

## Research paper

# The temporal stability and variability across frequency bands in neural synchrony between primary and secondary somatosensory areas following somatosensory stimulation

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## ABSTRACT

**Objectives:** To examine the temporal stability and variability of neuronal synchronization among the contralateral primary somatosensory cortex (cSI) and contralateral (cSII) and ipsilateral secondary somatosensory cortex (iSII) in response to median nerve stimulation.

**Methods:** Both the spontaneous magnetoencephalography (MEG) signals as the pre-stimulus condition and somatosensory evoked magnetic-fields (SEF) were recorded in eleven healthy subjects. We calculated a phase-locking value (PLV) between two areas among cSI, cSII, and iSII in five frequency bands (theta: 5–7 Hz, alpha: 8–12 Hz, beta: 15–29 Hz, gamma-1: 30–59 Hz, and gamma-2: 60–90 Hz), and compared the PLV among in pre-stimulus and stimulus conditions.

**Results:** The PLV between cSI and cSII for the theta band activity varied within 2 s from the stimulus onset. On the other hand, the PLV between cSI and iSII for the alpha band did not vary within 2 s.

**Conclusion:** The fluctuation of neuronal synchrony among sensory-related cortices in response to median nerve stimulation depends on the induced frequency band and inter-region.

**Significance:** This study is the first to report the temporal characteristic of stimulus-driven neural synchrony following somatosensory stimulation.

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## 1. Introduction

Recently, neural networks among brain areas have been of marked interest. There have been mainly two methodological approaches: functional magnetic resonance imaging (f-MRI) and magnetoencephalography (MEG), to investigate the neural networks, recordings of the resting state, and task-related brain activities. The resting state brain activity includes activities of resting state networks (RSNs), in which widely distributed brain areas function with temporal coherences at rest (Biswal et al., 1995; Brookes et al., 2011a; Brookes et al., 2011b; de Pasquale et al., 2010; Fox and Raichle, 2007; Liu et al., 2010;). For the somatosensory neural system, MEG (de Pasquale et al., 2010; Yuan et al., 2012) and f-MRI (Biswal et al., 1995; Brookes et al., 2011b) studies have shown a sensorimotor network at rest as well as other RSNs, such as a default mode network and dorsal attentional network. Furthermore, a stimulus-driven neuronal network among sensory-related cortices has been identified (Bardouille and Boe,

2012; Brookes et al., 2011a; Kujala et al., 2007). Neuronal synchrony from the alpha to gamma frequency bands was observed between the primary (SI) and secondary (SII) somatosensory cortices until 200–500 ms following median nerve stimulation (Hagiwara et al., 2010; Simões et al., 2003).

Following the identification of the neural network between spatially separate brain regions, some studies exploring the temporal and spectral evolution of coupling regions in a resting state suggested that temporally and spectrally variable neuronal dynamics underlie the resting state networks detected (Britz et al., 2010; Brookes et al., 2014; Hillebrand et al., 2012; Smith et al., 2009). Concerning the stimulus-driven neural network between somatosensory-related cortices, the characterizing phase locking between SI and SII in the early-stage somatosensory processing following electrical stimulation has been investigated, but the temporal variability across frequency bands remains unknown. Given the temporal and spectral non-stationarity in resting state networks, it is hypothesized that dynamic neural synchronization across frequency bands contributes to the stimulus-driven neural network between SI and SII following median nerve stimulation. To assess the temporal instability in the stimulus-driven neural network,

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we applied MEG, which shows significant advantages with excellent time resolution in characterizing temporal non-stationarity, and the phase-locking value (PLV) approach (Lachaux et al., 1999). It was reported that the PLV does not rely on stationarity, unlike spectral coherence, and it enables the accurate estimation of synchronization among networks (Lowet et al., 2016). In this study, we traced the neural synchrony of the MEG signals among the contralateral SI (cSI), contralateral SII (cSII), and ipsilateral SII (iSII) until 2 s following median nerve stimulation as well as the spontaneous signals under the non-stimulus condition. We estimated the PLV using source-reconstructed MEG signals, which yielded more information based on the brain anatomy than the sensor-level signals. Then, we compared the PLV between stimulus and non-stimulus conditions. This paper focuses on the temporal variability across frequency bands in the stimulus-driven neural network between SI and SII. Assessing the temporal instability in the stimulus-driven neural network can provide valuable insights into the interaction between the resting state and stimulus-driven neural networks.

