



Coupling between visual alpha oscillations and default mode activity[☆]

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ABSTRACT

Although, on average, the magnitude of alpha oscillations (8 to 12 Hz) is decreased in task-relevant cortices during externally oriented attention, its fluctuations have significant consequences, with increased level of alpha associated with decreased level of visual processing and poorer behavioral performance. Functional MRI signals exhibit similar fluctuations. The default mode network (DMN) is on average deactivated in cognitive tasks requiring externally oriented attention. Momentarily insufficient deactivation of DMN, however, is often accompanied by decreased efficiency in stimulus processing, leading to attentional lapses. These observations appear to suggest that visual alpha power and DMN activity may be positively correlated. To what extent such correlation is preserved in the resting state is unclear. We addressed this problem by recording simultaneous EEG-fMRI from healthy human participants under two resting-state conditions: eyes-closed and eyes-open. Short-time visual alpha power was extracted as time series, which was then convolved with a canonical hemodynamic response function (HRF), and correlated with blood-oxygen-level-dependent (BOLD) signals. It was found that visual alpha power was positively correlated with DMN BOLD activity only when the eyes were open; no such correlation existed when the eyes were closed. Functionally, this could be interpreted as indicating that (1) under the eyes-open condition, strong DMN activity is associated with reduced visual cortical excitability, which serves to block external visual input from interfering with introspective mental processing mediated by DMN, while weak DMN activity is associated with increased visual cortical excitability, which helps to facilitate stimulus processing, and (2) under the eyes-closed condition, the lack of external visual input renders such a gating mechanism unnecessary.

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Introduction

Field oscillations in the alpha range (8–12 Hz) are a prominent feature of human electroencephalogram (EEG) over the occipital-parietal cortex. The genesis and function of alpha have been the subject of intense study since the 1920s (Berger, 1929; Bollimunta et al., 2008, 2011; Lopes da Silva, 1991; Shaw, 2003). It is generally believed that for a given brain state (e.g., attention versus relaxed wakefulness), the magnitude of alpha is an inverse indicator of cortical excitability, with smaller alpha associated with improved visual processing. Goal-oriented increase of alpha over task-irrelevant cortices, therefore, has been interpreted as reflecting a mechanism of active inhibition (Jensen et al., 2002; Klimesch, 1996). In tasks demanding externally-oriented attention, alpha power, on average, is reduced over task-relevant cortices (Rajagovindan and Ding, 2010; Sauseng et al., 2005). Momentary increase of alpha power over these task-relevant cortices is indicative of decreased level of attention and worsened task performance (Macdonald et al., 2011).

A recent study examining the neural signature of attention lapses has found increased alpha band oscillation up to 20 s prior to the occurrence of an error (O'Connell et al., 2009).

The level of BOLD activity in the default mode network (DMN), a key system mediating introspective processes such as mind wandering (Christoff et al., 2009; Mason et al., 2007), appears to exhibit behavior similar to that of alpha. It is suppressed or deactivated on average when subjects are actively engaged in demanding cognitive tasks (Buckner et al., 2008). Stronger deactivation of the DMN is associated with greater activation of the sensory cortices (Greicius and Menon, 2004). Attentional lapses, characterized by ineffective stimulus processing and decreased task performance, are associated with momentarily insufficient deactivation of the DMN (Eichele et al., 2008; Weissman et al., 2006).

Based on these functional data, it seems reasonable to expect that alpha power and DMN activity be positively correlated, and this property should persist even in the absence of tasks (resting-state). This hypothesis has been subjected to experimental test using the simultaneous EEG-fMRI technique. Despite repeated attempts (Goldman et al., 2002; Laufs et al., 2003a,b, 2006; Moosmann et al., 2003), however, supporting evidence remains lacking. A closer examination of the literature suggests one possible reason, namely, resting-state data were often recorded with the eyes closed. Such data may not be ideally suited to model observations made under conditions of active

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visual processing. From a functional standpoint, positive alpha and DMN BOLD correlation, implying concurrent increase and decrease of alpha power and DMN BOLD, may serve to gate out sensory input to protect introspective processes from external interference. This protection is only necessary in the presence of visual input. Moreover, the act of opening the eyes has physiological consequences, including some reorganization of brain network activity. In particular, it has been shown that eyes-opening (1) suppresses alpha (Berger, 1929; Moosmann et al., 2003) and (2) increases functional connectivity within DMN (Yan et al., 2009).

