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Large-Scale Spontaneous Fluctuations and Correlations in Brain Electrical Activity Observed with Magnetoencephalography

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Abstract

Knowledge about the intrinsic functional architecture of the human brain has been greatly expanded by the extensive use of resting-state functional magnetic resonance imaging (fMRI). However, the neurophysiological correlates and origins of spontaneous fMRI signal changes remain poorly understood. In the present study, we characterized the power modulations of spontaneous magnetoencephalography (MEG) rhythms recorded from human subjects during wakeful rest (with eyes open and eyes closed) and light sleep. Through spectral, correlation and coherence analyses, we found that resting-state MEG rhythms demonstrated ultraslow (<0.1 Hz) spontaneous power modulations that synchronized over a large spatial distance, especially between bilaterally homologous regions in opposite hemispheres. These observations are in line with the known spatio-temporal properties of spontaneous fMRI signals, and further suggest that the coherent power modulation of spontaneous rhythmic activity reflects the electrophysiological signature of the large-scale functional networks previously observed with fMRI in the resting brain.

Keywords

Functional Connectivity; Resting State; Magnetoencephalography; Band-limited Power; Correlation; Coherence

Introduction

The notion that spontaneous activity patterns of the human brain are intrinsically organized is supported by a growing body of neuroimaging data obtained in the absence of any external stimulus or task. Notably, fMRI based on the blood oxygen level dependent (BOLD) contrast (Bandettini et al., 1992; Kwong et al., 1992; Ogawa et al., 1992) has been the dominant imaging tool for studying brain activity and connectivity at rest. A number of resting-state fMRI studies have demonstrated widely distributed low-frequency (<0.1 Hz) spontaneous fluctuations in BOLD signals and strong temporal correlations between such fluctuations at functionally related brain regions (Biswal et al., 1995; Cordes et al., 2000; Fox et al., 2006; Greicius et al., 2003; Hampson et al., 2002; Lowe et al., 1998). These observations have led to an active and rapidly growing branch of neuroimaging research, which holds great potential to unveil intrinsic brain networks and their dynamic interactions in a variety of arousal, behavioral and pathological conditions (Fox and Raichle, 2007).

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However, a central unresolved issue is the origin of the resting-state BOLD fluctuations and their inter-regional correlation. Since fMRI measures the secondary effect of neural activity on cerebral metabolism and hemodynamics, the BOLD signal might fluctuate due to a purely vascular effect (Sirotnik and Das, 2009) or other non-neuronal physiological variations, such as respiratory (Birn et al., 2006) and cardiac (Shmueli et al., 2007) activity. In contrast, direct measurements of neural activity at rest typically show electrophysiological signal oscillations that are orders of magnitude faster than the BOLD signal. If the spontaneous BOLD fluctuation is indeed driven by slow neural modulation, we may also expect some components of electrophysiological signals to exhibit low-frequency spontaneous fluctuations with large-scale correlation patterns similar to those observed with resting-state fMRI.

Several electrophysiology studies suggest that rhythmic neuronal activity, although oscillating at high frequencies (up to 250 Hz), may exhibit a much slower fluctuation in power (or modulation amplitude) that generally coincides with the frequency range of spontaneous BOLD fluctuations (Anderson, 2008; Leopold et al., 2003; Linkenkaer-Hansen et al., 2001; Nir et al., 2008; Shmuel and Leopold, 2008). Such power modulations may also synchronize in widespread cortical regions (He et al., 2008; Leopold et al., 2003) or even across hemispheres (Lu et al., 2007; Nir et al., 2008). However, the observations of large-scale neuronal correlation patterns have been mainly based on measurements of intracranial electrical potentials with depth or cortical-surface electrodes, which are inherently constrained by their invasive nature as well as the limited spatial coverage. It is highly desirable to use noninvasive electrophysiological measurements, particularly whole-head high-density MEG or electroencephalography (EEG), to study the spontaneous neural activity fluctuations and their correlations, allowing for a comprehensive comparison with the functional networks known to exhibit coherent BOLD fluctuations in the resting human brain.

