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Identifying Granger causal relationships between neural power dynamics and variables of interest

Irene Winkler [a,*], Stefan Haufe [a,b,c], Anne K. Porbadnigk [a,c,d], Klaus-Robert Müller [a,c,d,e,*], Sven Dähne [a,d,*]

[a] Machine Learning Laboratory, Berlin Institute of Technology, Marchstr. 23, 10587 Berlin, Germany
[b] Neural Engineering Group, Department of Biomedical Engineering, The City College of New York, New York City, NY, USA
[c] Bernstein Focus Neurotechnology, Berlin, Germany
[d] Bernstein Center for Computational Neuroscience, Berlin, Germany
[e] Department of Brain and Cognitive Engineering, Korea University, Anam-dong, Seongbuk-gu, Seoul 136-713, Republic of Korea

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ABSTRACT

Power modulations of oscillations in electro- and magnetoencephalographic (EEG/MEG) signals have been linked to a wide range of brain functions. To date, most of the evidence is obtained by correlating bandpower fluctuations to specific target variables such as reaction times or task ratings, while the causal links between oscillatory activity and behavior remain less clear. Here, we propose to identify causal relationships by the statistical concept of Granger causality, and we investigate which methods are bests suited to reveal Granger causal links between the power of brain oscillations and experimental variables.

As an alternative to testing such causal links on the sensor level, we propose to linearly combine the information contained in each sensor in order to create virtual channels, corresponding to estimates of underlying brain oscillations, the Granger-causal relations of which may be assessed. Such linear combinations of sensor can be given by source separation methods such as, for example, Independent Component Analysis (ICA) or by the recently developed Source Power Correlation (SPoC) method.

Here we compare Granger causal analysis on power dynamics obtained from i) sensor directly, ii) spatial filtering methods that do not optimize for Granger causality (ICA and SPoC), and iii) a method that directly optimizes spatial filters to extract sources the power dynamics of which maximally Granger causes a given target variable. We refer to this method as Granger Causal Power Analysis (GrangerCPA).

Using both simulated and real EEG recordings, we find that computing Granger causality on channel-wise spectral power suffers from a poor signal-to-noise ratio due to volume conduction, while all three multivariate approaches alleviate this issue. In real EEG recordings from subjects performing self-paced foot movements, all three multivariate methods identify neural oscillations with motor-related patterns at a similar performance level. In an auditory perception task, the application of GrangerCPA reveals significant Granger-causal links between alpha oscillations and reaction times in more subjects compared to conventional methods.

Introduction

Oscillatory neural activity is a fundamental property of neuronal networks and has widely been linked with distinct brain functions (Jensen et al., 2007; Nikulin et al., 2007; Rieder et al., 2011; Başar, 2012). Bandpower fluctuations in electro- and magnetoencephalography (EEG/MEG), as well as electrocorticography (ECoG), signals have been shown to be correlated with behavioral measures of task performance or perceptual experience in humans and have been related to a variety of cognitive phenomena, including attention (Debener et al., 2003; Bauer et al., 2006; Womelsdorf and Fries, 2007; Haegens et al., 2011), memory (Klimesch, 1999; Osipova et al., 2006), vigilance (Oken et al., 2006; Berka et al., 2008) and perception (Kaiser et al., 2006; Thut et al., 2006; Babiloni et al., 2006; Schubert et al., 2009). As most of the evidence is of correlative nature, the functional role of oscillatory activity and its causal effects on behavior remain a field of intense research (Buzski and Draguhn, 2004; Thut and Miniussi, 2009).

An intriguing way to investigate the functional role of oscillations is to induce them with brain stimulation techniques such as repetitive Transcranial Magnetic Stimulation (rTMS) and Transcranial Alternating Current Stimulation (TACS) (Thut et al., 2012; Herrmann et al., 2013). Accumulating evidence suggests that rhythmic stimulation induces behavioral consequences, for instance on visual perception (Romei et al., 2010), motor performance (Joundi et al., 2012), mental rotation

* Corresponding authors.
E-mail addresses: irene.winkler@tu-berlin.de (I. Winkler), shaufe@ccny.cuny.edu (S. Haufe), klaus-robert.mueller@tu-berlin.de (K.-R. Müller), sven.daehne@tu-berlin.de (S. Dähne).

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(Klimesch et al., 2003), working memory (Zaehle et al., 2011), and sleep stages (Massimini et al., 2007).

A fundamentally different approach to studying the causal effects of oscillations that does not require direct intervention in the nervous system is the following: identification of causal relationships based on temporal precedence as revealed by a concept called 'Granger causality' (Granger, 1969). Granger causality is a standard statistical method from the field of econometrics and has been applied in neuroscience to infer functional brain connectivity (e.g. Roebroeck et al., 2005; Astolfi et al., 2007; Bressler and Seth, 2011). Assume we simultaneously measure EEG bandpower ϕ and a target variable z over time. Then ϕ is said to Granger cause z if ϕ helps to predict the future z above what is predicted by the past of z alone. Here, z can be any signal of interest, such as a behavioral output (e.g., reaction time, sensory detection, task rating, evoked potentials), a physiological measure (e.g., muscular activity, heart rate variability) or a second power time course.

