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Differential sets of cortical muscle synergy signatures during adult locomotion *

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Abstract— **Muscle synergy assessments are often employed to evaluate the modular organization of the spinal cord during a locomotion task. While they provide valuable insights into the pattern formation of the α-motoneurons at the spinal cord, by construction they cannot capture control from supra-spinal layers. We examined how locomotor muscle synergies are represented in the sensorimotor cortex, with particular focus on the cortico-synergy coherence as a measure of coupling along the cortico-spinal tract. Non-negative matrix factorization served to decompose multivariate electromyographic signals into muscle synergies. Their representations were localized in the cortex using coherence-based beamforming. Overall, the cortico-synergy coherence was maximal in sensorimotor areas especially in the beta-frequency band. However, only for the synergies timed to heel strike, that are related to the double support phases, the coherence was significant. These coherences were closely related to the timing of the activation patterns of the synergies, suggesting sensorimotor cortex to be strongly involved in emergence and control of these synergies.**

I. Introduction

A major question in motor control is how the central nervous system (CNS) regulates muscular activation during locomotion. The CNS combines neural patterns of simultaneously operating muscles allowing for controlling them using low-dimensional commands [1]. That is, such combinations effectively reduce the dimensionality of the neural activity generated by spinal circuitries, typically coined *muscle synergies*. Although the exact neural mechanisms underlying the muscle synergies remain enigmatic [2, 3], human electrophysiological recordings have shown the existence of such a modular organization in the spinal cord during walking [4]. Such recordings often consist of co-registering many electromyographic (EMG) signals. Subsequent multivariate statistics (e.g., non-negative matrix factorization (NNMF)) revealed that four to five muscle synergies suffice explain the EMG's envelope dynamics during walking [5]. This approach adequately captures the modular organization of α-motoneuronal populations [6], but which neural structures primarily control the locomotor muscle synergies remain unclear.

Neural activity in the spinal cord arguably stems from central pattern generators (CPGs) [7]. Yet, in human locomotion the input of sensory and supra-spinal control seems to be crucial [8-10]. Thanks to recent advances in data analysis, non-invasive electrophysiological recordings of the cortical areas, i.e. electro-encephalography (EEG), have proven valuable tools to assess dynamical motor control tasks like walking [11]. Recent experimental findings of a dynamic postural control task indicated a pivotal role for the sensorimotor cortex in the formation of muscle synergies [12]. There, muscle synergy activity was shown to be phase-locked with neural oscillations in the sensorimotor cortex. The cortico-synergy coupling appeared most in the beta- and (part of the) gamma-frequency bands (13-30 Hz and ~40 Hz, respectively). When it comes to walking, beta-band activity in the motor cortex has been reported to synchronize with the activity of shank muscles (bilateral tibialis anterior), especially during double support phases [13]. To what extent this also applies to cortico-synergy coupling during walking and, hence, whether one may speak of cortical-synergy control, remains to be elucidated.

Based on our recent findings on postural control, we hypothesized that locomotor muscle synergies also manifest in the phase-locked beta-band oscillations of the sensorimotor cortex. To investigate this, we employed cortico-synergy coherence as a measure of functional connectivity along the cortico-spinal tract.

II. Methods

A. Participants and experimental protocol

The experimental protocol of this study was approved by the local ethical committee of the Faculty of Behavioural and Movement Sciences (reference #VCWE-2020-006). Twelve healthy adults (seven females; mean age: 23.0±8.0 years [mean±SD]; weight: 63.9±6.0 kg, height: 1.74±0.08 m) participated in the study. Participants were recruited from a student pool at the Faculty of Behavioural and Movement Sciences and received educational credits. Participants were asked to walk at a comfortable walking speed. Data were acquired during 30 over-ground trials and 6 treadmill trials, corresponding to a total of 403±22 strides, and a resting state trial recorded at the beginning of the experiment.

B. Data acquisition

Kinematic and video data were acquired with a Vicon motion capturing system (Oxford, UK) sampled at a rate of 100 Hz. Twenty-three reflective passive markers with a diameter of 14 mm were attached to the participant's skin. As this study is integrated into a larger project, we focused on the markers that were bilaterally placed on the following landmarks: lateral malleolus, heel, and fifth metatarsophalangeal joint.