In the present study, we recorded and analyzed human MEG data in three distinct rest conditions (eyes-open and eyes-closed wakefulness and light sleep). In order to identify the possible neural correlates of coherent spontaneous BOLD signals, several spatio-temporal features that were characteristic of resting-state BOLD-fMRI activity and connectivity were assessed with neuronal signal fluctuations by performing spectral, correlation and coherence analyses to the power modulations of various MEG rhythms. Specifically, we addressed the following questions: i) whether the power of a specific MEG rhythm fluctuates over very long time scales (>10 s), ii) whether such power modulations are temporally synchronized across hemispheres, in particular between bilaterally homologous regions, and iii) how the correlation (or coherence) structure compares between distinct arousal states and frequency bands.

Methods and Materials

Subjects

Seven healthy human subjects (age 29 ± 12 , 5 female) were studied after giving informed written consent in accordance with a protocol approved by the Institutional Review Board at the National Institutes of Health.

Experimental Design

All subjects were instructed to lie on a bed in a dark and magnetically shielded room (Vacuumschmelze, Germany). For six of these subjects, the experimental paradigm started with two cycles of alternating eyes-closed and eyes-open wakeful rest periods of two minutes each, followed by an undisturbed 32-minute eyes-closed period during which the subjects tried to fall asleep. One subject was instructed to sleep from the very beginning of the experiment. For all subjects, the entire experiment lasted 40–45 minutes.

Data Acquisition

The MEG data were continuously recorded at 600 Hz with an analog bandwidth of 150 Hz using a CTF MEG system (CTF Systems, Inc., Canada) composed of a whole-head array of 275 radial first-order gradiometer channels. Synthetic third gradient balancing was used to remove background noise on-line. Foam padding was used to immobilize the head with respect to the MEG sensors. The MEG sensor locations were measured with respect to three coils attached to the nasion and two preauricular points. For all subjects, the difference between the sensor locations measured before and after the experiment was insignificant (2.9 ± 2.1 mm), confirming a relatively stable head position during the experiment.

MEG Preprocessing

The MEG raw data were first band-pass filtered between 0.02 and 70 Hz. A notch filter was also applied to remove the 60-Hz power-line noise. An independent component analysis (ICA), implemented in EEGLAB (Delorme and Makeig, 2004), was used to decompose the data into a number of independent components (ICs). As illustrated in Fig. 1.A, the ICs of cardiac or respiratory origin were identified in a semi-automatic manner. An autocorrelation function was computed based on the time course of each IC. An IC was identified as a cardiac artifact if a positive peak autocorrelation coefficient (≥ 0.3) was found at a time lag between 0.6 and 1.5 s, or as a respiratory artifact if a positive peak correlation coefficient (≥ 0.3) was found at a time lag between 2.5 and 5 s. These particular intervals were chosen to cover the expected ranges of cardiac and respiratory rate. The automatically detected artifact ICs were further confirmed or rejected by visual inspection of the IC time course. The identified artificial ICs were removed and the remaining ICs were reassembled to produce a “cleaner” dataset with an effective exclusion of cardiac and respiratory artifacts. The data were then down-sampled to 300 Hz. See Fig. 1.B and 1.C for a comparison between the example signals before and after the cardiac and respiratory artifact removal.

Identification of the Sleep Period

Transition from wakefulness to light sleep is characterized by an attenuation in the alpha rhythm and an elevation in the theta and delta rhythms in both EEG (Horovitz et al., 2009; Horovitz et al., 2008) and MEG (Simon et al., 2000). Such a transition was readily discernible by visually examining the time-frequency power and z-score diagrams, and was further quantified by using the inverse index of wakefulness (IIoW) defined as the ratio of the power of the delta and theta bands to that of the alpha band computed over 2-min intervals (Horovitz et al., 2009; Horovitz et al., 2008). Accordingly, the period of light sleep was identified by combining both the visual inspection and the quantitative scoring described as above.