In this study we sought to examine the relationship between occipital alpha oscillations and DMN activity by recording simultaneous EEG-fMRI in two types of resting-state sessions: a more traditional eyes-closed session and a less traditional eyes-open session. Alpha power fluctuations were extracted from visual EEG channels using short-time Fourier transforms and convolved with a canonical hemodynamic response function (HRF). The HRF-convolved alpha power time series was then correlated with the concurrent BOLD activity to assess their coupling.

Methods

Experimental procedure and data acquisition

Fourteen healthy college students with normal or corrected-to-normal vision participated in the study in exchange of course credit. The experimental protocol and data acquisition procedure were approved by the Institutional Review Board of the University of Florida. Prior to experiment, written informed consent was obtained from all participants.

The experiment consisted of two resting-state fMRI sessions each lasting 7 min. Participants were instructed to remain still, stay awake, not to think any systematic thoughts, and keep their eyes closed during one session. During the other session, they were asked to open their eyes and fixate on a fixation cross presented at the center of an MR-compatible monitor, and the instructions were otherwise the same. The order of the two sessions was randomized across participants.

EEG acquisition

EEG data were recorded using a 32-channel MR-compatible EEG system (Brain Products GmbH). Thirty one sintered Ag/AgCl electrodes were placed according to the 10–20 system and one additional electrode was placed on the participant's upper back to monitor electrocardiogram (ECG). ECG was used subsequently to aid the removal of the cardioballistic artifact. The impedance from all scalp channels was kept below 10 k Ω during the entire recording session as recommended by the manufacturer. The online band-pass filter had cutoff frequencies at 0.1 and 250 Hz. The filtered EEG signal was then sampled at 5 kHz, digitized to 16-bit, and transferred to the recording computer via a fiber-optic cable. The EEG recording system was synchronized with the scanner's internal clock throughout the recording session. The synchronization, along with the high sampling rate, was essential to ensure the successful removal of the gradient artifact.

fMRI acquisition

Functional images were acquired on a 3-Tesla Philips Achieva whole-body MRI system (Philips Medical Systems, Netherlands) using a T2*-weighted echoplanar imaging (EPI) sequence (echo time (TE) = 30 ms; repetition time (TR) = 1980 ms; flip angle = 80°). Two hundred and twelve (212) volumes of functional images were acquired during each experimental session, with each whole-brain volume consisting of 36 axial slices (field of view: 224 mm; matrix size: 64 × 64; slice thickness: 3.50 mm; voxel size: 3.5 × 3.5 × 3.5 mm). A T1-weighted high resolution structural image was obtained for each subject after the two resting-state sessions.

Data preprocessing

Dataset from two participants was excluded as they self-reported of falling asleep during at least one of the sessions. The final dataset analyzed in this study contained 12 participants (5 females; mean age: 22.9 ± 4.54).

EEG data

There were two sources of artifacts in EEG data specifically associated with simultaneous acquisition: gradient and cardioballistic. The gradient artifact was removed by subtracting an average artifact template from the EEG data as implemented in Brain Vision Analyzer 2.0 (Brain Products GmbH). The gradient artifact template was constructed by using a sliding-window approach which involved averaging the EEG signal across 41 consecutive volumes. The cardioballistic artifact was removed by an average artifact subtraction method proposed in Allen et al. (1998). In this method, the R peaks were detected in the ECG recordings in a semiautomatic way and then utilized to construct a delayed average artifact template over 21 consecutive heartbeat events. The cardioballistic artifact was then removed by subtracting the average artifact templates from the EEG data. After these two steps, the EEG data were then band-pass filtered between 0.5 and 50 Hz, down-sampled to 250 Hz, and re-referenced to the average reference. The MR-corrected EEG data were then exported to EEGLAB (Delorme and Makeig, 2004) to correct for eye-blinking, residual cardioballistic, and movement-related artifacts using SOBI (Second Order Blind Identification; Belouchrani et al., 1993). Recent work has shown that SOBI was effective in removing the cardioballistic artifact (Vanderperren et al., 2010), as well as in separating EEG data into interpretable neural components (Klemm et al., 2009; Tang et al., 2005).

