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Coordinative task difficulty and behavioural errors are associated with increased long-range beta band synchronization

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ABSTRACT

The neural network and the task-dependence of (local) activity changes involved in bimanual coordination are well documented. However, much less is known about the functional connectivity within this neural network and its modulation according to manipulations of task complexity. Here, we assessed neural activity via high-density electroencephalography, focussing on changes of activity in the beta frequency band (~15–30 Hz) across the motor network in 26 young adult participants (19–29 years old). We investigated how network connectivity was modulated with task difficulty and errors of performance during a bimanual visuomotor movement consisting of dial rotation according to three different ratios of speed: an isofrequency movement (1:1), a non-isofrequency movement with the right hand keeping the fast pace (1:3), and the converse ratio with the left hand keeping the fast pace (3:1). To quantify functional coupling, we determined neural synchronization which might be key for the timing of the activity within brain regions during task execution. Individual source activity with realistic head models was reconstructed at seven regions of interest including frontal and parietal areas, among which we estimated phase-based connectivity. Partial least squares analysis revealed a significant modulation of connectivity with task difficulty, and significant correlations between connectivity and errors in performance, in particular between sensorimotor cortices. Our findings suggest that modulation of long-range synchronization is instrumental for coping with increasing task demands in bimanual coordination.

1. Introduction

Task difficulty in bimanual coordination depends on the spatio-temporal characteristics of the submovements and overall movement speed. Simultaneous (in-phase) or alternated movement (anti-phase) of the limbs are the easiest bimanual coordination patterns that belong to the intrinsic motor repertoire, and deviations from these require more attention and practice (Kelso, 1984; Zanone and Kelso, 1992; Lee et al., 1995; Treffner and Turvey, 1995; Serrien and Swinnen, 1997). There are two principal ways in which the central nervous system copes with the task demands: via increased neural activation (either within the same region or recruiting additional regions) and via modulations of the strength of interaction among those regions, i.e. functional connectivity. The latter has received little attention, in spite of evidence showing that modulated communication among brain regions is key for successful multi-sensory integration or execution of cognitive tasks (e.g. Roelfsema et al., 1997; Maier et al., 2008; Pesaran et al., 2008).

Increased neural activation in bimanual movements compared to rest has been reported in what is referred to as the bimanual neural network. Among other regions, this network comprises the primary motor cortex (M1), supplementary motor area (SMA), premotor cortex (PMC), cingulate motor area, basal ganglia and cerebellum (Swinnen and Wenderoth, 2004; Pollok et al., 2007). A higher movement frequency during stable execution involves activation in the bilateral SMAs, premotor dorsal (PMd) and left middle cingulate cortex (Sadato et al., 1996; Deiber et al., 1999; Debaere et al., 2004; Goble et al., 2010)

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and a linear decrease of power in the beta frequency band (approx. 13–30 Hz) in bilateral M1s (Houweling et al., 2010). It should be noted that decreases of power in the alpha (8–12 Hz) and beta bands in electrophysiological measures are considered markers of neural activation in motor-related tasks (Pfurtscheller and Neuper, 1994; Stancák and Pfurtscheller, 1996).

Task difficulty manipulated via phase relations revealed that anti-phase movements are accompanied by increased activity in the SMA and PMC compared to in-phase (Sadato et al., 1997; Goerres et al., 1998; Stephan et al., 1999; Immisch et al., 2001; Gross et al., 2005; Aramaki et al., 2006; Pollok et al., 2007), as well as in the brain stem, cerebellum, and M1 (Aramaki et al., 2006). Besides activity increases, EEG activity during in-phase and anti-phase movements results from temporal modulations of unimanual-related EEG activity (Banerjee et al., 2012). Phase relations that differ from anti-phase and in-phase come with activity increases in the SMA, superior parietal cortex, thalamus, cerebellum and PMd (Debaere et al., 2003; Debaere et al., 2004). Similarly, bimanual movements whereby each hand moves at a different frequency, i.e. non-isofrequency rhythms or polyrhythms, are associated with activity increases in bilateral M1s and medial brain regions (Lang et al., 1990; Ullén et al., 2003).

Besides increases of local activation as a function of task difficulty, alterations in functional connectivity may be an additional means to cope with task difficulty. Inter-hemispheric connectivity between bilateral primary sensorimotor cortices (S1/M1) in the beta frequency band has been reported when increasing the task demands from unimanual, to bimanual in-phase and anti-phase, mostly at the sensor level, in magneto- and electro-encephalography (M/EEG) studies (Andres et al., 1999; Serrien and Brown, 2002; Serrien et al., 2003; Serrien, 2008b; 2009; Houweling et al., 2010). Higher inter-hemispheric connectivity was also observed in bimanual compared to unimanual movements or rest in studies using functional magnetic resonance imaging (fMRI) (Rissman et al., 2004; Grefkes et al., 2008; Maki et al., 2008). However there are dissenting findings. Walsh et al. (2008) did not find any changes in inter-hemispheric connectivity between bilateral M1s, but found bilateral SMA connectivity increases. Also, Serrien (2008a) reported decreased inter-hemispheric connectivity in the beta band during the in-phase coordination mode compared to the anti-phase and unimanual ones.