Time-Frequency Analysis

For each channel, a multi-taper spectral estimation algorithm, implemented in Chronux (Mitra and Bokil, 2008), was used to compute a spectrogram representing the power of the MEG signal as a function of both time and frequency. Specifically, we calculated a moving estimate of the power spectrum using a short sliding time window (window length $T=4$ s, step size $\Delta T=0.5$ s) and five orthogonal tapers (time-bandwidth product $TW=3$) provided by the discrete prolate spheroidal sequences (DPSS) (Percival and Walden, 1993). The spectrogram was then normalized to time-frequency z scores, giving rise to a mean of zero and a standard deviation of one for the time course at each frequency value. The time-frequency diagram of the resulting z scores allowed us to examine the frequency-specific power modulation independent of the inter-frequency difference in the absolute power value. The “second order spectrum” (Drew et al., 2008), defined as the spectrum of the temporal modulation in z-score at each frequency value, was further computed separately for the eyes-open, eyes-closed and sleep periods.

Band-limited Power Calculation

The band-limited signals were extracted by band-pass filtering the preprocessed MEG data into five frequency bands: delta (0.5~4 Hz), theta (4~8 Hz), alpha (8~13 Hz), beta (13~30 Hz) and gamma (30~70 Hz). The band-limited power (BLP), defined as the envelope of the band-limited signal (Leopold et al., 2003), was calculated by first applying the Hilbert transform to the band-limited signal and then taking the absolute value of the resultant complex helical sequence. The BLP signal was further low-pass (<8 Hz) filtered to eliminate ringing. Subsequently both zero- and first-order trends were removed from the BLP signal. This was done to remove any possible effect of instrumental drift (a common phenomenon in BOLD fMRI data) despite the fact that this was not apparent in the BLP data.

Correlation and Coherence Analysis

For each frequency band, we measured the temporal correlation between the BLP signals from every pair of channels using the Pearson's linear correlation coefficient. The pairwise correlation coefficients were stored and visualized as a color-coded correlation matrix organized in a way as illustrated in Fig. 3.A. Note that the main diagonal elements (running from top left to bottom right) of the correlation matrix were the auto-correlation coefficients and therefore always equal to one; the counter-diagonal elements (running from bottom left to top right) were the cross-correlation coefficients between symmetric pairs of channels in opposite hemispheres, thus representing the inter-hemispheric correlations. A specific column (or row) of the correlation matrix was also visualized as a color-coded topographic map showing the spatial distribution of the correlation coefficients between the corresponding "seed" channel and all other channels.

Also for each frequency band, we further computed the BLP coherence functions for all channel pairs. Specifically, the magnitude squared coherence, $C_{xy}(f)$, between the BLP signals from two channels, denoted as x and y , was calculated according to the following formula.

$$C_{xy}(f) = \frac{|\rho_{xy}(f)|^2}{\rho_{xx}(f)\rho_{yy}(f)}$$

where $\rho_{xx}(f)$ and $\rho_{yy}(f)$ represent the power spectrum of x and y respectively, and $\rho_{xy}(f)$ represents their cross spectrum. Spectral estimation was based on a multi-taper algorithm (five DPSS tapers and TW=3) (Mitra and Bokil, 2008). The resulting coherence function provided an additional measure of signal co-variation as a function of frequency (Nunez et al. 1997; Leopold et al. 2003), allowing us to examine the frequency-dependent coupling of the BLP signals.

The pairwise coherence values were also displayed as color-coded matrices and seed-derived topographic maps. Both the correlation and coherence analyses were performed separately for each rest condition (i.e. eyes-open, eyes-closed or sleep), and the results were averaged across subjects (n=7 for sleep and n=6 for wakeful rest).

Results

Slow Power Fluctuations

For all MEG channels, spectrograms were computed for the entire 40-minute dataset. Fig. 2.A shows the mean spectrogram averaged across channels for a representative subject. Different rest conditions were characterized by distinct time-frequency distributions. Relative to the eyes-open condition, the MEG signals during the eyes-closed wakeful periods were more dominated by the alpha rhythm. During the eyes-closed condition further into the experiment,

the alpha-band activity generally decreased and slower waves increased. This electrophysiological feature, also quantified by the sleep index shown in Fig. 2.C, defined the transition from wakeful rest to light sleep.

