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On optimal spatial filtering for the detection of phase coupling in multivariate neural recordings

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ABSTRACT

Introduction: Neuronal oscillations synchronize processing in the brain over large spatiotemporal scales and thereby facilitate integration of individual functional modules. Up to now, the relation between the phases of neuronal oscillations and behavior or perception has mainly been analyzed in sensor space of multivariate EEG/MEG recordings. However, sensor-space analysis distorts the topographies of the underlying neuronal sources and suffers from low signal-to-noise ratio. Instead, we propose an optimized source reconstruction approach (Phase Coupling Optimization, PCO).
Methods: PCO maximizes the 'mean vector length', calculated from the phases of recovered neuronal sources and a target variable of interest (e.g., experimental performance). As pre-processing, the signal-to-noise ratio in the search-space is maximized by spatio-spectral decomposition. PCO was benchmarked against several competing algorithms and sensor-space analysis using realistic forward model simulations. As a practical example, thirteen 96-channel EEG measurements during a simple reaction time task were analyzed. After time-frequency decomposition, PCO was applied to the EEG to examine the relation between the phases of pre-stimulus EEG activity and reaction times.
Results: In simulations, PCO outperformed other spatial optimization approaches and sensor-space analysis. Scalp topographies of the underlying source patterns and the relation between the phases of the source activity and the target variable could be reconstructed accurately even for very low SNRs (−10 dB). In a simple reaction time experiment, the phases of pre-stimulus delta waves (< 0.1 Hz) with widely distributed fronto-parietal source topographies were found predictive of the reaction times.
Discussion and conclusions: From multivariate recordings, PCO can reconstruct neuronal sources that are phase-coupled to a target variable using a data-driven optimization approach. Its superiority has been shown in simulations and in the analysis of a simple reaction time experiment. From this data, we hypothesize that the phase entrainment of slow delta waves (< 1 Hz) facilitates sensorimotor integration in the brain and that this mechanism underlies the faster processing of anticipated stimuli. We further propose that the examined slow delta waves, observed to be phase-coupled to reaction times, correspond to the compound potentials typically observed in paradigms of stimulus anticipation and motor preparation.

Introduction

There is a considerable interest in understanding the relation between neuronal oscillations and human perception, memory, and behavior (for a review: Buzsaki, 2006). Synchronized membrane oscillations in neuronal populations lead to mutually shared temporal windows of increased or decreased firing probability (McLelland and Paulsen, 2009; Haegens et al., 2011). Thereby, neuronal oscillations carry the potential to synchronize neuronal firing rates over larger spatiotemporal scales and enable interactions between different func-

Abbreviations: BFGS, Broyden-Fletcher-Goldfarb-Shanno algorithm; BP, Bereitschaftspotential; CCAvReg, canonical correlation average regression analysis; CI, confidence interval; CNV, contingent negative variation; CSD, current source density; cSPoC, canonical source power correlation analysis; ECoG, electrocorticography; EEG, electroencephalography; ICA, independent component analysis; LDA, linear discriminant analysis; MEG, magnetoencephalography; MI, modulation index; nRT, normalized reaction time; PCA, principal component analysis; PCO, phase coupling optimization; RT, reaction time; SEM, standard error of the mean; SSD, spatio-spectral decomposition; SNR, signal-to-noise ratio; ta-MR, temporally adjusted multiple regression; tf, time-frequency

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tional pathways (for a review: Fries, 2005).

Here, we focus on the analysis of the coupling between the phases of neuronal source activities and behavioral/perceptional measures, an approach that has attracted considerable interest in recent years. It has—for example—been shown that the phases of alpha and theta oscillations are related to performance in a visual detection task (Busch et al., 2009) and that the phases of pre-stimulus alpha oscillations influence the perception of temporal concurrence in the visual system (Cravo et al., 2015; Milton and Pleydell-Pearce, 2016). Similar findings were described in the somatosensory domain (Ai and Ro, 2014; Baumgarten et al., 2015). It has been argued that these findings indicate a discrete perceptual sampling of our environment (for a review: VanRullen, 2016).

Many of the previous analyses, however, have a major disadvantage since they are usually carried out in sensor-space of magneto- or electroencephalography (M/EEG). Yet, MEG and EEG measure a noise-afflicted far-field superimposition of the electromagnetic activity generated by distant neuronal sources in the brain. The exact projection of these neuronal sources to the sensors (the 'forward problem') depends on the individual anatomy and electromagnetic properties of the subject's brain and enclosing hulls, and it has been shown that distinctly different source configurations may give rise to the same electromagnetic field on the scalp (Fender, 1987). Additionally, maximal activity in one EEG/MEG sensor does not imply that its source is located in the brain region directly underneath that sensor (Michel et al., 2004). This problem, albeit to a lesser extent, is also relevant for electrocorticography (ECoG) recordings (Fuchs et al., 2007). Accordingly, analysis of M/EEG and ECoG data in sensor space might fail to detect and localize the neuronal sources of phase-coupling to behavior or perception.

Fig. 1 summarizes the limitations of sensor-space analysis and illustrates the utility of the proposed spatial filtering approach, denoted as Phase Coupling Optimization (PCO). PCO is a data-driven filter optimization approach to recover neuronal sources showing phase-coupling to an external target variable (e.g., experimental task performance). The approach is analogous to established spatial filtering approaches based on data-driven optimization. As examples: independent component analysis (ICA; Hyvarinen and Oja, 2000) maximizes the mutual independence between recovered sources, principle component analysis (PCA; Pearson, 1901) maximizes the variance of recovered sources, and common spatial pattern (CSP) analysis (Fukunaga, 1990; Blankertz et al., 2008) maximizes the ratio of variances between two experimental conditions. In analogy, PCO recovers neuronal sources by maximizing the coupling between the phases of the recovered sources and the target variable of interest (e.g., experimental performance). The scalp projection of the recovered source activity is authentically reflected by the spatial pattern corresponding to the constructed spatial filter.

