NEUROSCIENCE

RESEARCH ARTICLE

Low Frequency Phase-locking of Brain Signals Contribute to Efficient Face Recognition

Yifeng Wang, [a*] Xinju Huang, [b] Xuezhi Yang, [b] Qi Yang, [b] Xinqi Wang, [b] Georg Northoff, [c] Yajing Pang, [b] Chong Wang, [b] Qian Cui [d] and Huafu Chen [b*]

[a] *Institute for Brain and Psychological Sciences, Sichuan Normal University, Chengdu 610066, China*

[b] *The Clinical Hospital of Chengdu Brain Science Institute, MOE Key Lab for Neuroinformation, School of Life Science and Technology, University of Electronic Science and Technology of China, Chengdu 611731, China*

[c] *The Royal's Institute of Mental Health Research & University of Ottawa Brain and Mind Research Institute, Centre for Neural Dynamics, Faculty of Medicine, University of Ottawa, 145 Carling Avenue, Rm. 6435, Ottawa, ON K1Z 7K4, Canada*

[d] *School of Public Affairs and Administration, University of Electronic Science and Technology of China, Chengdu 611731, China*

Abstract—Low frequency phase synchronization is an essential mechanism of information communication among brain regions. In the infra-slow frequency range (<0.1 Hz), inter-regional phase lag is of importance for brain function (e.g., anti-phase between the default mode network and task positive network). However, the role of phase lag in cognitive processing remains unclear. Based on the frequency tagging experimental paradigm and functional magnetic resonance imaging (fMRI) technique, we investigated inter-regional phase lag and phase coherence using a face recognition task ($n = 30$, 15 males/15 females). Phase coherence within the face processing system was significantly increased during task state, highlighting the importance of regular inter-regional phase relationship for face recognition. Moreover, results showed decreased phase lag within the core and extended face areas (face processing system) and increased phase lag between the face processing system and frontoparietal network, indicating a reorganization of inter-regional relationships of the two systems. Inter-regional phase lag was modulated by the task at ascending and descending phases of the fMRI signal, suggesting a phase-dependent inter-regional relationship. Furthermore, phase lags between visual cortex and amygdala and between visual cortex and motor area were positively related to reaction time, indicating better task performance depends on both rapid emotional detection pathway and visual-motor pathway. Overall, inter-regional phase synchronization in the infra-slow frequency range is of important for effective information communication and cognitive performance. © 2019 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: face recognition, fMRI, infra-slow, low frequency steady-state brain response, phase-locking.

INTRODUCTION

Cognitive performance requires the integration of information among brain regions (Friston et al., 1997; Gonzalez-Castillo et al., 2015). Phase-locking of low frequency neural oscillations has been suggested to be an effective mechanism in gating information communication across regions (Fries, 2015; Maris et al., 2016). Studies targeting faster frequencies (1–80 Hz) have shown that the phase of brain signal fluctuations plays important roles in cognitive performance and information communication

(Canavier, 2015; Maris et al., 2016). Specifically, phase-locking appears not only during cognition (Bonnefond and Jensen, 2015) but also before stimuli presentation (Busch et al., 2009) to modulate subsequent cognition in various ways. Unlike in the faster frequencies, the role of phase-locking remains to be explored in the infra-slow frequency domain (<0.1 Hz) (Aladjalova, 1957) as mainly measured with functional magnetic resonance imaging (fMRI) technique.

Recent fMRI studies have highlighted phase information in resting state or cognitive-related brain functions. For instance, phase-based functional connectivity (FC) has been uncovered with a dynamic variation at ultra-slow (<0.02 Hz) frequency range during resting state (Ponce-Alvarez et al., 2015; Omidvarnia et al., 2016; Huang et al., 2017). Instantaneous phase has been shown to be modulated in task activated regions (Laird et al., 2002). Recently, Mitra

---

[*]Corresponding authors. Fax: +86-28-83208238 (H. Chen).
E-mail addresses: wyf@sicnu.edu.cn (Y. Wang), chenhf@uestc.edu.cn (H. Chen).
Abbreviations: EEG, electroencephalograph; EPI, echo-planar imaging; FC, functional connectivity; FDR, false discovery rate; fMRI, functional magnetic resonance imaging; GSR, global signal regression; HT, Hilbert Transform; lfSSBR, low frequency steady-state brain response.

and colleagues (2015a, 2017) reported stable time delay between brain regions during resting state in the infra-slow frequency range, suggesting multiple possible phase lags between in-phase (e.g., in the same network) and anti-phase (e.g., between the default mode network and task positive network) relationships (Kelly et al., 2008; Cottereau et al., 2011; Abbas et al., 2019). Huang and colleagues (Huang et al., 2017) have demonstrated intra-regional phase-locking with regard to stimulus-onset during task-evoked activity. Other studies have shown phase-dependent cognitive performance and FC in the infra-slow frequency range of electroencephalograph (EEG) and fMRI signals (Monto et al., 2008; Wang et al., 2016a). This leaves open though whether and how inter-regional phase-locking in the infra-slow frequency range mediates cognition.

Low frequency steady-state brain response (lfSSBR) is a steady-state evoked potential (SSEP)-like phenomenon in the low frequency range (< 1 Hz) (Wang et al., 2014). It has been proved that lfSSBR is frequency and phase sensitive (Wang et al., 2016a,b) and occurs during both basic and higher-order cognitions in widespread brain regions (Wang et al., 2015; Gao et al., 2018). During lfSSBR, phase lag could be reliably detected in adjacent brain regions (Lewis et al., 2016). These characteristics make lfSSBR a suitable carrier for the study of phase synchronization during various cognitions.