In addition to the spectral alteration across conditions, the power of various rhythmic signals showed different degrees of temporal fluctuations even within the same rest condition. Fig. 2.B depicts the mean time-frequency z-score distribution averaged across channels. Slow power modulation over a time scale of tens of seconds was readily observable for a broad frequency range and for all three rest conditions. Fig. 2.D depicts the second spectrum averaged across channels and subjects for each rest condition ($n=7$ for sleep and $n=6$ for wakeful rest). Both gamma (>30 Hz) and sub-gamma (<30 Hz) rhythms demonstrated dominant low-frequency (<0.1 Hz) power fluctuations, whereas the frequency spectra of the sub-gamma power modulations showed multiple peaks at frequencies <0.05 Hz. Such low-frequency modulations were noticeably stronger during the sleep period than during the eyes-open or eyes-closed periods.

Correlation of BLP signals

During the distinct period of each rest condition, the temporal correlation of BLP signals was computed for each frequency band (i.e. delta, theta, alpha, beta or gamma) and every pair of MEG channels. Fig. 3.B illustrates the pairwise correlation patterns as color-coded correlation matrices. Note that the counter-diagonal elements represent the inter-hemispheric correlations between bilaterally homologous channels (see Fig. 3.A for detailed specifications). All three rest conditions exhibited similar correlation patterns, except that the correlation coefficients were overall higher during the sleep period than during the eyes-open and eyes-closed periods. Inter-hemispheric correlations were apparent for most frequency bands except the gamma band.

To examine the spatial distribution of the BLP correlation, the correlation coefficients between a selected “seed” channel and all other channels were further displayed as a 2-D topographic map. Figs. 4.A through 4.D depict the correlation maps with a seed channel selected from the left-temporal, right-temporal, left-central and left-occipital regions, respectively. For all three rest conditions, the BLP signals of all sub-gamma bands showed strong inter-hemispheric correlations regardless of a long spatial distance between channels, whereas the gamma BLP was mainly coupled locally with much weaker long-range inter-hemispheric correlations. Bilaterally symmetric correlation patterns were consistently observed for different seed channel selections.

Fig. 5 summarizes the difference in the inter-hemispheric BLP correlation across scalp regions, frequency bands and rest conditions. The inter-hemispheric correlation was strongest between temporal regions and weakest between frontal regions; the regional variation was more evident during eyes-open and eyes-closed periods than during sleep; the gamma band showed the weakest inter-hemispheric correlations relative to other frequency bands.

Coherence of BLP signals

To further characterize the dependence of the BLP coupling property on the BLP modulation frequency, we also computed the coherence between the BLP signals from every pair of MEG channels. Fig. 6 depicts the seeded coherence maps during sleep for ten 0.1-Hz frequency ranges up to 1 Hz. The frequency range displaying the strongest large-scale coherences was between 0 and 0.1 Hz. For such ultraslow BLP signals, strong inter-hemispheric coherence was found for the gamma band as well as other lower frequency bands; the beta and alpha bands demonstrated a larger degree of global synchrony than other frequency bands. Similar observations were also made under the eyes-open and eyes-closed conditions.

Fig. 7 illustrates the comparison between the average inter-hemispheric coherence for homologous channels and the mean of the coherence for all other channel pairs, the latter of which served as a measure of global synchrony. For all three rest conditions, both the homologous inter-hemispheric and global coherences peaked at frequencies <0.1 Hz; the coherence values were generally larger for bilaterally homologous pairs relative to other pairs. The coherence matrices averaged within the frequency range between 0 and 0.1 Hz are also shown as the panel insets in Fig. 7. In general, the counter-diagonal elements had larger coherence values than the off-diagonal elements; the beta and alpha bands had a relatively higher degree of global synchrony than other frequency bands; the gamma band had the least global and inter-hemispheric coherences.

