



Nonlinear coupling between occipital and motor cortex during motor imagery: A dynamic causal modeling study

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ABSTRACT

We demonstrate the capacity of dynamic causal modeling to characterize the nonlinear coupling among cortical sources that underlie time–frequency modulations in MEG data. Our experimental task involved the mental rotation of hand drawings that ten subjects used to decide if it was a right or left hand. Reaction times were shorter when the stimuli were presented with a small rotation angle (fast responses) compared to a large rotation angle (slow responses). The grand-averaged data showed that in both cases performance was accompanied by a marked increase in gamma activity in occipital areas and a concomitant decrease in alpha and beta power in occipital and motor regions. Modeling directed (cross) frequency interactions between the two regions revealed that after the stimulus induced a gamma increase and beta decrease in occipital regions, interactions with the motor area served to attenuate these modulations. The difference between fast and slow behavioral responses was manifest as an altered coupling strength in both forward and backward connections, which led to a less pronounced attenuation for more difficult (slow reaction time) trials. This was mediated by a (backwards) beta to gamma coupling from motor till occipital sources, whereas other interactions were mainly within the same frequency. Results are consistent with the theory of predictive coding and suggest that during motor imagery, the influence of motor areas on activity in occipital cortex co-determines performance. Our study illustrates the benefit of modeling experimental responses in terms of a generative model that can disentangle the contributions of intra-areal vis-à-vis inter-areal connections to time–frequency modulations during task performance.

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Introduction

Studying task-dependent communication between brain regions is essential to link behavior with its accompanying neural activity. Using non-invasive recording techniques like M/EEG recordings one can characterize distinct rhythmic activities that differ with region and modulate with task. To estimate the coupling strength between regions or sources, most studies concentrate on iso-frequency connections, which are relatively easy to address and to interpret. For example, cross-regional information transfer can be treated by assuming a simple linear response system and connectivity can be determined through standard regression techniques. However, by definition, these approaches are blind to cross-frequency interactions. Moreover, directionality of connections is often ignored although it is

considered important, if not essential, for neural functioning. Recent advances that address directionality in the analysis of M/EEG data include, e.g., Granger causality, the directed transfer function, and the phase slope index (Nolte et al., 2008). Likewise the introduction of generalized phase coupling (Tass et al., 1998), and empirical findings of cross-frequency phase–amplitude (Canolty and Knight, 2010; Jensen and Colgin, 2007), and amplitude–amplitude correlations (Bruns and Eckhorn, 2004; de Lange et al., 2008), underscore the relevance of multi-frequency coupling for neural functioning.

Alternatively, one might follow a slightly different route by first formalizing explicit models that are supposed to generate empirically observed neural activity and use the structure and parameters of these models to infer effective connectivity in a (small) network of regions. In doing so, knowledge about neuroanatomy and the neurophysiological processes at work can be incorporated. Fitting the model to observed data gives an estimate of its parameters that quantify the coupling strength within and between regions. This is standard procedure in the vast field of system identification and forms the rationale behind dynamic causal modeling (DCM); where different configurations of sources and their connections are tested to find the most likely network generating observed task-related responses.

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DCM was initially developed for the analysis of fMRI data (Friston et al., 2003) that – to a good approximation – can be modeled with first-order, linear differential neuronal state equations, and more detailed hemodynamic response functions. In more recent work this approach has been extended to model evoked responses in both EEG and MEG (David et al., 2006). Due to high temporal resolution of M/EEG recordings, the neural state equations are replaced by neurophysiologically more realistic, neural mass models based on studies by Jansen and Rit (1995). Subsequently, DCM has been adjusted to other data features: cross-spectral densities underlying steady state-responses (Moran et al., 2009), complex-valued cross-spectral densities (Friston et al., 2012), time-resolved modulations of spectral power (Chen et al., 2008), and synchronization by means of phase coupling (Penny et al., 2009).

Here, we demonstrate the capacity of DCM to investigate time–frequency modulations in visual and motor areas during motor imagery. The experimental task under study involved the mental rotation of hand drawings as described by de Lange et al. (2008). Subjects used mental rotation in order to report whether the drawing contained a left or right hand. Reaction times typically increased when the images were shown with a larger rotation angle. Executing the task induced a strong increase in gamma activity over visual areas, and a decrease in alpha and beta activity in both visual and motor areas. de Lange et al. (2008) also found a negative correlation between occipital gamma and beta activity in the motor cortex that became stronger over time after stimulus onset and dissolved just before response onset. To disentangle directional cross-frequency couplings underlying these time–frequency modulations, we employed DCM and contrasted trials with short and long reaction times. Do trials with fast and slow reaction times differ in time–frequency modulations after stimulus presentation, and if so, are slow reaction times associated with altered forward (from visual to motor cortex) and/or backward (from motor to visual cortex) information processing?