## 2. Materials and methods

### 2.1. Participants

Eleven healthy volunteers (2 males and 9 females, mean age: 21.0 years, range: 20–22 years) participated in the experiment. All subjects showed right-hand dominance based on the Edinburgh Handedness Questionnaire (Oldfield, 1971), and they had no history of neurological or psychiatric disease. Each participant gave informed consent for the study and experimental protocol prior to its commencement. This study was approved by the ethical committee of the Faculty of Medicine, Nagoya University.

### 2.2. Experimental design

Each participant lay down on a bed in a magnetically shielded room during the recording. The right median nerve was stimulated at the wrist with 0.5-ms constant-current square-wave pulses by an electrical stimulator (S-2727B, Nihon-Koden, Japan), at an intensity 20% above the motor threshold ( $44.2 \pm 6.3$  V) with an inter-stimulus interval of 2 s. (If cortical activity were being recorded from SII, an inter-stimulus interval of 2 s may be short. However, this study investigated the temporal stability and variability in neural synchrony focused on the phase between brain areas, and not the amplitude of cortical activity. Further, the PLV can be calculated from a spontaneous condition, it is therefore likely that there is little effect of the inter-stimulus interval on the results.) Participants were asked to ignore the stimuli, keeping their attention on a silent video projected on a screen 30 cm in front of them.

### 2.3. Data acquisition

We used a whole-head MEG system (PQ1160C, Yokogawa Electric Co., Japan) with 160 axial-type first-order gradiometers and a 50-mm-long baseline detection coil. The initial bandpass filter was between 0.3 to 500 Hz, at a sampling rate of 2000 Hz, with a notch filter at 60 Hz. An electro-ocular gram (EOG) with a pair of disk electrodes placed on the lateral canthus and 2 cm below the infra-orbicular edge of the right eye, and electrocardio gram (ECG) with a pair of electrodes on both sides just beneath the clavicle, were recorded for artifact rejection at the pre-processing stage, as described below.

Firstly, spontaneous signals were recorded as the pre-stimulus condition with no stimulus (NS) for three minutes in a dark and

noise-shielded room. The participants were instructed to stay awake with their eyes open and relax. Somatosensory evoked fields (SEF) were recorded following right median nerve stimulation. MEG signals were continuously collected for 400 s during the administration of 200 stimuli.

Prior to the MEG recording in each participant, his/her scalp shape was digitally traced using a 3D digitizer (SR system-R, YOKOGAWA, Japan), which enabled us to fit the MEG coordinates to those of the standardized brain, as described below.

### 2.4. Data analysis

All data analyses including the preprocessing, source imaging, and calculation of PLV were performed with the software Brainstorm (Tadel et al., 2011), which is open-source software (<http://neuroimage.usc.edu/brainstorm/>). All implementation details are therefore readily documented and can be verified in Brainstorm.

Firstly, using the EOG and ECG data, artifacts caused by the heart-beat and eye movement/blinking were attenuated by designing signal-space projections from selected segments of data about each artifact event (Nolte and Curio, 1999). Furthermore, segments with residual artifacts of extra-cephalic origin were rejected by visual inspection from datasets before further analysis.