Discussion

The results presented in this study show that over a range of conditions, resting-state MEG rhythms demonstrate ultraslow (<0.1 Hz) spontaneous power modulations that tend to synchronize over a long spatial distance, especially between bilaterally homologous regions in opposite hemispheres. These spatio-temporal properties mimic those of spontaneous fMRI signals. Therefore, we posit that the coherent power modulation of spontaneous rhythmic activity reflects the electrophysiological signature of the large-scale functional networks, as was previously suggested with fMRI in the resting brain. While the reported findings lend strong support for the use of resting state fMRI as a tool for mapping functional connectivity, they also suggest that MEG may serve as an alternative modality with potential to offer supplementary or confirmative information regarding the brain's intrinsic functional architecture.

Is there a specific frequency band of which the power modulation serves as the best candidate for the neuronal correlate of spontaneous fMRI fluctuations? This question is of substantial interest to the understanding of the mechanism by which spontaneous neural activity results in the BOLD signal fluctuation and correlation in rest. In an attempt to address this question, previous studies have arrived at differing conclusions in support of the power (or amplitude) modulations of electrical activity in the gamma (Leopold et al., 2003; Nir et al., 2008; Shmuel and Leopold, 2008), delta (Lu et al., 2007) or beta (Nikouline et al., 2001) band as the electrophysiological correlates of spontaneous BOLD-fMRI fluctuations. Although a definitive answer requires simultaneous recordings of both fMRI and electrical signals, unavailable in the present study, we found that the MEG rhythms of different frequency bands shared largely similar spatial patterns of pairwise correlations and coherences (e.g. the inter-hemispheric correlation/coherence) in analogy with that of the fMRI signal during rest. This finding suggests that the spontaneous fMRI fluctuations may come from the complex interplay of multiple frequency bands (Mantini et al., 2007), which in turn may reflect different aspects of neuronal processing.

However, several distinctions among different frequency bands should also be noticed. In particular, the gamma and sub-gamma bands demonstrated significant differences in terms of the strength and scale of their power synchrony. For the gamma-band power, the intrahemispheric synchrony decayed sharply with an increasing distance, whereas the long-range inter-hemispheric synchrony was generally weak but became more visible when assessed with its ultraslow (<0.1 Hz) component. This observation agrees with the notion that correlated neural activity with high temporal precision is confined to a limited spatial scale (Smith and Kohn, 2008), but not in full agreement with the previous findings obtained with intracranial electrical recordings (Leopold et al., 2003; Nir et al., 2008) perhaps due to the lower SNR of gamma-band activity measured by MEG in the present study.

In contrast, the sub-gamma (i.e. delta, theta, alpha and beta) power synchrony extended much farther in space with sometimes global reach. This global component was strongest in the low-frequency (<0.1 Hz) beta power modulation. This finding echoes the critical role of the beta rhythm in large-scale neuronal interactions as supported by previous modeling (Kopell et al., 2000) and electrophysiology (Bassett et al., 2009) studies. In addition, it raises an important hypothesis that the globally coherent BOLD signals, consistently present in resting-state fMRI data and being commonly regressed out in data preprocessing, might arise from neuronal origins other than non-neuronal physiological processes. Future studies are needed to test this hypothesis, which would help interpret the source of the global fMRI signal as well as the effect of its removal in mapping functional connectivity during resting state (Fox et al., 2009; Murphy et al., 2009).

Another observation in the present study that rings familiar is the inter-hemispheric synchronization in the power modulations of multiple MEG rhythms. Similar inter-hemispheric connectivity patterns are also revealed by resting-state fMRI (Salvador et al., 2005). Such inter-hemispheric synchrony reflects one of the defining features of the brain's functional architecture: most sensory systems consist of two symmetric parts in opposite hemispheres. Functional coupling across hemispheres, likely sub-served by the corpus callosum or sub-cortical common inputs (Drew et al., 2008), are often thought to facilitate the integrative processing of sensory inputs. Interestingly, our results also demonstrate a considerable variation across regions in terms of the strength of inter-hemispheric coupling. Correlation was strongest between bilateral temporal regions and weakest between frontal regions. Such regional variation generally agrees with the fact that higher order cognitive functions are predominantly lateralized in the frontal cortex (Toga and Thompson, 2003), while cortical regions beneath the bilateral temporal MEG channels are mainly responsible for primary sensory and motor functions that are more functionally coupled, as suggested by a recent resting-state fMRI study (Stark et al., 2008).