As real-world example, we examine the relation between reaction times (RTs) and the phases of EEG oscillations. A previous independent study demonstrated that the phases of delta waves (0.5–3 Hz) encode the degree of expectation of the anticipated imperative stimuli and are subsequently coupled to reaction times (RTs; Stefanics et al., 2010). In the used experimental paradigm, both a contingent negative variation (CNV; Walter et al., 1964; Tecce, 1972) and Bereitschaftspotential (BP; Kornhuber and Deecke, 1965; Shibasaki and Hallett, 2006) can in principle be produced (Kornhuber and Deecke, 1965; Tecce, 1972). The BP displays the readiness of the motor system to respond to the imperative stimulus ('S2'). However, each stimulus can simultaneously be regarded as a preparatory stimulus ('S1') for the upcoming GO-stimulus, resembling the classical S1–S2-paradigm to evoke the CNV (Walter et al., 1964). The relation between the recovered slow delta waves and the BP/CNV compound potentials will be discussed.

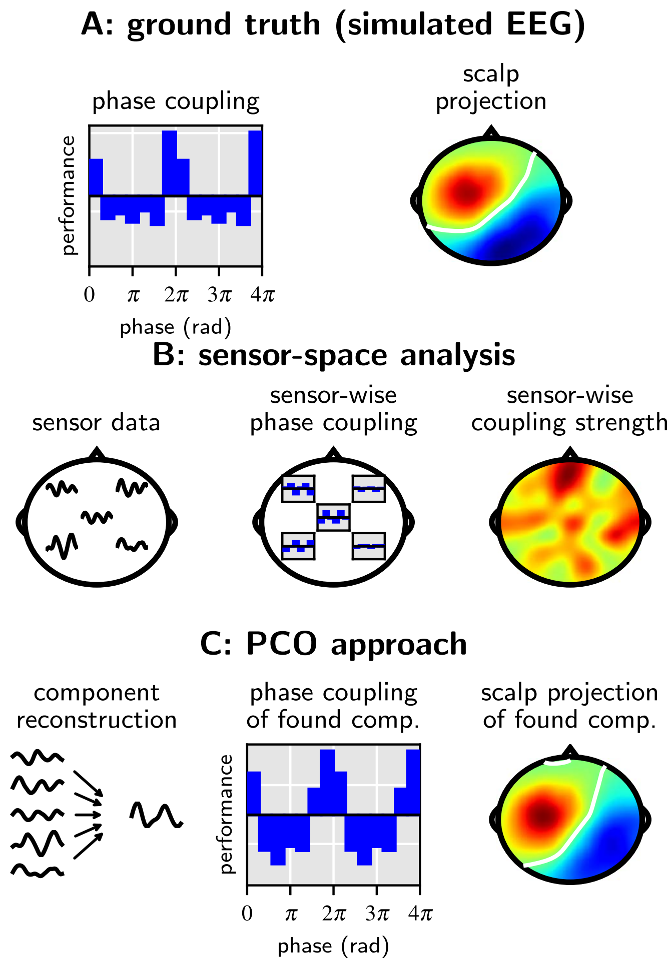

Fig. 1. Motivation of the PCO approach: insights from realistic forward modeling. A: The relation between the phases of a simulated neuronal source and a modeled measure of experimental performance can be visualized by a phase–performance histogram (top row, left). The scalp-projection of the modeled neuronal source displayed a bipolar configuration above the right parietal cortex (top right). B: In conventional sensor-space analysis, the coupling between the phases of neuronal oscillations and experimental performance is analyzed in the individual sensor data (middle row, center), composed of the superimposition of a multitude of neuronal sources and additional technical (e.g. amplifier) noise. The spatial distribution of the obtained phase-coupling strength (middle row, right) distorts the source pattern and cannot localize the phase–performance-coupled source correctly. C: The PCO approach reconstructs the phase–performance-coupled source component by linear spatial filtering of the sensor data (bottom row, left). Contrary to sensor-space analysis, this approach can reliably reproduce the underlying phase–performance relation (bottom row, center) and scalp projection (bottom row, right). The underlying modeling process is explained in Section 2.2.

Methods

Phase coupling optimization (PCO)

We model M/EEG as linear superimposition of neuronal brain sources onto the scalp. Let the activity of N neuronal generators at discrete time t be reflected by the vector $s_{N\times1}(t)$. In a linear forward model, the projection of the N neuronal sources to C sensors at the scalp is described as linear mixing process:

$$\boldsymbol{x}_{C\times1}(t) = \boldsymbol{A}_{C\times N}\boldsymbol{s}_{N\times1}(t), \tag{1}$$

where we denote $\boldsymbol{x}_{C\times1}(t)$ as *sensor-space activity*, $\boldsymbol{s}_{N\times1}(t)$ as *source-space activity*, and the matrix $\boldsymbol{A}_{C\times N}$ as *mixing matrix*. A column $\boldsymbol{a}_{C\times1}$ of the mixing matrix describes the projection of an individual source to the sensor space and is denoted as *spatial pattern* of that source.

The idea of spatial filtering techniques is to recover source activities from the sensor space: