



EEG correlates of spontaneous self-referential thoughts: A cross-cultural study

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ABSTRACT

The default mode network (DMN) has been mostly investigated using positron emission tomography and functional magnetic resonance imaging (fMRI) and has received mixed support in electroencephalographic (EEG) studies. In this study, after sLORETA transformation of EEG data, we applied group spatial independent component analysis which is routinely used in fMRI research. In three large and diverse samples coming from two different cultures (Russian and Taiwanese), spontaneous EEG data and retrospective questionnaire measures of subject's state, thoughts, and feelings during the EEG registration were collected. Regression analyses showed that appearance of spontaneous self-referential thoughts was best predicted by enhanced alpha activity within the DMN. Diminished theta and delta activity in the superior frontal gyrus and enhanced beta activity in the postcentral gyrus added to the prediction. The enhanced alpha activity prevailed in the posterior DMN hub in Russian, but in the anterior DMN hub in Taiwanese participants. Possible cross-cultural differences in personality and attitudes underlying this difference are discussed.

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1. Introduction

Till recently, the investigation of spontaneous mental processes was beyond the scope of most neuroimaging studies. The situation has changed drastically during the last decade. This became possible owing to two parallel developments. Firstly, fMRI and PET studies of synchronized spontaneous low-frequency oscillations between the brain's areas have revealed a number of so-called resting state networks (RSNs) (Biswal et al., 1995; Lowe et al., 1998) whose possible role in spontaneous mental processes is hotly debated. Second development started after the discovery of the so-called default-mode network (DMN). The DMN concept comes from an emergent body of evidence showing a consistent pattern of deactivation across a network of brain regions that occurs during the initiation of task-related activity (Raichle et al., 2001; Raichle and Snyder, 2007). The DMN includes the precuneus/posterior cingulate cortex (PCC), the medial prefrontal cortex (MPFC), and medial, lateral, and inferior parietal cortex (although some other brain regions, e.g., the medial temporal lobe, are also frequently included in the DMN). Although deactivated during task performance, this network is active in the resting brain. A notable exception to this general pattern occurs in relation to tasks requiring self-referential thought and social cognition (Buckner et al., 2008; Mitchell, 2006; Raichle et al., 2001). Correspondingly, many authors suggested that the DMN is somehow

involved in self-referential processes and social cognition (Boly et al., 2008; Christoff et al., 2003; David et al., 2007; Golland et al., 2007; Gusnard et al., 2001; Mitchell, 2006; Wicker et al., 2003). The study of task-related activation/deactivation and studies of synchronized spontaneous low-frequency oscillations have converged in admitting the DMN as one of RSNs (Raichle et al., 2001).

The quest to fully elucidate the function of DMN and other RSNs requires a solid understanding of the link between neuroimaging findings and their electrophysiological underpinnings. Electroencephalogram (EEG) and fMRI represent different aspects of brain activity. Their relationship can thus yield insights not available from one modality alone. If DMN is involved in self-referential processes, as existing fMRI evidence appears to suggest, the study of EEG correlates of these processes may bring important information on how the same psychological processes are reflected in the EEG and fMRI domains. There could be different approaches to the study of fMRI and EEG manifestations of such phenomenon as DMN. Firstly, because simultaneous registration of both signals is now available, raw fMRI and EEG measures could be correlated with each other. Secondly, instead of raw fMRI and EEG measures, patterns of temporally or spatially synchronized networks could be revealed in one or both domains and the correlations could be calculated between these patterns. Lastly, measures of DMN-related behavioral or psychological processes could be used as the criterion variable that could be correlated with respective fMRI or EEG measures (Laufs, 2008).

Many simultaneous EEG–fMRI studies have noted correlations between the DMN blood-oxygen-level-dependent (BOLD) signal and EEG gamma (Mantini et al., 2007), beta (Laufs et al., 2003b; Mantini et al., 2007), alpha (Laufs et al., 2003a; Mantini et al., 2007), and theta (Meltzer et al., 2007; Scheeringa et al., 2008) oscillations.

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Most of the studies have found mainly negative correlations between EEG spectral power (particularly in alpha band of frequencies) and BOLD signal in cortical areas (see e.g., Laufs, 2008 for a review). Laufs (2008) notes that the failure across studies to identify an average cortical BOLD signal pattern which is positively correlated with alpha power may be explained by nonuniform brain activity at the population level during periods of prominent alpha oscillations which fMRI group analysis must fail to detect (Laufs et al., 2006).

In the study by de Munck et al. (2007, 2008), time variations of the occipital alpha band amplitudes were correlated to the fMRI signal variations to obtain insight into the hemodynamic correlates of the EEG alpha activity. It was found that: (1) the alpha band response function of the thalamus is mainly positive. (2) The response functions at the occipital and left and right parietal points are similar in amplitude and timing. (3) The peak time of the thalamus is a few seconds earlier than that of occipital and parietal cortex. A general negative correlation was found between heart beat intervals and alpha power, but inclusion of this confounder had a negligible effect to alpha-BOLD correlations. Wu et al. (2010) found widespread alpha hemodynamic responses and high functional connectivity during eyes-closed rest, while eyes open resting abolished many of the hemodynamic responses and markedly decreased functional connectivity.

Jann et al. (2010) note that when investigating BOLD correlates of EEG rhythms, these correlates resembled the RSNs, suggesting that the different RSNs assemble through synchronization of electric activity as measured by EEG. Namely, BOLD correlates of electrical activity in the alpha (8–12 Hz) and beta (17–23 Hz) frequency bands displayed striking similarity with the DMN as it was described in other publications, suggesting that the RSNs may be organized by neuronal activity at specific frequencies. Martinez-Montes et al. (2004) demonstrated a method correlating EEG 'atoms' with fMRI 'atoms' and identified the alpha-band atom to include parieto-occipital cortex, thalamus, and insula. Mantini et al. (2007) incorporated into their analysis EEG bands between 1 and 50 Hz averaged across the entire scalp and correlated with these bands the fMRI time courses of resting state networks identified by the use of independent component analysis (ICA). RSNs 1 (DMN) and 2 (dorsal attentional network) had stronger relationship with alpha and beta rhythms, albeit in opposite directions, with RSN1 showing positive whereas RSN2 showing negative correlation with alpha and beta rhythms. Jann et al. (2009) show that the BOLD correlates of global EEG synchronization in the alpha frequency band are located in brain areas involved in the DMN. These results confirm the hypothesis that specific RSNs are organized by long-range synchronization at least in the alpha frequency band (Jann et al., 2009). Jann et al. (2010) report on the topographic association of EEG spectral fluctuations and RSN dynamics using EEG covariance mapping. T-mapping of the covariance maps indicated that the strongest effects were again in the alpha and beta bands. DMN activity was found to be associated with increased alpha and beta1 band activity. Sadaghiani et al. (2010) showed that global field power of upper alpha band oscillations is positively correlated with activity in a network overlapping with the DMN and is negatively correlated with activity in the dorsal attention network which is most prominently involved in selective spatial attention. Brookes et al. (2011) analyzed magnetoencephalographic (MEG) data using a unique combination of beamformer spatial filtering and independent component analysis. This method resulted in RSNs with significant similarity in their spatial structure compared with RSNs derived independently using fMRI. In this study, the DMN was identified using MEG data filtered into the alpha band.

In sum, this evidence suggests that alpha and beta oscillations appear to positively correlate with fMRI-DMN and negatively with attentional networks (although, correlations with other frequency bands have also been noted, e.g., Mantini et al., 2007; Meltzer et al., 2007; Scheeringa et al., 2008). Most of these studies correlated temporal dynamics of averaged or 'global' spectral EEG variables with time courses

of spatially correlated networks derived from spontaneous fluctuations of fMRI BOLD signal by means of ICA and similar techniques. The reported correlations imply that in resting condition, the spontaneous fluctuations of 'global' EEG alpha and beta activity notably covary with spontaneous fluctuations of DMN's BOLD signal. Whatever important these observations may be, they in themselves do not speak anything about behavioral or psychological processes underlying this covariance. As Laufs (2008) noted, of the neural processes reflected in both EEG and fMRI there may be measurable behavioral manifestations. It could be argued that from both theoretical and practical point of view these behavioral manifestations are most important.

Unfortunately, studies investigating EEG correlates of self-referential processes are very scarce and few of them did it in resting condition and analyzed spectral EEG information. Mu and Han (2010) used wavelet analysis to calculate non-phase-locked time-frequency power associated with encoding of trait adjectives referenced to the self or the familiar other. Relative to other-referential traits, self-referential traits induced event-related synchronization of theta-band activity over the frontal area and of alpha-band activity over the central area. In contrast, event-related desynchronization associated with self-referential traits was observed in beta-band activity over the central-parietal area and in gamma-band activity over the fronto-central area. eLORETA analysis during eyes-closed rest and Transcendental Meditation identified sources of alpha activity in midline cortical regions that overlapped with the DMN (Travis et al., 2010). Congedo et al. (2010) used group ICA of rest EEG data on large sample of subjects and found several components whose topography overlapped with DMN. Two components which were characterized by clear peak in alpha frequencies had maximal activity in posterior cortical regions including the cuneus/precuneus and PCC. The authors suggest that these components may represent activity involved in self-centered mental imagery, during both personal past and personal future thinking.

It should be noted that differences in EEG and fMRI results could be partly explained by different analysis approaches that are traditionally used in the two domains. Thus, blind source separation techniques are increasingly becoming popular both in EEG and in fMRI research, but there are several principal differences in how these techniques are applied in the two domains. In EEG research, temporal ICA (TICA) is usually used, whereas in fMRI research, spatial ICA (SICA) is almost exclusively applied. There are several reasons for this, of which the most important is that the spatial dimension is much larger than the temporal dimension in fMRI, whereas for EEG, the temporal dimension is much larger than the number of sources (Calhoun et al., 2001a). SICA and TICA yield similar results if there is one predictable task-related component or two components that are uncorrelated in both space and time. However, SICA and TICA diverge if the predictable components are highly correlated in space or time, respectively (Peterson et al., 2000). Another difference is that in EEG research, ICA is usually applied to each subject's data separately. Obtained independent components (ICs) are said to represent temporally independent signal sources and have scalp maps that nearly perfectly match the projection of a single equivalent brain dipole (Delorme and Makeig, 2004). Thus, such approach is perfectly suited for studying temporally uncorrelated spatially local processes that could be modeled by a single equivalent brain dipole, but it is less suitable for studying more spatially extended or temporally correlated processes. Besides, following such ICA, there is no natural and easy way to identify a component from one subject with a component from another subject (Makeig et al., 2004). A strategy that is most frequently used is to combine individual ICs across subjects with clustering techniques (Esposito et al., 2005; Onton et al., 2006). In fMRI research, another approach, which is called group ICA, is mostly used. Aggregate data containing observations from all subjects are created, then, a single set of ICs is estimated and back-reconstructed in the individual data (Calhoun et al., 2001b; Schmithorst and Holland, 2004). Knyazev et al. (2011) used group SICA of sLORETA-transformed EEG data in rest and

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