fMRI data

fMRI data preprocessing was performed in SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). The first 5 scans of each session were discarded in order to eliminate the transient effects. Other preprocessing steps included slice timing, motion correction, normalization to the Montreal Neurological Institute (MNI) template, and re-sampling of the functional images into a voxel size of 3 × 3 × 3 mm³ (Friston et al., 1995). Normalized images were spatially-smoothed by using an 8 mm FWHM (Full Width at Half Maximum) Gaussian kernel. Global scaling was applied to remove the global signal from the BOLD time series. The BOLD time series was then high-pass filtered with a cutoff frequency at 1/128 Hz.

Estimation of alpha power time series

The scalp EEG voltage data from the three occipital channels O1, O2, and Oz were selected. The overall average power spectra for the eyes-closed session and for the eyes-open session were obtained using the Welch's method. The alpha power time series from each subject was extracted as follows. First, EEG signals for each channel were segmented into 500 ms non-overlapping epochs. Second, the EEG power spectrum for each single epoch was calculated using a nonparametric multitaper approach (Mitra and Pesaran, 1999), and the alpha band power was obtained by integrating the power spectrum between 8 and 12 Hz. Epochs that contained motion or muscle artifacts were interpolated using adjacent epochs. Third, the channel-level alpha power time series from each of the three occipital channels was averaged to yield the subject-level alpha power time series, which was convolved with a canonical hemodynamic response function (HRF). The HRF-convolved alpha power time series was then downsampled to the same sampling frequency as the BOLD signal, and normalized by 1) subtracting the mean and 2) dividing the mean-removed data by its standard deviation.

Correlation between alpha power and BOLD activity

To identify brain regions whose BOLD activity co-varied with EEG alpha power, we examined the temporal correlation between HRF-convolved alpha power time series and BOLD time series from all voxels (Fox et al., 2005; Goldman et al., 2002; Mantini et al., 2007). Brain regions showing significant alpha-BOLD correlation at the group level were identified for the eyes-open and eyes-closed conditions by a voxel-wise one-sample t-test performed on the Fisher transformed correlation coefficients from all subjects. To assess the systematic difference in alpha-BOLD coupling between the two resting-state conditions, we constructed a group-level contrast map by performing a paired t-test with the experimental condition treated as a within-subjects factor. The test results were further adjusted for multiple comparisons using a whole brain cluster-extent FDR correction method (Chumbley and Friston, 2009).

To test the robustness of the correlation analysis, we considered an alternative approach to construct the alpha-BOLD coupling map based on the general linear model (GLM). HRF-convolved alpha power time series was incorporated as a parametric regressor in the GLM, modeling the coupling effects between alpha and BOLD. Six additional regressors accounting for the six degrees of freedom of the rigid body movement were included as nuisance covariates in the model. Regions showing significant alpha-BOLD correlation were identified within each subject by testing the corresponding coefficient in the linear regression model. Group-level statistical parametric maps were obtained by performing second-level analyses based on the statistical maps obtained from the within-subjects analyses.

Analysis based on current source density (CSD)

It is known that scalp EEG is subject to volume conduction. To minimize the effect of volume conduction, current source density data were derived by applying the Laplacian spatial filter to the EEG voltage data (Tenke and Kayser, 2012). The correlation map between the CSD alpha power time series from Oz and BOLD was then obtained by the same analysis procedure detailed above.

Results

EEG spectra

For a typical subject, from the artifact-free EEG voltage data in Fig. 1A, alpha oscillations are clearly seen in both eyes-closed and eyes-open conditions. At the group level, average power spectra combining the three occipital channels are shown in Fig. 1B, where the mean peak frequency is centered around 10 Hz (eyes-closed: 8.87 ± 1.14 Hz; eyes-open: 9.03 ± 0.85 Hz). The average alpha power under the eyes-open condition was significantly lower than

that under the eyes-closed condition ($p < 0.05$), demonstrating the well-established “alpha blockade” phenomenon, initially described by Berger (Berger, 1929; Moosmann et al., 2003).