Methods

Behavioral task and recordings

de Lange et al. (2008) have described the experiment in detail. Briefly, twelve subjects performed a motor imagery task in which they needed to identify line drawings of a human hand as a left or right hand. The drawings were presented with five different rotation angles between 40 and 180°. Each trial started with a 3 s baseline period, after which a drawing of a hand was presented. The task required mental rotation of the hand drawing, since subjects were instructed to respond as fast as possible after recognizing the laterality of the hand by pressing one of two buttons with the right hand. The hand was presented either with the palm or the back facing forward and was displayed until a response was given. In total, 800 trials were performed in a random order. Brain activity was recorded using a 151-channel CTF MEG system. Data were sampled at a rate of 1200 Hz after online low-pass-filtering with 300 Hz. The electro-oculogram was co-recorded to identify trials with excessive eye movements and trials containing artifacts were discarded offline. Head position was localized at the start and end of the recording session, using coils on the nasion and pre-auricular points. In addition, individual structural MRI scans were obtained. Here we re-analyzed the data from the original paper using Matlab (version R2007b, MathWorks, Natwick, MA) and SPM8 (Update revision number 4667, <http://www.fil.ion.ucl.ac.uk/spm>, Litvak et al., 2011).

Source localization

de Lange et al. (2008) found an increase in gamma activity (50–80 Hz) over occipital areas peaking shortly after stimulus onset, and a sustained decrease in beta activity (16–24 Hz) over occipital/

parietal and motor areas before response onset. To localize the origin of these modulations, we used a linearly constrained minimum variance beamformer (Hillebrand and Barnes, 2005). For the gamma band we selected the time interval between 100 and 600 ms after stimulus onset (at 0 ms) and for the beta band the time interval –700 to –200 ms before response onset. The localized power in these intervals was contrasted against that during the –500 to 0 ms pre-stimulus baseline interval. The beamformer grid resolution was set to 10×10×10 mm using the individual MRI scans. To allow post-hoc averaging over subjects (see below) the individual beamformer averages were transformed to template space. Values on the grid were then interpolated using linear interpolation to produce volumetric images with 2 mm resolution (without further smoothing). The resulting images of source power differences between active and baseline intervals were averaged over subjects. We found large power differences in left and right visual cortex (from here on referred to as ‘O’ for occipital) as well as sources in left and right sensorimotor cortex (referred to as ‘M’ for motor). See Fig. 1 for their specific locations. In addition, left and right parietal sources could be discerned, which revealed time–frequency spectra that closely resembled that of the sources in sensorimotor areas. Given the similarity between parietal and motor responses, we focused on the motor regions in subsequent DCM analyses. Locations of the sources in individual subjects were identified as the closest to the mean peak location over subjects. For one subject no clear right O source could be identified. Likewise, for three subjects no right M source could be detected. In these cases, unilateral sources were used for subsequent analyses. Finally, source time series were extracted for all selected trials using beamformer weights that were

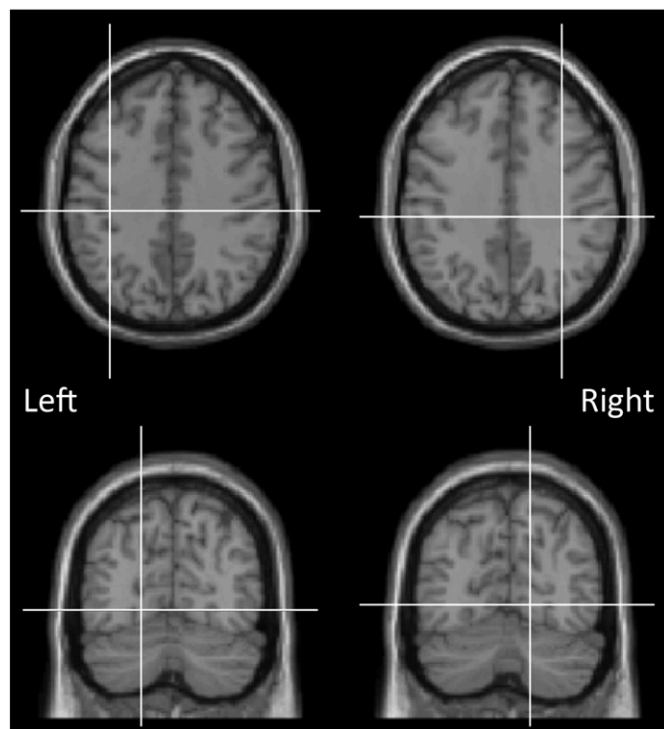


Fig. 1. Source locations used for DCM. The crosshairs indicate the peak locations of the grand-averaged power contrast images. Top row: beta band (16–24 Hz) decrease in M [left: –37 –25 39 mm; right: 34 –28 37 mm]. Bottom row: gamma band (50–80 Hz) increase in O [left: –18 –71 –5 mm; right: 14 –69 –2 mm]. Sources in individual subjects were identified as the closest to these locations (mean Euclidean distance from the grand-averaged peak locations: left M: 15 mm; right M: 18 mm; left O: 14 mm; right O: 13 mm).

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