



The reorganization of corticomuscular coherence during a transition between sensorimotor states



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ARTICLE INFO

Article history:

Accepted 22 June 2014

Available online 30 June 2014

Keywords:

Motor control

Corticomuscular coherence

Dual-band synchronization

Prediction errors

ABSTRACT

Recent research suggests that neural oscillations in different frequency bands support distinct and sometimes parallel processing streams in neural circuits. Studies of the neural dynamics of human motor control have primarily focused on oscillations in the beta band (15–30 Hz). During sustained muscle contractions, corticomuscular coherence is mainly present in the beta band, while coherence in the alpha (8–12 Hz) and gamma (30–80 Hz) bands has not been consistently found. Here we test the hypothesis that the frequency of corticomuscular coherence changes during transitions between sensorimotor states. Corticomuscular coherence was investigated in twelve participants making rapid transitions in force output between two targets. Corticomuscular coherence was present in the beta band during sustained contractions but vanished before movement onset, being replaced by transient synchronization in the alpha and gamma bands during dynamic force output. Analysis of the phase spectra suggested a time delay from muscle to cortex for alpha-band coherence, by contrast to a time delay from cortex to muscle for gamma-band coherence, indicating afferent and efferent corticospinal interactions respectively. Moreover, alpha and gamma-band coherence revealed distinct spatial topologies, suggesting different generative mechanisms. Coherence in the alpha and gamma bands was almost exclusively confined to trials showing a movement overshoot, suggesting a functional role related to error correction. We interpret the dual-band synchronization in the alpha and gamma bands as parallel streams of corticospinal processing involved in parsing prediction errors and generating new motor predictions.

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Introduction

Synchronous brain rhythms represent a dynamic mechanism for coordinating neural activity across large-scale neuronal networks and controlling the timing of neuronal firing (Buzsaki and Draguhn, 2004; Engel et al., 2001; Wang, 2010). Evidence from the past two decades of research suggests that neural oscillations subservise important cognitive functions, including motor control (Fetz, 2013; Fries, 2005; Schnitzler and Gross, 2005). During sustained contractions, primary motor cortex shows oscillations in alpha (8–12 Hz) and beta (15–30 Hz) bands (Baker et al., 2003; Murthy and Fetz, 1992; Sanes and Donoghue, 1993). Although oscillations in both frequency bands are effectively carried down the corticospinal tract (Baker et al., 2003), most studies using sustained contractions find that only beta-band oscillations are coherent between motor cortex and muscle activity (Baker et al., 1997; Conway et al., 1995; Gross et al., 2000; Halliday

et al., 1998). Corticomuscular beta-band coherence is most prominent during tonic muscle contractions and disappears during movement (Baker et al., 1997, 1999; Kilner et al., 2000; Riddle and Baker, 2006) and beta-band activity is enhanced when higher precision is required (Gilbertson et al., 2005; Kristeva et al., 2007; Kristeva-Feige et al., 2002; Witte et al., 2007). These findings suggest that the beta-band activity is related to a mechanism that maintains the current sensorimotor state (Baker, 2007; Engel and Fries, 2010; Van Wijk et al., 2012).

Research findings of corticomuscular coherence at other frequencies are inconclusive. A few studies have reported alpha-band coherence during sustained contractions (Raethjen et al., 2002) and during slow finger movements (Gross et al., 2002; Williams et al., 2009). It has recently been proposed that a spinal circuit may reduce 10-Hz oscillations in descending cortical input to the spinal motor neurons (Williams et al., 2010). In particular, computational analyses have shown that recurrent inhibition via Renshaw cells in the spinal cord leads to partial cancellation of 10 Hz oscillations, markedly reducing corticomuscular coherence at this frequency (Williams and Baker, 2009). Corticomuscular gamma-band coherence has been observed during dynamic force output (Cheyne et al., 2008; Omlor et al., 2007), as well as during movement

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preparation (Schiffelen et al., 2005, 2011). These results indicate that the frequency of corticomuscular coherence varies across motor tasks and may hence be dependent on the moment-to-moment motor state (Marsden et al., 2000).

An overarching framework suggests that different carrier frequencies reflect different types of neural processing, predicting changes in the frequency of corticomuscular coherence during transitions in sensorimotor state, e.g. from sustained contractions to dynamic force output (Engel and Fries, 2010). Here we test this hypothesis by investigating corticomuscular coherence while participants make fast transitions between two distinct force levels. We hypothesized that corticomuscular coherence in the beta band would disappear during dynamic motor output and that coherence at other frequencies would appear during the transition between force levels. Phase spectra are used to characterize the type of interaction underlying the observed functional connectivity. Capturing the reorganization of the dynamics in the sensorimotor loop speaks to the functional role of corticomuscular coherence and its role in coordinating the information transfer between sensorimotor cortex and spinal populations.

Materials and methods

Participants

Twelve healthy right-handed adults (age: 28.5 ± 2.7 years; 8 males and 4 females) participated as paid volunteers in this study. The protocol was approved by the Human Research Ethics Committee of The University of New South Wales. All participants gave voluntary and informed consent according to National Health and Medical Research Council guidelines.