It is important to keep in mind that MEG has intrinsically limited spatial specificity and resolution. MEG sensors on the scalp surface have a varying degree of overlap in their lead fields, meaning that the same neuronal population likely contributes to signals recorded from different sensors. It is possible that apparent synchrony between macro recordings from two sensors might simply reflect a common source signal, instead of true interaction between distinct brain regions. For this reason, caution should be taken in interpreting MEG signal correlation/coherence as underlying source coupling/synchrony. However, it is reasonable to believe that the lead-field overlap is much less of concern for our observed large-scale synchrony in slow power modulations of rhythmic MEG signals. Note that the lead fields as well as their spatial overlap are mainly confined to superficial brain areas, because the amplitude of the detected magnetic field decreases dramatically with the distance between the neuronal current source and the recording sensor (Hämäläinen et al., 1993; Lachaux et al., 1999). While the magnetic field arising from superficial source activity can travel to neighboring sensors with relatively short inter-sensor distances, its field spread to far-field sensors at the opposite hemisphere is essentially too weak to cause robust yet spurious inter-hemispheric correlations across long distances (Stam et al., 2006). Therefore, we would like to argue that electrophysiological rhythms in the source space should possess similar connectivity patterns as those observed in the MEG sensor space in terms of their general spatiotemporal properties (i.e. slow power fluctuations and large-scale synchrony), whereas a lack of precise anatomical correspondence may be anticipated.

Nevertheless, a reliable technique capable of correcting the aforementioned confounding effect would be highly valuable and desirable. Unfortunately, there is to date no universal way to unambiguously distinguish true synchrony from spurious synchrony due to overlapping lead fields. This is in spite of currently active research aimed at solving this problem. Two main

types of techniques have been under development. The first technique attempts to de-convolve scalp surface signals to estimate source activity within the brain, utilizing forward models that mimic the human head in both geometries and electromagnetic properties (Baillet et al. 2001). The second technique attempts to improve spatial precision of surface signals by computing spatial derivative (Bastiaansen and Knosche 2000) or laplacian (He 1999) of MEG or EEG. It follows that connectivity analysis can be performed on either the reconstructed source-space data (Babiloni et al., 2005; Lin et al., 2004) or the spatially transformed signal-space data (Montez et al., 2009). However, both types of techniques have known limitations. For example, source reconstruction techniques often introduce false positive cross-talk (or “source leakage”) (Dale et al., 2000), especially if brain activity is extensive. Computing the spatial gradient of the sensor-space data decreases the SNR, and it is mainly effective to reveal focal and superficial sources that are well separated (Bastiaansen and Knosche 2000). It remains unclear how these limitations would confound any subsequent connectivity analysis, or whether applying these techniques would indeed make data interpretation easier. Extensive and systematic future studies are necessary to address these questions.

It is also worth noting that cardiac and respiratory artifacts were removed using ICA. The artifact removal was intended to preclude such non-neuronal sources from dominating the correlation/coherence patterns. Any remaining artifacts were unlikely to contribute to the observed large-scale synchrony, as their temporal frequencies were outside the relevant frequency band (<0.1 Hz).

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Fig. 1.