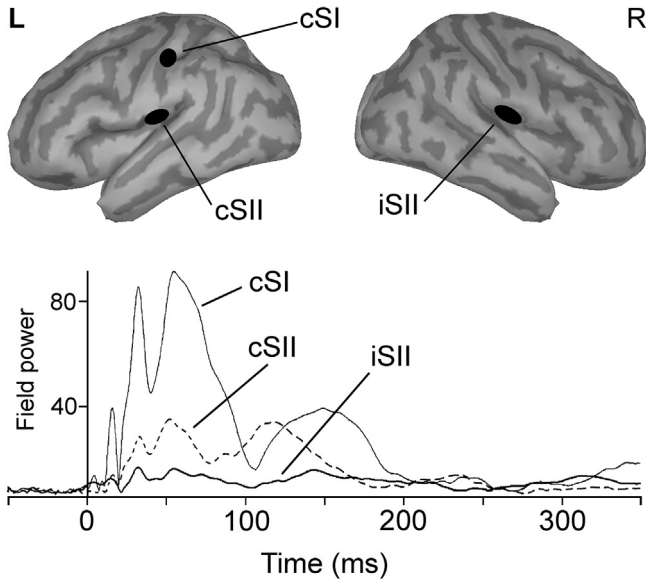
For the spontaneous MEG data, epochs for 1 s were segmented and collected (Pre-stim). For the SEF data, epochs from the stimulus onset to 1 s after the stimulus (Seg-1) and from 1 to 2 s after the stimulus (Seg-2) were separately collected. Over 160 epochs (NS:  $173.0 \pm 4.6$ , SEF (Seg-1 and -2):  $173.6 \pm 5.7$  trials) were used to estimate source activities. In Brainstorm, the depth-weighted minimum norm model (Hämäläinen and Ilmoniemi, 1994) was used with the default parameter settings, including a set of elementary current dipoles, up to 7500 dipoles, distributed over the individual cortical envelope. Each individual cortical envelope projecting the source activities was created from Brainstorm's default anatomy, Colin 27, which is the Montreal Neurological Institute (MNI) brain template, based on each individual scalp shape digitized. We manually selected three regions of interest (ROIs) on the cortex with 15 vertices (mean size:  $3.47 \text{ cm}^2$ ): the contralateral primary somatosensory cortex (cSI) and contralateral (cSII) and ipsilateral (iSII) secondary somatosensory cortex (Fig. 1).

The PLV between two areas among the three cortical areas in five frequency bands (theta: 5–7 Hz, alpha: 8–12 Hz, beta: 15–29 Hz, gamma-1: 30–59 Hz, and gamma-2: 60–90 Hz) was calculated for each epoch of Pre-stim, Seg-1, and Seg-2 source time-series. The PLV, ranging from 0 to 1, estimates the variability of phase differences between two brain areas. In each participant, the calculated PLV was averaged in Pre-stim, Seg-1, and Seg-2, respectively. To remove the influence of individual differences, the PLV ratio was calculated by dividing values of the three conditions by the value of Pre-stim for each participant. The PLV ratio in each frequency band was statistically analyzed among the conditions using one-way repeated measures ANOVA with post hoc multiple comparison tests (Bonferroni correction). All statistical analyses were performed with the SPSS statistical package (version 22). *P*-values of  $<0.05$  were set as significant.

## 3. Results

In all participants, SEF were clearly identified until approximately 200 ms, and were included in Seg-1 (Fig. 2). On the other hand, there was no prominent SEF component in Seg-2. The regional field power in cSI, cSII, and iSII lasted until 300 ms after stimulus onset (Fig. 1 lower panel).

The PLV between cSI and cSII in the theta band significantly varied among conditions ( $F(2, 20) = 9.387$ ,  $p = 0.001$ ). Multiple

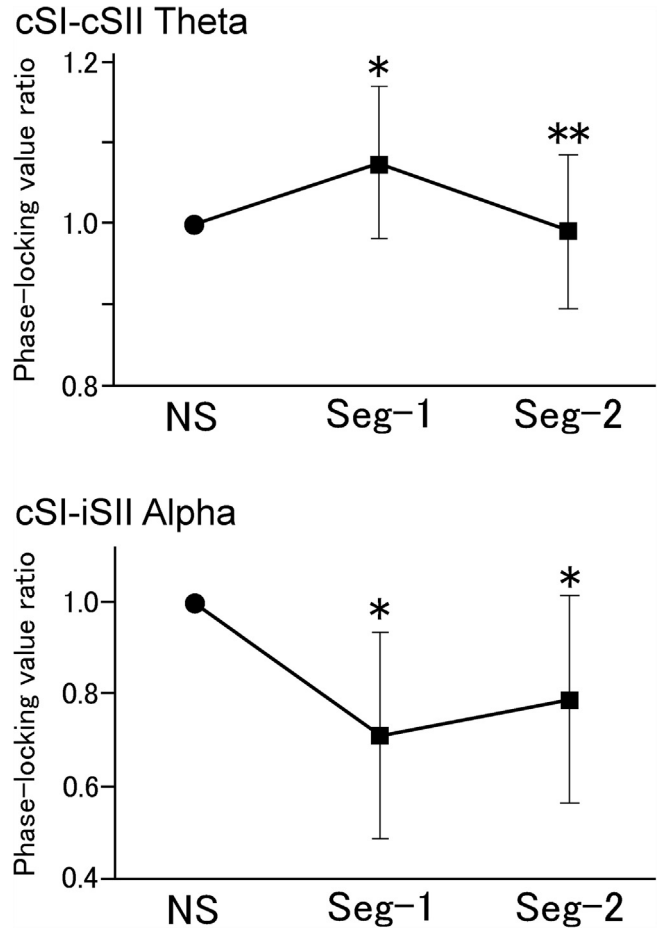


**Fig. 1.** Cortical areas selected for PLV analysis (top) and regional field power in each cortical area (bottom). The mean size of each region was 3.47 cm<sup>2</sup> based on the Montreal Neurological Institute (MNI) Colin 27 brain template (top). The temporal changes of the regional field power in each selected cortical area in a representative participant (bottom). cSI: contralateral primary somatosensory cortex, cSII: contralateral secondary somatosensory cortex, iSII: ipsilateral secondary somatosensory cortex.

comparisons showed that the theta PLV in Seg-1 was significantly higher than that in Pre-stim and Seg-2 ( $p = 0.018$  and  $p = 0.002$ , respectively) (Fig. 3 upper). Additionally, the PLV between cSI and iSII in alpha band also varied among conditions ( $F(2, 20) = 9.83$ ,  $p = 0.001$ ). The alpha PLV in Seg-1 and Seg-2 was lower than that in Pre-stim ( $p = 0.006$  and  $p = 0.045$ , respectively), and there was no difference between Seg-1 and Seg-2 (Fig. 3 lower). In beta, gamma-1, and gamma-2 bands, there was no significant difference among conditions.

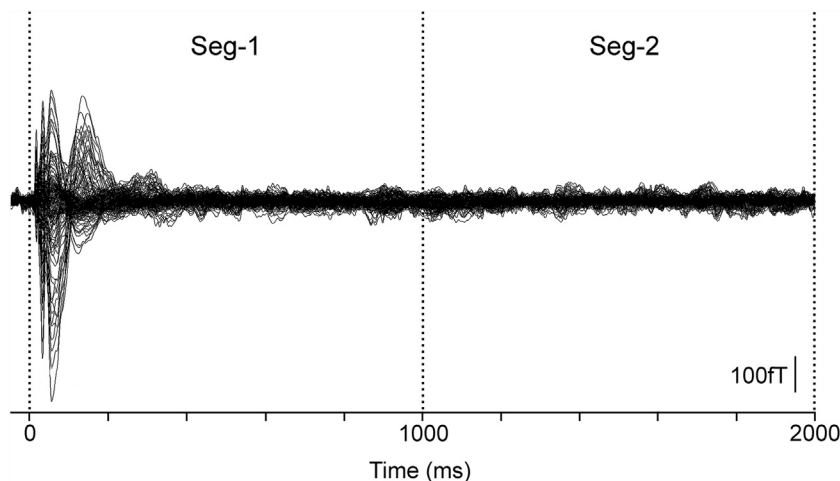
**4. Discussion**

The stimulus-driven neuronal network among sensory-related cortices has been identified (Bardouille and Boe, 2012; Brookes et al., 2011a; Kujala et al., 2007). The neuronal synchrony from



**Fig. 3.** The phase-locking value (PLV) ratio to no stimulus (NS) in Seg-1 and Seg-2. Upper: The theta PLV between cSI and cSII in Seg-1 was significantly higher than that in NS and Seg-2 ( $p = 0.018$  and  $p = 0.002$ , respectively). Lower: The alpha PLV between cSI and iSII in Seg-1 and Seg-2 was significantly lower than that in NS ( $p = 0.006$  and  $p = 0.045$ , respectively). \*: vs. NS. \*\*: vs. Seg-1. NS: non-stimulus condition.

the alpha to gamma frequency bands was observed between SI and SII until 200–500 ms following median nerve stimulation (Hagiwara et al., 2010; Simões et al., 2003). Recently, some studies explored the temporal and spectral evolution of coupling regions in



**Fig. 2.** The SEF waveforms in a representative participant. The SEF waveforms averaged from 160 epochs with a bandpass filter between 0.5 and 100 Hz. The first segment for 1 s (Seg-1) includes large deflections of the SEF components, while there was no deflection identified in the latter segment for 1 s (Seg-2).

a resting state, and suggested that temporally and spectrally variable neuronal dynamics underlie the resting state networks detected (Britz et al., 2010; Brookes et al., 2014; Hillebrand et al., 2012; Smith et al., 2009). However, temporal variability across frequency bands in the stimulus-driven neural network between somatosensory-related cortices remains unknown. In this study, we assessed the PLV among somatosensory-related cortices until 2 s following median nerve stimulation, and our results provide evidence for temporal variability across frequency bands in the stimulus-driven neural network between somatosensory-related cortices. To our knowledge, our study is the first to demonstrate temporal variability across frequency bands in the stimulus-driven neural network between SI and SII following somatosensory stimulation. Therefore, temporal variability in the stimulus-driven neural network is induced in theta and alpha band activity, and this variability changes depending on the inter-region.

Previous studies reported that the brain process in response to somatosensory stimuli was reflected by the phase synchrony in the alpha frequency band (Cheng et al., 2015; Dockstader et al., 2010; Hari et al., 1997; Palva et al., 2005; Ploner et al., 2006; Simões et al., 2003). Moreover, Jensen and Mazaheri (2010) proposed that oscillatory alpha activity reflected functional inhibition in task-irrelevant brain areas. Conversely, the alpha activity was decreased in the engaged primary sensorimotor cortex during a cognitive somatosensory information-processing task (Haegens et al., 2010). Although we are not able to simply compare it with this study because the employed task was different, the decreased alpha PLV in both Seg-1 and Seg-2 may reflect the brain process in response to median nerve stimuli. It should be noted that the alpha PLV between cSI and iSII did not vary within 2 s from the stimulus onset. The phase synchrony in alpha as well as in other frequency bands could be associated with a specific inter-region phase difference, which facilitates or suppresses neural communication between these regions (Fries, 2005). We demonstrated that this neural synchrony in the alpha frequency band between cSI and iSII could last for at least 2 s, whereas the stimulus-time locked magnetic fields did not show marked neuromagnetic activity after 500 ms following the stimulus onset. There is a discrepancy between the duration of inter-regional neural synchrony and measured stimulus time-locked cortical activity. Because the early cortical activity evoked by somatosensory stimulation was well time-locked, the first to third components, especially from 0 to 100 ms, were steep. Thus, it is plausible that the time dispersion expanded with increasing time, which resulted in the disappearance of time-locked components in the averaged waveforms. We cannot discuss how long this phase synchrony continues or when it fluctuates. A previous study demonstrated the temporal non-stationarity of the connectivity within the sensorimotor network in a resting state, showing that periods of high correlation alternated with periods of low correlation in a cycle of several tens of seconds (Brookes et al., 2014). Taking this result into consideration, the steady alpha PLV in this study might be a part of succeeding alternation. Further studies are needed to answer these questions by calculating the PLV in a segment with a longer time window.

It is well-known that not only alpha but also beta frequency bands are characteristic of the functional connectivity among the sensorimotor cortexes (Hari et al., 1997; Palva et al., 2005; Simões et al., 2003). These results differ from ours in that there was no significant PLV difference in the beta frequency band among the conditions. The alpha and beta frequency band oscillations were spatially and temporally different, and they played different functional roles in sensorimotor processing (Pfurtscheller and Lopes da Silva, 1999; Salmelin et al., 1995; Simões et al., 2003). Actually, the beta band oscillation is associated with the motor cortical function and the alpha band predominantly reflects

the somatosensory cortical function (Salmelin et al., 1995). The reason why the PLV in beta did not vary among conditions in this study is that we employed an electrical stimulation, which evokes cortical activation of mainly somatosensory-related areas.

The cortical theta band activity plays an important role in sensorimotor integration in humans (Cruikshank et al., 2012), and is associated with conscious somatosensory perception over the primary sensory area (Palva et al., 2005). Taking these results into consideration, the theta PLV variability within 2 s after sensory stimulation in this study may reflect information processing of perceived sensory stimulus. Therefore, along with the disappearance of clear time-locked cortical activity, this phase synchrony enhancement was attenuated and approached the pre-stimulation level in the subsequent second. Our findings suggest that the phase synchrony in the theta band within somatosensory-related cortices may be disconnected in a shorter time compared with that in the alpha band. In accordance with our assumption, a similar reset of theta activity was reported under a repetitive somatosensory stimulation paradigm (Dietl et al., 1999). A phasic increase in the theta band activity coincident with the stimulus train onset was reset to the pre-stimulation level with a short time duration (0.9 Hz) (Dietl et al., 1999). This inter-stimulus interval is very similar to the time course of theta PLV variability in this study.

In conclusion, the present study investigated temporal variability across frequency bands in stimulus-driven neural synchrony between sensory-related cortices. We demonstrated that the theta PLV between cSI and cSII showed variability within 2 s after stimulus onset. On the other hand, the alpha PLV showed temporal stability. The present results suggest that temporally and spectrally variable neural dynamics underlie the stimulus-driven neural synchrony between sensory-related cortices.

#### Conflict of interest statement

The authors declare that there is no conflict of interest.

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#### References

- Bardouille, T., Boe, S., 2012. State-related changes in MEG functional connectivity reveal the task-positive sensorimotor network. *PLoS ONE* 7 (10), e48682. <http://dx.doi.org/10.1371/journal.pone.0048682>.
- Biswal, B., Yetkin, F.Z., Haughton, V.M., Hyde, J.S., 1995. Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magn. Reson. Med.* 34 (4), 537–541.
- Britz, J., Van De Ville, D., 2010. Michel CM.BOLD correlates of EEG topography reveal rapid resting-state network dynamics. *Neuroimage* 52 (4), 1162–1170.
- Brookes, M.J., Hale, J.R., Zumer, J.M., Stevenson, C.M., Francis, S.T., Barnes, G.R., Owen, J.P., Morris, P.G., Nagarajan, S.S., 2011a. Measuring functional connectivity using MEG: methodology and comparison with fMRI. *Neuroimage* 56 (3), 1082–1104.
- Brookes, M.J., Woolrich, M., Luekhoo, H., Price, D., Hale, J.R., Stephenson, M.C., Barnes, G.R., Smith, S.M., Morris, P.G., 2011b. Investigating the electrophysiological basis of resting state networks using magnetoencephalography. *Proc. Natl. Acad. Sci. U.S.A.* 108 (40), 16783–16788.
- Brookes, M.J., O'Neill, G.C., Hall, E.L., Woolrich, M.W., Baker, A., Palazzo Corner, S., Robson, S.E., Morris, P.G., Barnes, G.R., 2014. Measuring temporal, spectral and spatial changes in electrophysiological brain network connectivity. *Neuroimage* 91, 282–299.
- Cheng, C.H., Chan, P.Y., Baillet, S., Lin, Y.Y., 2015. Age-related reduced somatosensory gating is associated with altered alpha frequency desynchronization. *Neural Plast.* 2015, 302878. <http://dx.doi.org/10.1155/2015/302878>.
- Cruikshank, L.C., Singhal, A., Hueppelshauer, M., Caplan, J.B., 2012. Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. *J. Neurophysiol.* 107 (1), 65–77.