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Surface EMG of a set of 24 muscles was acquired, which included the bilateral activity of the tibialis anterior (TA), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), soleus (SOL), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), biceps femoris (BF), semitendinosus (SEM), tensor fasciae latae (TFL), gluteus maximus (GLM), and erector spinae (ES; recorded at L2). After cleaning the skin with alcohol, Ag/AgCl electrode pairs were attached according to SENIAM guidelines [14]. Movement artifacts were minimized by fixating electrodes and sensor boxes using adhesive tape. Two 16-channel wireless systems (Cometa Mini Wave Plus Wireless, Bareggio, Italy) served to record the EMG signals that were digitized at 2 kHz after an online band-pass filtering (10 Hz - 500 Hz).

Cortical activity was recorded using a 64-channel EEG cap (eego^{TM} mylab, ANT B.V., Enschede, the Netherlands). Electrode placement was based on the 10-20 system with CPz as reference (impedance values were below 10 kΩ). The EEG was sampled at a rate of 2,048 Hz. Sampling of kinematic, EMG and EEG data were synchronized.

C. Data analysis

The gait cycle (stride) was defined with respect to the right leg movement, beginning with right foot contact with the surface (heel strike) to the consecutive right foot contact, and thus equaled two steps. Foot-strike and foot-off onsets were automatically detected using a peak-detection algorithm based on the bilateral heel marker and its first time derivative [15].

For data pre-processing and artefact rejection we proceeded as follows. EEG time series were band-pass (5-250 Hz) and notch filtered (at 50, 100, …, 200 Hz). Bad channels (defined as mean values outside the 10·mean or SD-values outside the 3·SD interval of all channels) were spherically interpolated using neighboring channels. Next, EEG data were decomposed using independent component analysis to identify and remove muscular and movement artefacts (e.g., components with spectral composition atypical for EEG were omitted). EMG data were high-pass filtered (30 Hz) and notch filtered (at 50, 100, …, 200 Hz).

The EMG signals were rectified with the Hilbert transform, low-pass filtered (10 Hz), and decomposed into muscle synergies using NNMF. For every subject, the NNMF was applied to the averaged muscle activation patterns over all strides to identify the underlying muscular coefficients and temporal activation patterns. To construct high-frequency temporal patterns of the muscle synergies, the rectified but not low-pass filtered EMG was weighted with the (pseudo-)inverse of the muscular coefficients. From hereon we refer to these patterns as virtual activation patterns that served as input for the subsequent cortico-synergy coherence estimates. As mentioned in the introduction, this approach helped identifying phase-locking between activity in motor areas and muscle synergies in terms of cortico-synergy coherence [12].

We employed dynamical imaging of coherent sources (DICS) beamformers to localize cortical areas with maximal cortico-synergy coherence with the virtual activation patterns. White and gray matter volumes (2-mm grid) were obtained from a template MRI [16] within which spatial filters maximizing coherence in beta-frequency band were constructed. The resulting sources were statistically evaluated using cluster-based permutation testing (1,024 random permutations). Critical alpha and cluster-alpha levels were both set to 0.001. The first served as significance threshold when contrasting coherence in the double support phases (i.e. maximal coherence during the gait cycle) vis-à-vis coherence during resting state. We used the LONI probabilistic brain atlas [17] to map anatomy.

Source time series of the cortical activity exhibiting maximal coherence were reconstructed and used for a subsequent analysis. In particular, time-frequency coherence was estimated between virtual activation patterns and superior frontal and precentral gyri (i.e. the cortical region revealing maximal coherence) using short-time Fourier transforms with 0.2 seconds Hanning windows.

