. 2009).

The results presented in Fig. 4B are very similar to those already published by Hug et al. (2010) for cycling. Synergy 1 of cycling (involving primarily hip flexor, knee extensor, and ankle dorsiflexor) mainly provided force to start the upstroke phase of cycling (Barroso et al. 2013). The energy generated by RF in this phase of cycling is transmitted to the crank by the activation of TA (Rausch and Zajac 1999). TA is excited early in this phase because of its participation in flexion of the limb. Synergy 2 (hip abductor, hip flexor, knee extensors, and ankle plantarflexors) contributed to the second part of upstroke phase and also to the initial downstroke phase. Despite being activated to a lower extent, SOL was found to be necessarily coactivated with hip and knee flexors during initial downstroke phase, to facilitate energy transfer from the limb to the crank (Rausch and Zajac 1999). Finally, synergy 3 (hip extensors, knee flexors, and ankle plantarflexors) activated muscles responsible for downstroke phase of cycling (Barroso et al. 2013), including the plantarflexion needed to transfer energy produced by gluteus maximus to the crank (Zajac et al. 2002). Moreover, GM and SOL act to oppose the strong acceleration of the leg verified during this phase (Zajac et al. 2002). In summary, SOL and TA play a very important role in the proper positioning of the feet to transfer energy from the limb to the crank, preventing ankle dorsiflexion during limb extension and controlling excessive plantarflexion during limb flexion (Rasch and Zajac 1999; Zajac et al. 2002).

Considering the case of four synergies (Fig. 4C), two different synergistic profiles were obtained: one for lower speeds (S42 and 70%MWS) and the other for higher speeds (80%MWS and MWS). For the late one, synergies 3 and 4 presented the same periods of activation (H3) as synergies 2 and 3 from Fig. 4B. Therefore, they can be considered the same synergy. Synergies 1 and 2 were fractions of synergy 1 from Fig. 4B. Interestingly, synergy compositions (W3) for S42 and 70%MWS were very similar to those presented by De Marchis et al. (2012). This may indicate a speed effect on synergistic composition in cycling when using four synergies.

Comparison Between Walking and Cycling

In light of the neural-mechanical components that are thought to be shared between walking and cycling (Hug et al. 2010; Rausch and Zajac 1999; Zehr et al. 2007), we hypothesized that pedaling should at least share some similar neural mechanisms involved in the coordination of walking.

The first similarity test was performed by correlating the four synergy vectors of walking with the four synergy vectors of cycling (see Table 1). Maximum correlation values were obtained for the MWS condition (mean correlation of 73.8%), in accordance with the values presented previously by us (Barroso et al. 2013) (mean r = 79.8% ± 6%).

We also correlated the three synergy vectors extracted in cycling with the three synergy vectors of walking (from the set of 4 synergies) that best correlated with the cycling synergy vectors (see Table 2). In this case, correlation values varied considerably for synergy 3. Four muscles (BF, ST, GM, and SOL) that are usually activated by synergy 3 of cycling (see Fig. 4BIV) are generally activated by synergies 3 and 4 in walking (see Fig. 4AIV). As synergies 1 and 2 from cycling usually were similar to synergies 1 and 2 from walking, the synergy of walking that better correlated with synergy 3 from cycling was synergy 3 or 4. Therefore, correlation values were lower for synergy 3 when compared with the other two synergies (see Table 2). Nevertheless, the correlation values in this case were better than those obtained with four synergies across all conditions, which may indicate a possible lower dimensionality for cycling.

We also tested the hypothesis that EMG envelopes obtained in cycling trials could be reconstructed with the four synergy vectors extracted from walking, and vice versa. The reconstruction of cycling EMG patterns by means of the four walking synergy vectors resulted in slightly higher VAFtotal values than the opposite reconstruction. Average VAFmuscle values when reconstructing walking EMG envelopes with the corresponding four synergies from cycling were high for GMed, RF, VL, and TA. On the other side, low VAFmuscle values were found for BF, ST, GM, and SOL, because these muscles are activated by the same synergy in cycling (see Fig. 4BIV) and by two synergies in walking (see Fig. 4AIV). In the future, caution should be used when using just VAFtotal as a metric to decide the number of synergies to use. A combination of VAFtotal with VAFmuscle (and maybe other metrics) will introduce more reliability. These results support our hypothesis that synergies extracted from walking can be used to reconstruct cycling EMG patterns.

Finally, the hypothesis that muscle synergies of cycling can result from merging synergies of walking was tested. According to our results, synergies 1 and 2 from walking could generally be merged in cycling (see Table 3). When synergies 1 and 2 of both motor tasks were compared for matched speeds, mean normalized scalar products ranged from 0.66 to 0.80 (see Table 1). Moreover, there is evidence that two synergies from walking, normally activated independently, can be merged (thus coactivated) into one synergy during cycling (see Table 3). This is the case of synergy 3 of cycling, which was always very well reconstructed with linear combinations from synergies 3 and 4 from walking (see Tables 3 and 4) across all speeds. MWS and 80%MWS were the speeds at which more similarities were found in the merging process (see Table 4). Apparently, the CNS may choose the appropriate subset of synergies from a larger set and, depending on the motor function, use them independently or in a merging state to cope with the required biomechanical task.

For the merging process, we used merging coefficients higher than 0.3. Cheung et al. (2012) used a threshold of 0.2. As they recorded EMG activity from 10–16 muscles, it is reasonable to use a higher threshold once we analyzed a set of 8 muscles. If we used a lower threshold, the similarity between reconstructed and original cycling synergies would be higher.
Globally, our results corroborate previous evidence defending the idea that both walking and cycling result from a modular control architecture (Barroso et al. 2013; Clark et al. 2010; Gizzi et al. 2012; Hug et al. 2011; Moreno et al. 2013; Routson et al. 2013). Nonetheless, we do not see muscle synergies as completely invariant profiles of spatial activation. As reported by Lacquaniti et al. (2012), this hypothesis may be too rigid to be physiologically plausible for human locomotion. Muscles belonging to the same anatomical group may have different biomechanical properties, which introduce competing demands on the appropriate way of activation of each one (Wakeling and Horn 2009). Therefore, it is thought that muscle synergies can incorporate the biomechanical properties of the limbs (Bizzi and Cheung 2013).

Methodological Considerations

Muscular activity from gluteus maximus was recorded during the experiment, but some data were corrupted because of the contact of this muscle with the chair. Therefore, our set of muscles did not include this muscle.

Other interesting muscles could have been analyzed, i.e., gracilis (as hip and knee flexor), psosas, or vastus medialis (monooarticular muscle in the knee but very similar to VL). For comparison with previous work on motor control of walking (Clark et al. 2010; Gizzi et al. 2012) and cycling (De Marchis et al. 2012; Hug et al. 2010), we chose a subset with the same number of muscles (except for Hug et al. 2010) and functionally matching muscular groups.

Baum and Li (2003) reported that load changes have an effect on EMG profiles during cycling. Hug et al. (2011) also reported a moderated similarity between EMG patterns in two different load conditions, although the extracted synergies presented higher similarity between the two conditions. Therefore, we used the same resistance value in the ergometer, in order to guarantee equal biomechanical constraints across subjects.

Conclusions

This work presents possible arrangements of existing synergies that, when adequately combined, can result in the typical muscular patterns verified at walking and cycling. Dimensionality of motor control in cycling seems to be reduced when compared with walking. Four synergies from walking can explain most of the EMG variability of cycling trials and also compared with walking. Four synergies from walking can

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