Experimental design

The experiment involves a sensorimotor loop (Wolpert and Ghahramani, 2000): Vibrotactile stimuli were delivered to the same index finger used for force generation. This setup was chosen to approximate a closed loop system, which requires minimal interactions with other brain systems. By using vibrotactile stimuli with linearly increasing amplitude the study seeks to investigate the reorganization of corticomuscular dynamics inherent to the sensorimotor loop and not those imposed through sudden, large amplitude perturbations. Participants were seated in a light- and sound-attenuated room with their right hand on a flat panel and their forearm supported. They were instructed to generate isometric force by abducting their index finger against a force sensor (Fig. 1C). Participants received visual feedback of the exerted force and were instructed to keep their force output within predefined force intervals (target 1: 0.5–0.9 N, target 2: 1.1–1.5 N) displayed on the computer screen (Fig. 1A). Both force targets were visible throughout the trial and participants had to make a transition between force targets upon perceiving the vibrotactile ‘go’ cue. Participants were instructed to move the cursor within target 1 at the start of each trial and keep it there until they perceived a vibration delivered to their index finger. After a variable time interval (4–7 s), a vibrotactile stimulus was delivered to the index finger that generates the force output. The amplitude of the stimulus linearly increased from zero (Fig. 1D) and once participants perceived the vibration, they had to move the cursor into target 2 as quickly as possible and keep it within target 2 until the end of the trial. The vibration was ceased immediately when a movement was performed.

Vibrotactile stimuli consisted of pure sinusoidal vibrations at a single frequency that were delivered to the index finger by a shaker attached to the force sensor. The amplitude of the stimuli increased linearly over a 8-s time interval. This slowly ramped increase was employed to avoid sensory evoked cortical activity associated with sudden supra-threshold stimuli. Each condition was repeated in 16 trials and each participant received 80 trials in total (16 trials \times 5 stimulus frequencies).

The stimulus frequency was varied across five stimulus conditions (14, 18, 22, 26, and 30 Hz). Prior to the experiment, the amplitude of the vibrotactile stimulus for each subject was titrated to the individual perception threshold such that the final amplitude of the stimulus (at 8 s) was equal to $3 \times$ threshold (Fig. 1D).

Data acquisition

A force sensor (LSB200 L2357, JR S-Beam load cell, FUTEK, California, USA) was used to measure the force exerted by the participant. The load cell was mounted onto a small mechanical shaker (Gearing and Watson Electronics, Hailsham, East Sussex, UK) that delivered the vibrotactile stimuli to the index finger. Participants were instructed to exert isometric force against the load cell by abducting their index finger. The locations of the thumb and fingers were fixed to ensure a 60° angle between thumb and index finger and avoid the generation of force by the other fingers by co-contraction of synergist hand muscles (Fig. 1C). The force signal was amplified (SCG110, Strain Gage Amplifier, FUTEK, California, USA) and digitized at 1 kHz (NI USB-6259 BNC, National Instruments, Austin, Texas).

Surface EEG and EMG were acquired using a 64-channel amplifier – BrainAmp MR Plus (Brain Products, Munich, Germany) and custom electrode caps (Easy Cap, Falk Minow Services, Herrsching-Breitbrunn, Germany, Fig. 1B). EEG electrodes were arranged according to the international 10–20 system. Two channels were used for the electrocardiogram, one for the electrooculogram, and two for EMG, leaving 59 scalp EEG channels. All data were referenced against an electrode centered on the midline between Fz and Cz and impedances at all electrodes were kept below $5 \text{ k}\Omega$. EEG data were band-pass filtered (0.5–80 Hz). An independent component analysis (ICA) algorithm, InfoMax (Cardoso, 1997), was used to identify and remove cardiac, ocular and muscular artifacts. EEG data were re-referenced to the average reference. A bipolar derivative was taken from the EMG electrodes and the resulting EMG signal was full-wave rectified using the Hilbert transform, which is optimal for assessing corticomuscular coherence at low force levels (Boonstra and Breakspear, 2012; Farina et al., 2013; Ward et al., 2013). The resulting EEG and EMG signals were then down-sampled to 1 kHz.

Data analysis

To capture the changes in corticospinal synchronization during the execution of the transition between the two force levels, time-frequency coherence was estimated pair-wise between all EEG channels and the rectified EMG signal. Time-resolved coherence quantifies linear correlations between two observables $x[n]$ and $y[n]$, as a function of time and frequency. Let $x[n]$ and $y[n]$ be a single EEG and rectified surface EMG signal respectively. As in Mehrkanoon et al. (2013), we define the complex-valued time-frequency coherency function as

$$\hat{r}_{xy}[t, f] = \frac{S\{\hat{p}_{xy}[t, f]\}}{\sqrt{S\{\hat{p}_{xx}[t, f]\}S\{\hat{p}_{yy}[t, f]\}}} \quad t = 1, 2, \dots, N, \quad (1)$$

where $\hat{p}_{xy}[t, f]$ denotes the Fourier cross-spectral density (CSD) estimate between signals $x[n]$ and $y[n]$, and $\hat{p}_{xx}[t, f]$ denotes the power spectral density (PSD) estimate. Fourier based spectral decomposition was performed by using a unit power Hamming window of 0.75-s duration. The smoothing operator $S\{\cdot\}$ used in this analysis is given by

$$K(n, k) = \exp\left(-\left(\frac{n^2}{2\sigma_n^2} + \frac{k^2}{2\sigma_k^2}\right)\right), \quad (2)$$

where $\sigma_n = 0.66 \text{ s}$ and $\sigma_k = 1.32 \text{ Hz}$ denote the time and frequency spreads of the Gaussian kernel. Smoothing was implemented by

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