Alpha-BOLD correlation based on EEG voltage data

To illustrate alpha power fluctuations, in Fig. 2A, EEG data filtered between 8 and 12 Hz was shown for a typical subject under the eyes-open condition. The alpha amplitude profile, subsequently referred to as alpha power time series, is superimposed. Over the 7-minute recording session, the alpha power time series exhibits strong fluctuations, as seen in Fig. 2B. In Fig. 2C, the HRF-convolved alpha power time series is plotted together with the simultaneously recorded BOLD time series from mPFC, a key hub of the DMN. The zero-lag cross correlation coefficient between the two time series is 0.43 ($p < 0.0001$).

When the eyes were closed, no significant positive correlation was found between the HRF-convolved alpha power time series and BOLD activity in DMN (Fig. 3A), whereas upon eyes opening, visual alpha power became positively correlated with BOLD activity within posterior cingulate cortex (PCC), medial prefrontal cortex (mPFC), bilateral inferior parietal lobule (IPL), and bilateral inferior temporal cortex (ITC) (Fig. 3B), all areas of the DMN (Buckner et al., 2008). Negative correlation between HRF-convolved alpha power time series and BOLD activity was also examined. The negative correlation map, shown in Fig. 3D, revealed a frontoparietal network, along with visual regions, consistent with the findings of a previous study (Laufs et al., 2003a). It is worth noting that the negative correlation map is not sensitive to the opening or closing of the eyes. The GLM-based approach yielded similar results for both the positive and the negative correlation maps.

The difference map contrasting eyes-open and eyes-closed conditions was derived from the 2nd level paired t-test. Clusters showing significant differences in positive alpha-BOLD correlation are shown in Fig. 3C. Again, DMN regions, including PCC, mPFC, bilateral IPL and left ITC, were revealed. Table 1 lists the coordinates of the DMN regions shown in Fig. 3C and associated statistical test results.

Alpha-BOLD correlation based on CSD data

CSD data exhibited similar frequency and amplitude characteristics as the voltage data. Applying the same analysis procedure used to generate alpha-BOLD correlation maps in Fig. 3, it was found that with eyes closed, there was again no significant positive correlation between the HRF-convolved CSD alpha power time series and BOLD activity in DMN (Fig. 4A). In contrast, upon eyes opening, CSD alpha power became positively correlated with BOLD activity in the DMN (Fig. 4B). The difference map obtained by contrasting eyes-open and eyes-closed conditions is shown in Fig. 4C. Table 2 lists the

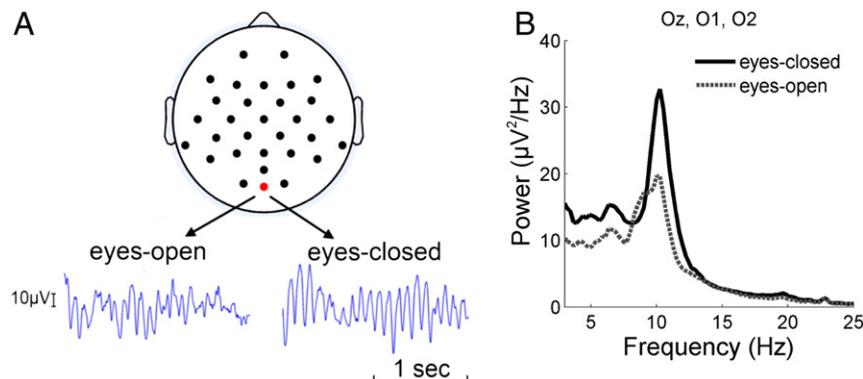


Fig. 1. Visual alpha oscillations under eyes-open and eyes-closed conditions. (A) EEG traces from a typical subject. (B) Power spectra from the three occipital channels averaged across subjects.

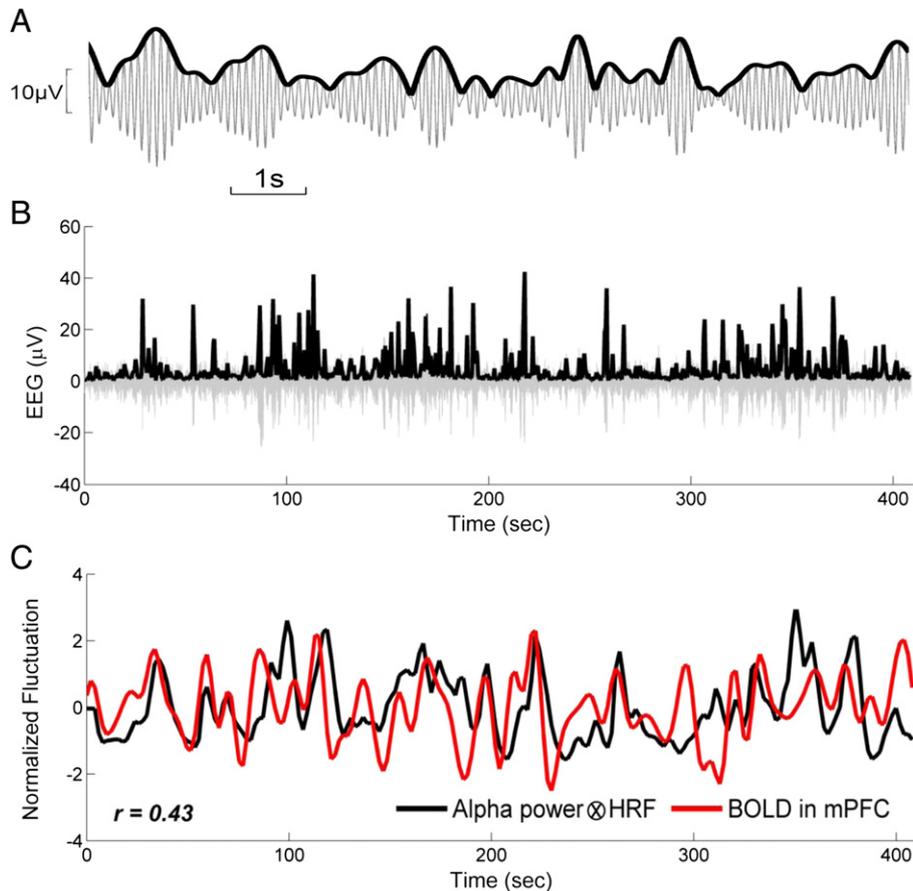


Fig. 2. Alpha power time series and BOLD time series. (A) Alpha oscillations and its amplitude profile; the latter is referred to as the alpha power time series (eyes-open). (B) Alpha power time series over the entire 7-minute recording session (eyes-open). (C) HRF-convolved alpha power time series, obtained from the same alpha power time course in (B), plotted together with the simultaneously acquired BOLD time series from mPFC. The zero-lag correlation between the two time series is $r = 0.43$ ($p < 0.0001$).

coordinates of the DMN regions shown in Fig. 4C and associated statistical test results. The negative correlation map using CSD alpha power, shown in Fig. 4D, is similar to Fig. 3D, and is again found to be not sensitive to the opening or closing of the eyes.

Discussion

The coupling between visual alpha oscillations and BOLD activity under both eyes-closed and eyes-open resting-state conditions was considered. Consistent with previous reports, the posterior alpha power was negatively correlated with BOLD activity in a frontoparietal network (Laufs et al., 2003a,b), and this negative correlation was further found to be not affected by whether eyes were open or closed. Positive alpha-BOLD correlation was found only for the eyes-open condition in mPFC, PCC, IPL, and ITC, key nodes of the default mode network, and such correlation was not found when the eyes were closed. The same DMN areas appeared also in the difference map when the eyes-open and eyes-closed conditions were contrasted.

