

Research Report

The oscillatory network of simple repetitive bimanual movements

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Accepted 8 June 2005
Available online 14 July 2005

Abstract

Bimanual synchronization relies on the precisely coordinated interplay of both hands. It is assumed that during temporal bimanual coordination, timing signals controlling each hand might be integrated. Although a specific role of the cerebellum for this integration process has been suggested, its neural foundations are still poorly understood. Since dynamic interactions between spatially distributed neural activity are reflected in oscillatory neural coupling, the aim of the present study was to characterize the dynamic interplay between participating brain structures. More specifically, the study aimed at investigating whether any evidence for the integration of bilateral cerebellar hemispheres could be found. Seven right-handed subjects synchronized bimanual index finger-taps to a regular pacing signal. We recorded continuous neuromagnetic activity using a 122-channel whole-head neuromagnetometer and surface EMGs of the first dorsal interosseus (FDI) muscle of both hands. Coherence analysis revealed that an oscillatory network coupling at 8–12 Hz subserves task execution. The constituents are bilateral primary sensorimotor and premotor areas, posterior-parietal and primary auditory cortex, thalamus and cerebellum. Coupling occurred at different cortical and subcortical levels within and between both hemispheres. Coupling between primary sensorimotor and premotor areas was observed directly and indirectly via the thalamus. Coupling direction suggests that information was integrated within the left premotor cortex corroborating a specific role of the left premotor cortex for motor control in right-handers. Most importantly, our data indicate strong coupling between both cerebellar hemispheres substantiating the hypothesis that cerebellar signals might be integrated during task execution.

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Theme: Motor systems and sensorimotor integration

Topic: Control of posture and movement

Keywords: Bimanual coordination; Coherence; Healthy; Human; MEG; Motor system; Oscillation

1. Introduction

A characteristic feature of bimanual coordination is the strong and spontaneous tendency to favor movements that are spatially and temporally symmetric (for an overview, see [4]). This observation gave rise to the assumption that bimanual coordination might be based on a common motor plan controlling both hands [35]. This generalized motor program (GMP) has been proposed specifically for temporal aspects of coordinated behavior [36]. An alternative explanation is the cross-talk model assuming independent motor programs for each hand [26]. According to this

approach, temporal and spatial couplings occur because of cross-talk between the signals controlling both arms. Since it is generally accepted that behavior is controlled in a network-like manner by spatially distributed neural activity, the dynamic systems approaches have become significant for the explanation of neural principles subserving human behavior. These theories are based on the assumption of cooperative interplay between different brain structures (for a detailed overview, see [4]). However, it remains still an open question how the brain coordinates information between different brain regions. The most likely candidate for the solution of this large-scale integration problem is synchronization of neural oscillatory activity, which is assumed to allow transient dynamic links between distributed areas [43].

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Synchrony between spatially distributed brain areas can be investigated non-invasively by using magnetoencephalography (MEG) together with the analysis tool Dynamic Imaging of Coherent Sources (DICS; [12]). So far studies on neural integration associated with bimanual coordination investigated the communication between cortical areas of both hemispheres [5,9,38,40]. However, imaging [42] as well as behavioral and clinical studies substantiate the pivotal role of subcortical [21] and cerebellar [7,19] structures for bimanual tasks. It has been suggested that timing of each hand is independently controlled by the lateral portions of the ipsilateral cerebellum [7,19]. Since it has been demonstrated that during bimanual execution the kinematic variability of each hand is reduced as compared to the same but unimanual task, it has been hypothesized that both timing signals are integrated prior to movement execution [7,17,19]. Although the neural basis of this process remains unclear, it has been suggested that both timing signals might be integrated on the level of the cerebellum or on the level of the basal ganglia [19]. Because of the assumed specific significance of cerebellar and subcortical structures for bimanual coordination, the investigation of the functional connectivity between these areas and cortical structures might reveal new insights into the neural foundations of bimanual coordination. The aim of the present study was to investigate the dynamic neural network associated with a synchronous bimanual auditorily paced synchronization task. Specifically, the study aimed to examine whether any evidence for the integration of bilateral cerebellar information could be found.

2. Method

Seven healthy right-handed subjects participated in this study (mean age 25.9 ± 0.9 years; range 22–28 years). Subjects had no history of neurological deficits and were naive with regard to the experiment's purpose. All individuals gave their written informed consent prior to the experiment. The study was performed with the approval of the local ethics committee and was in accordance with the declaration of Helsinki.

Subjects performed brisk finger flexions and extensions with their right and left index finger simultaneously. Finger-taps were synchronized with a regular auditory pacing signal (400 Hz, 74 dB, 10 ms duration). The pacing signal was presented with a constant interstimulus interval (ISI) of 800 ms and was ingrained in white noise (55 dB). Pacing signal and noise were delivered by two different synthesizers (HP 33120A) and were presented binaurally through plastic tubes. Subjects performed the task for 7 min.

2.1. Data collection

We recorded neuromagnetic activity with a helmet-shaped 122-channel whole-head neuromagnetometer (Neuromag™) in a magnetically shielded room while subjects performed the

synchronization task. Simultaneously, muscle activity using surface EMG electrodes placed on the first dorsal interosseus (FDI) muscle of both hands was recorded. MEG and EMG signals were recorded with a bandpass filter of 0.03–170 Hz, digitized with 513 Hz and stored digitally for off-line analysis. EMG signals were high-pass filtered at 60 Hz and rectified offline. Eye blinks were controlled by vertical EOG. Following visual inspection, contaminated epochs were excluded from further data analysis. Repeated eye blinks occurred mainly at the beginning of the experimental run.

The exact position of the head with respect to the sensor-array was determined by measuring magnetic signals from four coils placed on the scalp. High-resolution T1-weighted magnetic resonance images (MRI) were obtained from each subject. Three anatomical landmarks (nasion, left and right preauricular points) were localized in each individual and used for the alignment of the MRI and MEG coordinate system.

Onsets of finger-taps were determined by a photoelectric barrier mounted on a pad to estimate tapping accuracy and temporal coupling between both hands.

2.2. Data analysis

To identify oscillatory activity subserving task execution, the analysis tool DICS (Dynamic Imaging of Coherent Sources) was used. DICS provides tomographic maps of power, cerebro-muscular coherence and coherence between brain sites in the entire brain (for a detailed description of DICS, see [12]). The fast Fourier transform (FFT) was applied to all EMG and MEG signals. FFT was calculated on 512 sample windows after applying a Hanning window. Windows overlapped with half the FFT size (i.e., 256 points). Analysis results in 243 FFT segments for each subject. The Fourier-transformed EMG and MEG windows were used to compute the cross spectral density (C), which allows an estimation of the dependencies between two signals (e.g., EMG and neural activity of one MEG sensor) by calculating coherence values. Coherence is the magnitude-squared cross-spectrum divided by the power spectra of both time series and represents a normalized measure quantifying dependencies in the frequency domain. Values can range between 0, indicating independence of two signals, and 1, indicating a perfectly linear relationship (for details, see [37]). This strategy allows (i) to quantify oscillatory activity and (ii) to estimate the interaction between two signals.

Cross-spectral density was computed for all signal combinations and finally averaged across the whole measurement period. Cerebro-muscular coherence was calculated at movement frequency, whereas coherence analysis between brain sites, was computed at alpha (i.e., 8–12 Hz) frequency, since the source with the strongest coherence to FDI muscle showed discernible peaks of oscillatory activity at this frequency.

To compute coherence measures at any location within the brain, a linear transformation acting as a spatial filter was

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