- de Pasquale, F., Della Penna, S., Snyder, A.Z., Lewis, C., Mantini, D., Marzetti, L., Belardinelli, P., Ciancetta, L., Pizzella, V., Romani, G.L., Corbetta, M., 2010. Temporal dynamics of spontaneous MEG activity in brain networks. *Proc. Natl. Acad. Sci. U.S.A.* 107 (13), 6040–6045.
- Dietl, T., Dirlich, G., Vogl, L., Lechner, C., Strian, F., 1999. Orienting response and frontal midline theta activity: a somatosensory spectral perturbation study. *Clin. Neurophysiol.* 110 (7), 1204–1209.
- Dockstader, C., Cheyne, D., Tannock, R., 2010. Cortical dynamics of selective attention to somatosensory events. *Neuroimage* 49 (2), 1777–1785.
- Fox, M.D., Raichle, M.E., 2007. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nat. Rev. Neurosci.* 8 (9), 700–711.
- Fries, P., 2005. A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends Cogn. Sci.* 9 (10), 474–480.
- Haegens, S., Osipova, D., Oostenveld, R., Jensen, O., 2010. Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Hum. Brain Mapp.* 31 (1), 26–35.
- Hagiwara, K., Okamoto, T., Shigeto, H., Ogata, K., Somehara, Y., Matsushita, T., Kira, J., Tobimatsu, S., 2010. Oscillatory gamma synchronization binds the primary and secondary somatosensory areas in humans. *Neuroimage* 51 (1), 412–420.
- Hämäläinen, M.S., Ilmoniemi, R.J., 1994. Interpreting magnetic fields of the brain: minimum norm estimates. *Med. Biol. Eng. Comput.* 32 (1), 35–42.
- Hari, R., Salmelin, R., Mäkelä, J.P., Salenius, S., Helle, M., 1997. Magnetoencephalographic cortical rhythms. *Int. J. Psychophysiol.* 26 (1–3), 51–62.
- Hillebrand, A., Barnes, G.R., Bosboom, J.L., Berendse, H.W., Stam, C.J., 2012. Frequency-dependent functional connectivity within resting-state networks: an atlas-based MEG beamformer solution. *Neuroimage* 59 (4), 3909–3921.
- Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186. <http://dx.doi.org/10.3389/fnhum.2010.00186>.
- Kujala, J., Pammer, K., Cornelissen, P., Roebroek, A., Formisano, E., Salmelin, R., 2007. Phase coupling in a cerebro-cerebellar network at 8–13 Hz during reading. *Cereb. Cortex* 17 (6), 1476–1485.
- Lachaux, J.P., Rodriguez, E., Martinerie, J., Varela, F.J., 1999. Measuring phase synchrony in brain signals. *Hum. Brain Mapp.* 8 (4), 194–208.
- Liu, Z., Fukunaga, M., de Zwart, J.A., Duyn, J.H., 2010. Large-scale spontaneous fluctuations and correlations in brain electrical activity observed with magnetoencephalography. *Neuroimage* 51 (1), 102–111.
- Lowet, E., Roberts, M.J., Bonizzi, P., Karel, J., De Weerd, P., 2016. Quantifying neural oscillatory synchronization: a comparison between spectral coherence and phase-locking value approaches. *PLoS ONE* 11 (1), e0146443. <http://dx.doi.org/10.1371/journal.pone.0146443>.
- Nolte, G., Curio, G., 1999. The effect of artifact rejection by signal-space projection on source localization accuracy in MEG measurements. *IEEE Trans. Biomed. Eng.* 46 (4), 400–408.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9 (1), 97–113.
- Palva, S., Linkenkaer-Hansen, K., Näätänen, R., Palva, J.M., 2005. Early neural correlates of conscious somatosensory perception. *J. Neurosci.* 25 (21), 5248–5258.
- Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110 (11), 1842–1857.
- Ploner, M., Gross, J., Timmermann, L., Pollok, B., Schnitzler, A., 2006. Oscillatory activity reflects the excitability of the human somatosensory system. *Neuroimage* 32 (3), 1231–1236.
- Salmelin, R., Hämäläinen, M., Kajola, M., Hari, R., 1995. Functional segregation of movement-related rhythmic activity in the human brain. *Neuroimage* 2 (4), 237–243.
- Simões, C., Jensen, O., Parkkonen, L., Hari, R., 2003. Phase locking between human primary and secondary somatosensory cortices. *Proc. Natl. Acad. Sci. U.S.A.* 100 (5), 2691–2694.
- Smith, S.M., Fox, P.T., Miller, K.L., Glahn, D.C., Fox, P.M., Mackay, C.E., Filippini, N., Watkins, K.E., Toro, R., Laird, A.R., Beckmann, C.F., 2009. Correspondence of the brain's functional architecture during activation and rest. *Proc. Natl. Acad. Sci. U.S.A.* 106 (31), 13040–13045.
- Tadel, F., Baillet, S., Mosher, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: a user-friendly application for MEG/EEG analysis. *Comput. Intell. Neurosci.* 2011, 879716. <http://dx.doi.org/10.1155/2011/879716>.
- Yuan, H., Zotev, V., Phillips, R., Drevets, W.C., Bodurka, J., 2012. Spatiotemporal dynamics of the brain at rest—exploring EEG microstates as electrophysiological signatures of BOLD resting state networks. *Neuroimage* 60 (4), 2062–2072.