Positive visual alpha-DMN BOLD correlation

Electrophysiological and functional imaging studies show that preceding momentary lapses in visual attention, both alpha power and DMN activity are high (Eichele et al., 2008; O'Connell et al., 2009; Weissman et al., 2006), and in contrast, low levels of alpha and DMN activities signify heightened attention towards external input and enhanced sensory processing (Foxe et al., 1998; Greicius and Menon, 2004; McKiernan et al., 2003; Thut et al., 2006). This observation appears to suggest that a positive correlation should exist between visual alpha power and DMN activity. To date, no evidence

has emerged to support the hypothesis. Noticing that in typical EEG-fMRI resting-state studies, mainly the eyes-closed condition is employed, and such a condition may not represent a good model for tasks involving active visual processing, we included the eyes-open resting state condition, which proves to be essential for establishing the positive correlation between visual alpha power and DMN activity.

Possible functional interpretation

Strengthened alpha oscillation is thought to be indicative of inhibition of visual cortices (Klimesch, 1996; Klimesch et al., 2007). Empirical evidence in support of this theory includes: (1) increased alpha during tasks requiring internally oriented attention such as mental imagery and working memory retention (Cooper et al., 2003, 2006; Sauseng et al., 2005), and (2) decreased alpha during tasks requiring externally-oriented visual attention such as anticipation of target discrimination (Rajagovindan and Ding, 2010; Thut et al., 2006; Worden et al., 2000). Increased alpha over the occipital regions during internal attention tasks suppresses visual activity to protect internal processes from being disrupted by external sensory input. Decreased occipital alpha during external attention tasks increases the excitability of visual cortex and facilitates sensory processing.

The default mode network is thought to mediate task-independent introspection and self-referential processes (Buckner et al., 2008). Phenomena such as mind wandering and attention lapses have been associated with higher levels of activity within the default mode network (Christoff et al., 2009; Eichele et al., 2008; Mason et al., 2007; Weissman et al., 2006). In addition, using fMRI, a prior study has

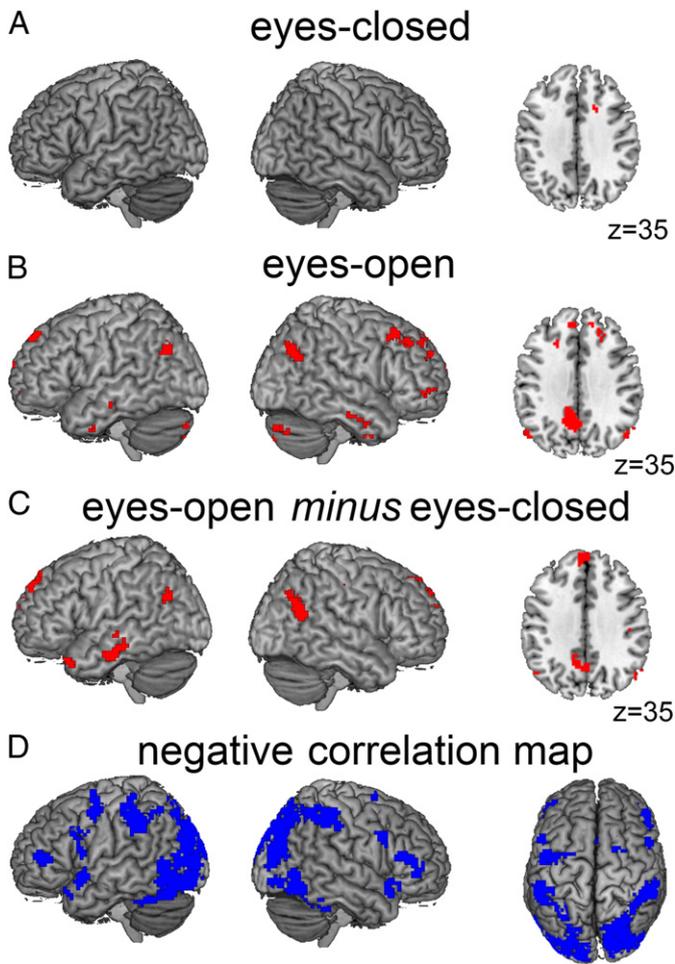


Fig. 3. Alpha-BOLD correlation maps (red: positive correlation and blue: negative correlation). Positive correlation maps for (A) eyes-closed condition and for (B) eyes-open condition. (C) Eyes-open map minus eyes-closed map. (D) Negative correlation maps (eyes-open). The maps are similar for the eyes-closed condition. All correlation maps are thresholded at $t=3.11$, $p<0.005$, uncorrected. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reported that higher DMN activity is associated with lower activation level in sensory cortices during a passive sensory stimulation task (Greicius and Menon, 2004).