III. Results

We identified four muscle synergies accounting for 94.1±1.2% of the reconstruction accuracy [12]. The temporal activation patterns and spatial distributions (i.e. muscle coefficients) of the decomposed patterns were in line with the findings of earlier studies (Figure 1). These temporal

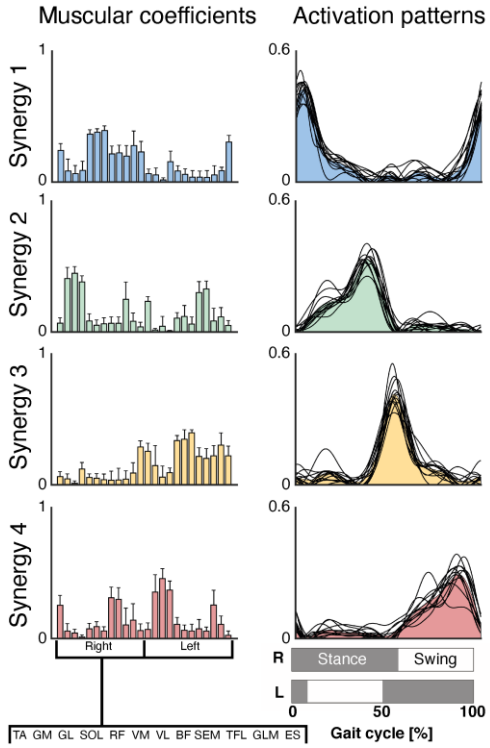

Figure 1. Spatial organization (left column) and activation patterns (right column) of the decomposed muscular activation patterns. Muscular coefficients are presented as mean and standard deviation (i.e. bars and error bars) over participants. Individual and group-average temporal activation patterns are shown as black curves and colored surfaces, respectively. R: right; L: left

activation patterns could be divided into two sets: Patterns 1 and 3 are timed during the double support phases and are involved in the touch-down and lift-off of the lower limbs; patterns 2 and 4 are primarily active during single support phases.

Coherence findings on sensor-level (not shown) identified that the maximal coherence for all synergies was expected during bilateral double support phases. The DICS beamforming yielded maximal statistical differences between beta-band coherences in double support phases versus resting state in bilateral premotor and sensorimotor areas of the cortex (Figure 2). The maximum T-statistic was localized in superior frontal gyrus (synergy 1) and precentral gyrus (synergy 3). In line with the findings of the synergy timings, their cortical representations could also be distinguished into two sets as only synergies 1 and 3 (i.e. the bilateral patterns timed at the double support phases) revealed statistically significant sources.

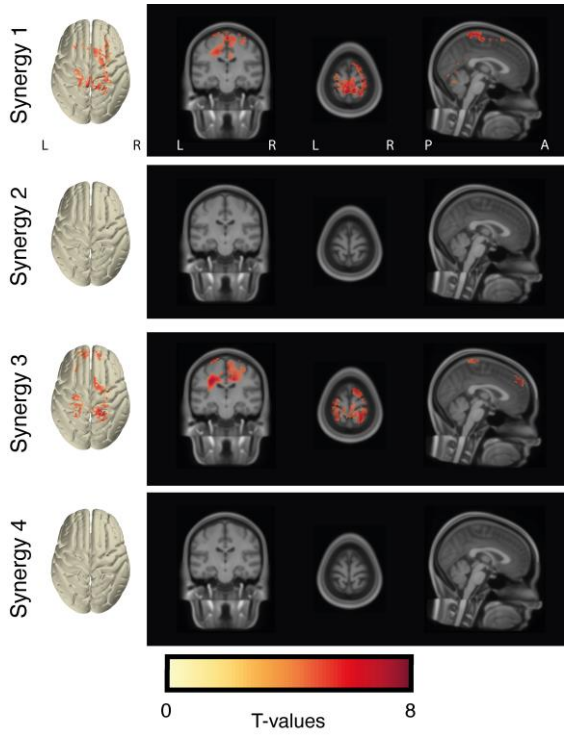

Figure 2. Localization of the muscle synergies in the cerebral cortex. Colored dimension represents the test statistic of the statistical contrast between the coherence during locomotion (i.e. double support phases) and resting state. L: left; R: right; P: posterior; A: anterior.

As shown in Figure 3, the beta-band coherences modulated as a function of the gait cycle for synergies 1 and 3. Here, we focus on synergies 1 and 3 because only they displayed significant sources at the cortex. For these synergies, beta-band coherences appeared to be maximal during the double support phases and their change in time agreed with that of the corresponding virtual activation patterns. For the single support phases, no significant beta-band coherence could be observed (see our note above).