With this study, we addressed three gaps in the literature. First, studies investigating modulations of brain activity associated with difficulty of bimanual tasks beyond the “simple” in-phase/anti-phase coordination modes have been limited to manipulating either the overall speed of movement (Houweling et al., 2010) or the phase relations (Debaere et al., 2004). Modulations of the bimanual neural network as a function of *manipulation of the spatiotemporal features* of bimanual movements (e.g. different non-isofrequency movements), implying different task assignments to each limb, have to date only been investigated with fMRI (Ullén et al., 2003). Compared to the preferred in- and anti-phase movements, non-isofrequency movements require preservation of the allocated pace in each hand within an integrated temporal framework across both hands. This is based on modulation of inter-hemispheric interactions between premotor and primary motor cortices to gate the different task assignments to each limb in contrast to isofrequency conditions where this is not the case (Fujiyama et al., 2016a, 2016b). Second, functional connectivity changes have been studied primarily between bilateral S1/M1s and SMA, with no focus on the involvement of a *broader network*. There are, however, a few exceptions to this. In an fMRI study, Grefkes et al. (2008) reported increased inter-and intra-hemispheric connectivity during bimanual movements compared to unimanual movements in a network including bilateral S1/M1s, PMCs and SMA. Using fMRI, Heitger et al. (2012, 2013) demonstrated increases of functional connectivity, with motor learning and in anti-phase compared to in-phase bimanual movements using the bimanual network extracted from activity profiles (i.e. a data-driven approach) including distant brain regions. Third, connectivity analysis at the *source level using M/EEG* has not been applied before to investigate modulations related to bimanual task difficulty. The local and long-range synchronization of neural dynamics as measured via M/EEG can be considered an information carrier between neural populations (Lopes da Silva, 2013). However most EEG literature on bimanual coordination uses sensor-level connectivity measures which can produce spurious patterns (Sakkalis, 2011).

Here we sought to address these gaps by applying a multivariate method to characterise the patterns of functional connectivity of source-level EEG and assess their modulations with task difficulty defined by different spatiotemporal characteristics. Additionally, given the limited literature on the topic, we also examined the underlying neural mechanisms of adaptation to task demands by investigating correlations of connectivity with behaviour. We first recorded high-density EEG during the execution of a bimanual visuomotor task, which consisted of circular wrist movements at different speeds for each hand. We estimated source activity using MRI-based individual head models, determined the synchronization level among the sources, and applied partial least squares analysis to examine network modulations with task difficulty and correlations of network modulations with error of performance (Boonstra et al., 2007; McIntosh et al., 2014). At the behavioural level, we expected an increase of performance error with increasing task difficulty. At the source level, we sought to reproduce the aforementioned motor network for bimanual motor behaviour, and hypothesised increases of activity in bilateral S1/M1s as a function of task difficulty. At the network level, we further hypothesised an increase of connectivity with increased task difficulty as this may support coping with the elevated task demands. Additionally, we expected correlations of connectivity with performance error to confirm network modulations with task difficulty.

2. Methods

2.1. Participants

Twenty-six participants were recruited and provided informed consent for this experiment (11 male; mean age 24.17 years; range 19–29 years) which had been approved by the ethics committee of KU Leuven. All participants were right-handed according to the Oldfield Handedness Questionnaire (mean 91.09; range: 56–100) (Oldfield, 1971).

2.2. Setup and task

Participants practiced a bimanual visuomotor task similar to the one previously used in our laboratory (Sisti et al., 2011; Gooijers et al., 2013; Pauwels et al., 2014; Solesio-Jofre et al., 2014; Beets et al., 2015). Participants were seated in front of a computer while their arms rested on two ramps covered with foam for comfort. At the end of each ramp, a shaft embedded into a rotating disc was placed. The rotating disc was glued to an encoder for registration of angular displacement (Avago Technologies, Fs=250 Hz, accuracy=0.089°). Participants were instructed to hold the dials as if they were pens. In order to prevent participants from seeing their hands/forearms, a wooden frame was positioned on top of their limbs. The data from the encoders was recorded and analysed with LabView 8.5 (National Instruments, Austin, Texas, USA).

The rotation of the dials, one for each hand, yielded a movement of a red cursor on the PC screen. Clockwise rotation of the right dial moved the cursor to the right; counter-clockwise rotation moved the cursor to the left (see Fig. 1). Clockwise rotation of the left dial moved the cursor upwards; counter-clockwise rotation moved the cursor downwards. Simultaneous rotation of both dials resulted in lines with different slopes being drawn on the PC screen, depending on the rotational speed of both hands. A blue line with a particular slope was