The foregoing suggests a possible functional interpretation of our results. It has been suggested that during rest, the brain spontaneously switches between a more externally-oriented state and a more internally-oriented state (Fransson, 2005). This is thought to manifest a basic survival mechanism that enables frequent interruptions of introspective and self-referential processes to allow individuals to be aware of their surrounding environments and respond to possible appetitive or threatening events. During the more externally-oriented

Table 1
ROIs in the DMN derived from the contrast between eyes-open and eyes-closed conditions (EEG voltage data).

ROI	Peak voxel	MNI coordinate (mm) x, y, z	Cluster extent ^a PFDR-corrected
	Puncorrected		
PCC	<0.001	-9, -57, 36	0.07
mPFC	<0.001	-3, 54, 36	0.01
Left IPL	<0.001	-51, -66, 30	0.09
Right IPL	<0.001	60, -57, 18	0.08
Left ITC	<0.001	-57, -18, -21	0.07

PCC: posterior cingulate cortex; mPFC: medial prefrontal cortex; IPL: inferior parietal lobule; ITC: inferior temporal cortex.

^a Whole brain cluster-extent FDR corrected.

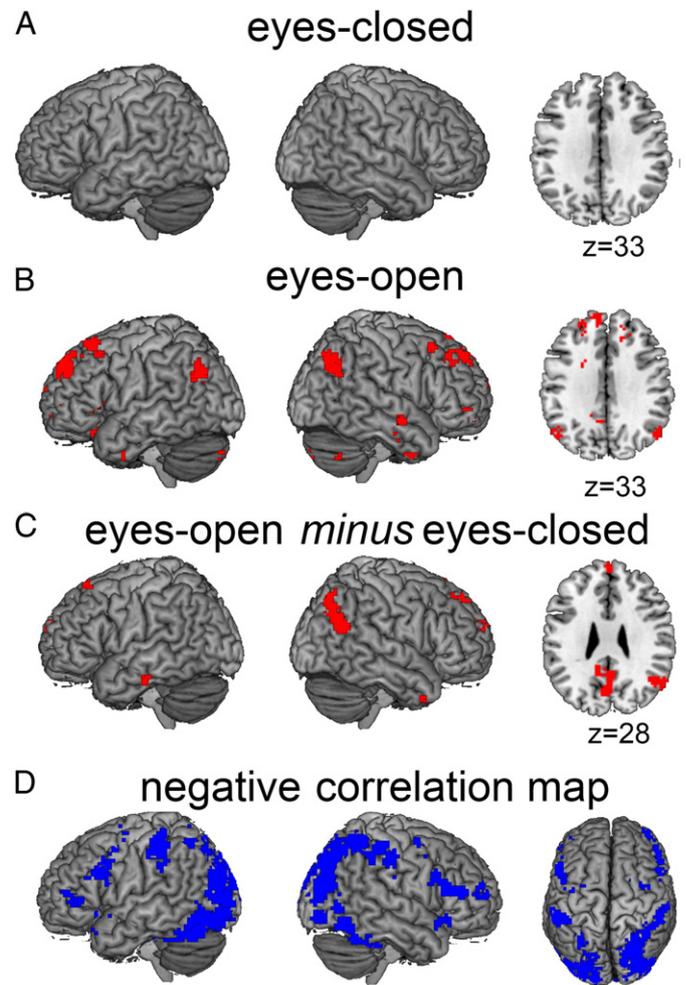


Fig. 4. Alpha-BOLD correlation maps based on EEG current source density data (red: positive correlation and blue: negative correlation). Positive correlation maps for (A) eyes-closed condition and for (B) eyes-open condition. (C) Eyes-open map minus eyes-closed map. (D) Negative correlation maps (eyes-open). The maps are similar for the eyes-closed condition. All correlation maps are thresholded at $t=3.11$, $p<0.005$, uncorrected. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