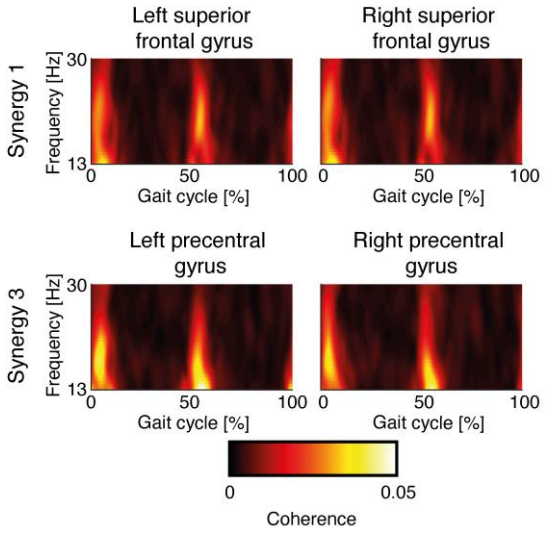

Figure 3. Cortico-synergy coherence between the bilateral superior frontal gyri and synergy 1, and bilateral precentral gyri and synergy 3. Coherence was estimated as the magnitude-squared coherence and as a function of normalized time (expressed as percentage of the gait cycle) and beta-band frequencies.

IV. Discussion

We examined how muscle synergies may be represented in the cerebral cortex during walking. To identify possible neural interactions, we focused on the cortico-synergy coherence as a measure to quantify the long-distance synchronization in the motor system. Our findings revealed that cortico-synergy synchronization was particularly evident in the sensorimotor cortex in the beta-frequency band.

Beta-band synchrony is a well-established signature within the motor system during voluntary movement and is apparent in both local and long-range synchronization in terms of cortical power and cortico-spinal synchronization [18]. Neural oscillations over long distances are thought to be conveyed via the monosynaptic pyramidal tracts of the cortico-spinal axis. Arguably, the main function of beta-band oscillations is to provide a stable outflow from the cortical motor nuclei to maintain a particular posture and/or movement state [19].

Thus far, the majority of experimental studies focused on the upper extremity tasks [18]. More recently, cortico-muscular coherence in the beta-band was identified during locomotion [13]. These beta-band oscillations are associated with the postural stability during locomotion [11].

Neural oscillations from the motor cortex are locked with the different synergies possibly via segregated cortico-synergy loops [20]. These loops activate cooperating groups of muscles through activation of α-motoneuronal populations. We found synchronization between sensorimotor cortex and muscle synergies to differ between (sets of) synergies. The coherences with synergies 1 and 3 were stronger than those with synergies 2 and 4. Hence, one may argue that the sensorimotor cortex is especially crucial in establishing the control of synergies 1 and 3.

One may speculate about the cause of the 2×2 grouping of the four muscle synergies. In fact, neonatal stepping can be represented by just two muscle synergies [4]. These stepping has also been reported in premature and anencephalic infants [21, 22] suggesting a primary role of spinal and brainstem mechanisms, arguably due to an immature infrastructure of the motor cortex and cortico-spinal tract at early age and/or in pathological cases. Needless to say, neonates cannot walk independently. Interestingly, however, the temporal organization of these neonatal synergies agree fairly well with our patterns 2 and 4 that are not signified by cortico-synergy coherence. Throughout the first year of development, the CNS undergoes many functional and structural reorganizations [10]. Around the onset of independent walking, two additional synergies emerge, whose shape and spatial organization largely correspond with our synergies 1 and 3. We consider the agreement(s) remarkable which lets us hypothesize that these two synergies emerge once the motor cortex and cortico-spinal tract are operational. Only then, the broadcasting of motor control commands from the cortex is properly developed to enable independent walking rather than 'reflex-like' muscle activation via synergies 2 and 4. If true, this organization may have major implications for our understanding of motor development, in particular, and the interaction between cortex and spinal circuitries, in general.

V. Conclusion

Our findings show that the locomotor muscle synergies are represented in the sensorimotor cortex. These cortical signatures are synergy-specific and differ in synchronization strength. With respect to timing of coupling during the gait cycle, the cortico-synergy connectivity is particularly evident at periods of double support. This indicates that the two muscle synergies that temporally align to these phases of the gait cycle receive higher cortical control than the other two synergies. Locomotor muscle synergies seemingly rely on the control of distinct neural circuitries.

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