The advantage of non-invasiveness warrants further pursuit of the Granger causality idea, as applied to power dynamics of EEG recordings. For example, an actively researched question in the field of Brain–Computer Interfaces (BCIs) is whether (and how) oscillatory sources influence the control performance of a user during a BCIs experiment (Grosse-Wentrup et al., 2011; Dähne et al., 2011; Maeder et al., 2012). Existing results suggest a causal role of gamma power in the modulation of BCIs control performance (Grosse-Wentrup, 2011). In the Granger causal setting, the target variable z would thus be the BCIs control performance per trial, while the goal would be to identify a neural source whose power time course Granger-causes z. Due to high inter-trial variability as well as low signal-to-noise ratio (particularly in high-frequency ranges such as the gamma band), finding predictive sources is a challenging task.

The simplest approach to testing for Granger causality is to consider each channel separately. However, the physics of EEG implies that the activity measured at a given channel is a mixture of contributions from several neuronal sources, whose activity is spread across the EEG channels due to volume conduction in the head (Baillet et al., 2001; Parra et al., 2005; Nunez and Srinivasan, 2006). This leads to a low signal-to-noise (SNR) ratio and may hinder physiological interpretation of the results, because the activity of a Granger causal neural source is not guaranteed to be best observable even in the sensors that are closest to the neural source. These considerations imply that testing Granger causality on sensor-level computed power time courses is potentially suboptimal.

The complications outlined above can be avoided by recovering the underlying neural source signals from scalp recordings prior to the computation of bandpower dynamics and the test for Granger causality. The task of recovering underlying signals from multivariate recordings is called (blind) source separation (BSS), and can only be solved using prior knowledge about the signals to be recovered. In the field of neuroscience, one of the most popular BSS algorithms is Independent Component Analysis (ICA), which seeks maximally statistically independent sources. However, here we are interested in recovering sources whose power dynamics Granger cause an external variable. Thus, we might benefit from basing the reconstruction of source activity exactly on this assumed dependency. This is especially important since an oscillatory source may Granger cause a behavioral output variable by modulating other brain rhythms — which contradicts the assumption of independence to all other sources. Moreover, a benefit of directly optimizing for the quantity of interest rather than statistical independence has been demonstrated recently in the context of correlation analysis (Dähne et al., 2013, 2014a,b).

In this paper, we investigate which methods are bests suited to reveal a Granger causal effect from neural oscillations to a given external target variable. To this end, we compare channel-wise Granger causality testing with three source separation methods. We propose a novel analysis method which extracts a source whose bandpower maximally Granger causes the target variable, and we compare it with ICA and the recently proposed SPoC method (Dähne et al., 2014a) which extracts neural sources whose bandpower is maximally correlated with the target variable. This comparison is carried out both in simulations and on two real EEG data sets.

Methods

Granger causality

Granger causality (Granger, 1969) is a statistical method to infer causality between time series based on the temporal argument that the cause should precede the effect. It has been widely applied to the study of economic variables and recently been adopted in the field of neuroscience (Roebroeck et al., 2005; Astolfi et al., 2007; Bressler and Seth, 2011). While Granger causality has gained popularity as a simple testable definition of causality, note that the scientific methodology for the inference of cause–effect relationships from data is subject to intense research. A significant Granger test is often thought not to reflect 'true causality', but what is sometimes termed 'predictive causality' or simply 'Granger causality'.

Let us consider two univariate time series ϕ and z (representing, for example, the EEG power and target variable time course). According to Granger's definition, ϕ is said to Granger cause z, if we are better able to predict z using 'all the information in the universe' than if all information apart from ϕ has been used (Granger, 1969). In practice, it is common to consider only the information in the past of ϕ and z (Hamilton, 1994; Bressler and Seth, 2011). The statistical test is then given by the comparison of the goodness of fit of two autoregressive (AR) models. First, z is modeled as a function of a predefined number P of its most recent past values. Second, z is modeled as a function of both its own past values and the past values of ϕ. Finally, Granger causality tests whether the second regression model explains significantly more variance of z than the first regression model.

In the linear case, the two regression models are given as

$$z(t) = \sum_{p=1}^{P} h_{res}(p) z(t-p) + \epsilon_{res}(t) \tag{2.1}$$

and

$$z(t) = \sum_{p=1}^{P} h_{full}(p) z(t-p) + \sum_{p=1}^{P} h_{full}(P+p) \phi(t-p) + \epsilon_{full}(t), \tag{2.2}$$

where P denotes the number of time lags, $h_{res} \in \mathbb{R}^P$ and $h_{full} \in \mathbb{R}^{2P}$ denote the regression coefficients, and ϵ_{res} and ϵ_{full} denote the residuals.

ϕ is said to Granger cause z if the variance of the residuals ϵ_{res} of the restricted model is significantly larger than the variance of the residuals ϵ_{full} of the full model. Granger causality from ϕ to z can be captured with Geweke's Granger causality index (Geweke, 1982), defined as

$$\mathcal{G}_{\phi \to z} = \log \frac{\mathrm{Var}\left(\epsilon_{res}\right)}{\mathrm{Var}\left(\epsilon_{full}\right)}. \tag{2.3}$$

Under the assumption of Gaussian distributed residuals, $\mathcal{G}_{\phi \to z}$ is asymptotically χ^2 distributed. Under the same assumption, an exact test is given by the F-test for regression (see Bressler and Seth, 2011, for instance). Under the null hypothesis of no Granger causality,

$$F_{\phi \to z} = \frac{\mathrm{Var}\left(\epsilon_{res}\right) - \mathrm{Var}\left(\epsilon_{full}\right)}{\mathrm{Var}\left(\epsilon_{full}\right)} \cdot \frac{N-2P}{P} \tag{2.4}$$

will have an F distribution with $(P, N-2P)$ degrees of freedom, where N denotes the number of available data points. If the distribution of the residuals is unknown, non-parametric methods such as permutation