state, there is increased excitability in the sensory regions as indexed by decreased alpha power, and at the same time there is also decreased internal interference or noise as indexed by DMN suppression, both being important for task execution. During the more internally-oriented state, higher DMN activity is accompanied by increased alpha power, which serves to protect internal information processing by gating out sensory input. It is worth noting, however, that in a recent EEG-fMRI study on working memory, Scheeringa et al. (2009) found neither positive correlation between alpha and BOLD activity in DMN nor negative correlation between alpha and BOLD activity in the frontoparietal network. This may suggest

Table 2
ROIs in the DMN derived from the contrast between eyes-open and eyes-closed conditions (EEG CSD data).

ROI	Peak voxel	MNI coordinate (mm) x, y, z	Cluster extent PFDR-corrected
	Puncorrected		
PCC	<0.001	0, -72, 30	<0.005
mPFC	<0.001	3, 63, 24	<0.05
Right IPL	<0.001	42, -75, 45	<0.005
Left ITC	<0.001	-60, -21, -21	>0.1

Notations are the same as in Table 1.

differences in physiological mechanisms between working memory task state and resting state (Hampson et al., 2006). A possible contributing factor for this discrepancy might be that the suppression of DMN to sustain task performance (Shulman et al., 1997) reduces the variability of BOLD signals. Sufficient signal variability is often needed to establish correlative relationships between variables.

Two types of resting-state conditions

Prior studies have generally failed to report any significant correlations between alpha power fluctuations and DMN BOLD activities (Goldman et al., 2002; Laufs et al., 2003a,b, 2006; Moosmann et al., 2003). A plausible explanation for this might be that resting-state data were often recorded with the eyes closed. During eyes-closed resting, as no visual information is present, the gating mechanism described above becomes unnecessary. The idea that eye-opening entails physiological changes in the brain is supported by EEG evidence, including the “alpha blockade” phenomenon (Berger, 1929) and changes in synchronization patterns (Kuhnert et al., 2012), and also by fMRI evidence showing enhanced functional connectivity within the DMN during eyes-open resting (Yan et al., 2009). In addition, simultaneous EEG-fMRI studies have revealed that occipital alpha power variation across eyes-open and eyes-closed conditions is negatively correlated with BOLD activity level within the visual cortex (Feige et al., 2005; Laufs et al., 2003a,b; Moosmann et al., 2003), indicating decreased visual cortical activity during eyes-closed compared to eyes-open conditions. The decreased visual cortical activity might allow more resources to be allocated to introspective processes, and render such processes less prone to be interrupted by external information. Taken together, while both considered resting state, eyes-closed resting and eyes-open resting may exhibit subtle differences in the functional organization of brain activity, with the eyes-open resting mimicking more strongly the experimental conditions where active visual processing is involved.

In closing, we make two comments. First, in a recent study, Wu et al. (2010) reported a significant reduction in alpha hemodynamic responses (de Munck et al., 2007) with the opening of the eyes in multiple brain regions including those in the DMN. In their approach, HRF functions were estimated from the data and may change between different brain states (e.g. eyes-open versus eyes-closed). Although it is hard to directly compare their findings with ours, owing to the differences in methodology, understanding the relation between various approaches aimed at the neural basis of BOLD activity is an important topic for future investigations. Second, in this study, we considered two types of data: voltage and CSD, and both types of data gave rise to similar correlation maps seen in Figs. 3 and 4. For mPFC and PCC, the two important hubs of DMN, whole brain FDR corrected cluster level statistics in Tables 1 and 2 further reveal that while mPFC is more significantly correlated with visual alpha based on voltage data, PCC is more significantly correlated with visual alpha based on CSD data. A possible explanation is that the spatial filtering procedure used to generate the CSD data helped to localize visual activity by minimizing the impact of volume conduction. Future investigations employing higher density electrode arrays and source space analysis (Yang et al., 2010, 2011) are essential to substantiate such observations.

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