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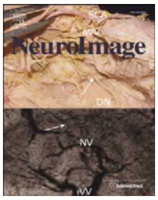

Corticokinematic coherence mainly reflects movement-induced proprioceptive feedback

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ABSTRACT

Corticokinematic coherence (CKC) reflects coupling between magnetoencephalographic (MEG) signals and hand kinematics, mainly occurring at hand movement frequency (F0) and its first harmonic (F1). Since CKC can be obtained for both active and passive movements, it has been suggested to mainly reflect proprioceptive feedback to the primary sensorimotor (SM1) cortex. However, the directionality of the brain–kinematics coupling has not been previously assessed and was thus quantified in the present study by means of renormalized partial directed coherence (rPDC).

MEG data were obtained from 15 subjects who performed right index-finger movements and whose finger was, in another session, passively moved, with or without tactile input. Four additional subjects underwent the same task with slowly varying movement pace, spanning the 1–5 Hz frequency range. The coupling between SM1 activity recorded with MEG and finger kinematics was assessed with coherence and rPDC.

In all conditions, the afferent rPDC spectrum, which resembled the coherence spectrum, displayed higher values than the efferent rPDC spectrum. The afferent rPDC was 37% higher when tactile input was present, and it was at highest at F1 of the passive conditions; the efferent rPDC level did not differ between conditions. The apparent latency for the afferent input, estimated within the framework of the rPDC analysis, was 50–100 ms.

The higher directional coupling between hand kinematics and SM1 activity in afferent than efferent direction strongly supports the view that CKC mainly reflects movement-related somatosensory proprioceptive afferent input to the contralateral SM1 cortex.

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Introduction

During fast repetitive hand movements, neuronal activity from the contralateral primary sensorimotor (SM1) cortex, as measured with magnetoencephalography (MEG), is coherent with hand kinematics at movement frequency (F0) and its first harmonic (F1), a phenomenon referred to as corticokinematic coherence (CKC) (Bourguignon et al., 2011, 2012b; Jerbi et al., 2007). During such repetitive movements, the SM1 cortex phasically produces motor output and integrates somatosensory input in overlapping time windows. Until recently, the brain oscillations emerging from the SM1 cortex at frequencies matching the frequencies of hand kinematics have been thought to be related to encoding of hand kinematics (Bourguignon et al., 2012a, 2012b; Jerbi et al., 2007; Kelso et al., 1998; Waldert et al., 2008), or to be a superposition of motor and somatosensory signals (Muller et al., 2000; Pollok et al., 2003, 2004). The hypothesis of motor encoding would imply descending motor commands that were backed up by monkey recordings showing that the firing rate of some motor-cortex neurons correlates with several kinematics parameters, such as direction (Georgopoulos et al., 1982), speed (Moran and Schwartz, 1999), and acceleration (Ashe and Georgopoulos, 1994; Reina et al., 2001). To which extent CKC reflects motor efferent vs. somatosensory afferent activity had, however, not been quantified.

We recently found evidence for strong involvement of afferent input in the generation of the CKC as both active and passive finger movements lead to similar CKC levels and neuronal generators at the hand area of the contralateral SM1 cortex (Piitulainen et al., 2013). We thus argued that CKC mainly reflects proprioceptive feedback to the SM1 cortex. However, this physiologically well-based interpretation was not backed up by any quantitative analysis of the relative afferent vs. efferent contributions to the CKC, nor was any directionality analysis carried out.

Here, we disentangled the relative contributions of motor output and somatosensory input to CKC by computing the directionality of coupling between MEG signals and finger kinematics. Such quantification can be performed with non-symmetric indices, such as partial directed coherence (PDC), which relies on the concept of Granger-causality to reveal information directionality between processes in a frequency-specific way (Baccala et al., 1998; Sameshima and Baccala, 1999).

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However, comparison of PDC values is fraught with caveats since a higher PDC value does not necessarily indicate a stronger coupling between the signals (Schelter et al., 2009). Renormalized PDC (rPDC), wherein PDC is normalized so that its null distribution follows a χ^2 distribution, has been designed to correct this shortcoming, allowing the inference of statistical significance and the comparison of two PDC values reflecting the direction of the information flow (Schelter et al., 2009).

Methods based on the concept of Granger causality were previously used to assess the directionality of the cortex–muscle coherence (Lim et al., 2014; Tsujimoto et al., 2009; Witham et al., 2010, 2011), which reflects coupling between activity of the primary motor cortex and surface electromyogram. During low-force isometric contraction the coherence peaks at ~20 Hz (Conway et al., 1995) and the cortex leads the muscle by about 20 ms to upper limbs and by about 40 ms to lower limbs (Salenius et al., 1997), in agreement with corticomuscular conduction times evident also from other types of measurements (Gross et al., 2000). Proprioceptive feedback does not appear essential for the generation of cortex–muscle coherence since the strength of the coupling assessed with methods based on Granger causality is considerably higher in the efferent direction than in the afferent direction (Lim et al., 2014; Tsujimoto et al., 2009; Witham et al., 2010), and because ischemic sensory deafferentation in the upper limb diminishes but does not abolish cortex–muscle coherence nor alter the frequency of its dominant component (Pohja and Salenius, 2003). Nevertheless, directionality analyses imply that significant coupling to upper-limb muscles exists in both afferent and efferent directions with a similar delay of on average 24 ms for both (Witham et al., 2011). This result argues for the ability of directionality analysis methods to separate the afferent and efferent contributions and to estimate the associated delays, whereas inferences obtained from the phase of the cross-spectrum may fail due to a non-trivial mixing of the afferent and efferent signals (Baker, 2007). Still, methods based on the Granger causality or other measures have not been used to assess the directionality of CKC.

In the present study, we applied rPDC to the previously reported CKC data where subjects performed ~4-Hz right forefinger movements (active) or where their finger was passively moved by an experimenter (passive), with or without tactile input (touch/no-touch) (Piitulainen et al., 2013). Here, rPDC measured the strength of the directional coupling between MEG signals picked up above the SM1 cortex and finger kinematics. To evaluate the relative contributions of motor output and somatosensory feedback, we compared rPDC values in the efferent and afferent directions. In addition, to determine the afferent and efferent delays between finger kinematics and brain signals, and to better link the CKC to movement evoked fields (MEFs) associated with discrete movements (Neshige et al., 1988), we carried out recordings on a new set of subjects who moved at varying rate within the same recording session.

Experimental procedures

Subjects

The dataset related to the first (fixed-pace) experiment is derived from Piitulainen et al. (2013) who studied 15 healthy adults (mean age 29.4 yrs, range 21–38; 8 males, 7 females). According to the Edinburgh handedness scale (Oldfield, 1971), 14 subjects were right-handed and one was ambidextrous.

Four additional healthy right-handed subjects (mean age 30 yrs, range 26–35; 3 males, 1 female) participated in the second (variable-pace) experiment.

The study had a prior approval by the ethics committee of the Helsinki and Uusimaa district, and the subjects gave written informed consent before participation. Subjects were compensated monetarily for the lost working hours and travel expenses.

Experimental protocol

In the fixed-pace experiment described in Piitulainen et al. (2013), subjects performed four randomized movement conditions (*active–touch*, *active–no-touch*, *passive–touch*, and *passive–no-touch*) involving fast repetitive flexion–extension movements of the metacarpophalangeal joint of the right forefinger for 3.5 min. In *touch* conditions, the tip of the index finger touched the table on which hand was resting, whereas in *no-touch* conditions, it did not. In *active* conditions, the subjects performed self-paced movements, whereas in *passive* conditions, an investigator moved the subjects' forefinger with a light aluminum stick. Before the recordings, we ensured that the subjects mastered the task. During the recordings, no cues were delivered about the movements. The movement pace was analyzed only afterward, and it ranged from 3 to 5 Hz in all conditions and subjects.

The variable-pace experiment was designed to assess the delay between finger kinematics and MEG signals. Both *active–touch* and *passive–touch* movements were performed with smoothly varying rate, spanning frequencies from 1 to 5 Hz in ~20-s-long cycles for 10 min. Subjects were instructed to start with tapping at ~1 Hz and then smoothly increase the pace up to their limit, then slowly decrease the pace back to ~1 Hz, and thereafter again starting the next cycle. The task performance was evaluated similarly as in the fixed-pace experiment. In a few cases, the experimenter asked the subject to start again because online monitoring of the acceleration signals and the video image of the subject indicated deviation from the requested task.

Measurements

The measurements were carried out at the MEG Core of the Brain Research Unit, Aalto University. Cortical activity was recorded with a 306-channel whole-scalp neuromagnetometer (Elekta Neuromag™, Elekta Oy, Helsinki, Finland) and the kinematics of the right forefinger was monitored with a 3-axis accelerometer (ADXL335 iMEMS Accelerometer, Analog Devices, Inc., Norwood, MA, USA) attached to the nail of the forefinger. The recording passband was 0.1–330 Hz for MEG signals and DC–330 Hz for accelerometer signals, and the signals were sampled at 1 kHz.

Data processing

Continuous MEG data were pre-processed off-line using the signal-space-separation method (SSS) to suppress external interferences and to correct for head movements (Taulu et al., 2005). Acceleration (Acc) was computed at every time bin as the Euclidian norm of the three band-passed (1–195 Hz) Acc signals (Bourguignon et al., 2011). Signals from gradiometer pairs indexed by $r \in \{1:102\}$ ($g_{r,1}$ and $g_{r,2}$) were used to estimate the signal of virtual gradiometers in the orientation $\theta \in [0; \pi]$:

$$g_{r,\theta}(t) = g_{r,1}(t)\cos\theta + g_{r,2}(t)\sin\theta.$$

Following Halliday et al. (1995), coherence based on the Fourier transform of artifact-free 2-s epochs was then computed between Acc and g_θ:

$$\mathrm{Coh}(r,f,\theta) = \frac{\mathrm{Acc}(f)g^{*}_{r,\theta}(f)^{2}}{|\mathrm{Acc}(f)|^{2}|g_{r,\theta}(f)|^{2}},$$

where * is the Hermitian conjugate and ⟨ · ⟩ the mean across epochs. Practically, $\mathrm{Coh}(r,f,\theta)$ was estimated from the cross-spectral density matrix formed with Acc, $g_{r,1}$ and $g_{r,2}$, and for θ spanning $[0;\pi]$ by

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