A) Cardiac and respiratory artifacts identified by ICA for a representative subject. In the left and middle sub-panels, the three rows depict three independent components (ICs) of cardiac (the top two) or respiratory (the bottom one) origin. The time courses of these ICs demonstrate characteristic temporal patterns of cardiac and respiratory events. In the right sub-panel, the autocorrelation functions of the various components are shown. The functions for the two cardiac components show peaks separated by approximately 1-s intervals (shown in blue and red). The respiratory component shows similar behavior with peaks separated by about 3.5-s intervals (shown in black). These autocorrelation functions are clearly distinct from those of other ICs, which show no such periodic behavior on these timescales, and presumably arise from underlying neural activity (shown in light gray). **B & C)** Beta-band MEG signals from ten channels within the right temporal region before (**B**) and after (**C**) removing the ICs associated with cardiac and respiratory events. Cardiac artifacts on MEG were most prominent in the beta-band signals, whereas the respiratory artifacts were not visually discernible from the raw MEG time courses. Before the artifact removal, regularly recurring rhythmic discharges were observed around every 1 second, which was presumably close to the cardiac pulse cycle. These periodic discharges were effectively eliminated after the artifact removal.

Fig. 2.

Time-frequency distributions and second order spectra. **A)** Mean spectrogram (in dB) averaged across channels based on the data from a single subject. Spectral alterations are noticeable at the transitions between the eyes-open (EO) and eyes-closed (EC) rest conditions, and between wakefulness and light sleep. **B)** Mean time-frequency z-score distribution averaged across channels for the same subject. Slow power modulation can be observed for all three rest conditions, especially during sleep. **C)** Plot of IloW for the same subject. A larger IloW value represents a larger degree of low-frequency (i.e. delta and theta bands) dominance (relative to the alpha band) in the MEG spectrum, which is associated with sleep. **D)** Second order spectra averaged across channels and subjects for each of the three rest conditions ($n=7$ for sleep and $n=6$ for both eyes open and eyes closed). Each diagram displays the frequency spectrum of the z-transformed power modulation (color coded along the abscissa) against the intrinsic frequency of the carrier rhythm (indicated by the ordinate).

Fig. 3.

BLP correlation matrix for each frequency band and each rest condition. **A)** Channels are clustered by their locations on the scalp surface. The number of channels belonging to each cluster is listed along the right edge of the correlation matrix illustration on the top-right. Elements in the correlation matrix are grouped by cluster. The ordering of these elements is mirrored for the left and right hemispheres. The counter-diagonal elements of the correlation matrix represent the inter-hemispheric correlations between symmetric locations from opposite hemispheres. **B)** Color-coded BLP correlation matrices for all three rest conditions (i.e. EO, EC and sleep) and five frequency bands (i.e. delta, theta, alpha, beta and gamma). The correlation matrices shown represent the group average of the individual-subject results ($n=7$ for sleep and $n=6$ for wakeful rest).

Fig. 4.

Seed-derived BLP correlation maps. **A-D)** Color-coded 2-D topographic maps of the correlation coefficients between a selected seed channel (marked by a white dot) and all other channels for each rest condition and each frequency band. Each panel corresponds to one of the four seed channel selections: left-temporal (top left panel), right-temporal (top-right panel), left-central and left-occipital (left and right bottom panels, respectively). The correlation maps shown represent the group average of the individual-subject results ($n=7$ for sleep and $n=6$ for wakeful rest).

Fig. 5.

Variation in inter-hemispheric BLP correlation across frequency bands, regions and rest conditions. Regions are color coded. Frequency bands are indicated by the ordinate. Results for different rest conditions are plotted separately in different panels. Data points shown in each panel represent the regional mean in inter-hemispheric correlations for each frequency band and each rest condition. The error bars indicate the corresponding standard errors of the mean.

Fig. 6.

Seed-derived BLP coherence maps during sleep. The seed channel was selected from the left-temporal region (marked by a white dot). For each frequency band (specified in the left column), coherence values were averaged within each frequency range (specified in the top row) before being visualized as a color-coded map. The maps shown in this figure represent the group average of the individual-subject results ($n=7$ for sleep and $n=6$ for wakeful rest).

Fig. 7.

Inter-hemispheric coherence and global coherence for the BLP signals of each frequency band (listed by columns) under each rest condition (listed by rows). The average BLP coherences for bilaterally homologous channel pairs (blue) and the average for all other channel pairs (red) are plotted as a function of frequency. The inset of each panel shows the corresponding BLP coherence matrix averaged within a frequency range from 0 to 0.1 Hz.