In the current study, we investigated phase synchronization in the infra-slow frequency range using a face recognition task presented in a fixed frequency (0.05 Hz). This frequency is located around the center of infra-slow frequency range and has minimal noises in fMRI signals (Glerean et al., 2012). If the lfSSBR is task- and phase-specific (Wang et al., 2016a, Gao et al., 2018), inter-regional phase relationship within the core face areas and extended face areas should be locked by the task reflecting the shift from a more random pattern during resting state to a more task-related pattern during task state. Furthermore, particular inter-regional phase lag should be associated with task performance (Huang et al., 2017). Overall, if low frequency phase synchronization is essential for information communication and cognitive performance, we would expect lower phase lag and higher phase coherence in the face processing system.

METHODS

Subjects and experimental design

Thirty healthy participants (mean age = 22.41 years, standard deviation (SD) = 2.11 years, range from 18 to 27 years; 15 males/15 females) participated in this study. All subjects had normal or corrected-to-normal vision, were right-handed (tested using the Chinese Edinburgh-Handedness Questionnaire; coefficients of all participants > 40) (Wang et al., 2013), reported free from any psychiatric and neurological disorders. The experiment was carried out in accordance with the Declaration of Helsinki. Written informed consent, approved by the research ethical committee of School of Life Science

and Technology at University of Electronic Science and Technology of China (UESTC), was obtained from each subject.

The face recognition task was used in previous studies (Wang et al., 2016a, 2018b) and was described as follows. A task lasting for 620 seconds (31 trials) and an equal-length resting scan were counterbalanced between subjects.

During the task, participants were required to judge whether the face has a neutral expression (right thumb response) or a happy expression (left thumb response) as accurately and fast as possible. Although there were only neutral faces in the experiment, subjects were told that the happy expression would appear no more than once to ensure that they paid attention during the entire task. All face pictures (16 males, 15 females) were selected from the Chinese Facial Affective Picture System. At a nine-point scale, the values of valence, arousal, dominance, and attraction were 4.40 ± 0.60 (mean ± SD), 3.65 ± 0.54, 4.98 ± 0.35, and 4.19 ± 0.45, respectively. In each trial, the face was presented on the center of black screen for 2 seconds and followed by a white crosshair of 18 seconds. Each trial lasted for 20 seconds, forming a task frequency of 0.05 Hz. The procedure was performed with E-Prime 2.0 software (http://www.pstnet.com).

During the resting scan, participants were asked to remain motionless, focus their eyes on a white crosshair against black screen, stay awake, and not think of anything in particular.

Behavioral data analysis

The accuracy and reaction time (RT) of behavioral performance were calculated for each subject and were used for the analysis of brain-behavioral relationship.

Imaging data acquisition

The fMRI data were acquired using a 3.0T GE 750 scanner (General Electric, Fairfield, Connecticut, USA) at UESTC with the gradient-recalled echo-planar imaging (EPI) sequence. An 8-channel prototype quadrature birdcage head coil fitted with foam padding was applied to minimize the head motion. The imaging parameters were as follows: repetition time/echo time = 2000 ms/30 ms, 90° flip angle, 43 axial slices (3.2 mm slice thickness without gap), 64 × 64 matrix, 22 cm field of view.

Imaging data preprocessing

Functional images were preprocessed using the Data Processing Assistant for Resting-state fMRI (DPARSF 2.3, http://rfmri.org/DPARSF) (Yan and Zang, 2010). The first 10 volumes were discarded to ensure signal equilibrium, allow evoked fluctuations to appear, and for the participants to familiarize themselves with the scanning environment (Wang et al., 2014). The remaining 300 images were slice-time corrected, spatially aligned, spatially normalized to Montreal Neurological Institute (MNI) EPI template and resampled to 3 × 3 × 3 mm^3 vox-

els. The images were then spatially smoothed using 8-mm FWHM Gaussian kernel. Friston's 24 head motion parameters, white matter signal, and cerebrospinal fluid signal were further extracted and regressed out using the DPARSF software. The data of six participants were removed due to large head motion (translation > 3 mm or rotation $> 3°$ or mean frame-wise displacement > 0.5) or data missing in any scan. It is worth noting that the global signal regression (GSR) should be took over under specific situations (Murphy and Fox, 2017). Recent studies have linked fluctuations of the GS to glucose metabolism (Thompson et al., 2016), vigilance (Wong et al., 2013), arousal mediated by ascending nuclei (Turchi et al., 2018), and various psychopathological effects (Yang et al., 2017; Zhang et al., 2019). Specifically, the phase of GS conveys important information about network state, indicating that the GS may contribute greatly to inter-regional phase synchronization (Gutierrez-Barragan et al., 2019). Another study has demonstrated that the GS is largely driven by phase coherence (Zhang et al., 2019), arguing that GSR may remove some phase lag information especially the long cycle durations that extend across space and different regions which are important for phase coherence. Therefore, lower phase coherence and relatively stronger phase lags were expected in the analysis with GSR. Based on aforementioned reasons, both results with GSR and without GSR were showed in the present study but the results without GSR were identified as main results.

As shown in previous studies (Wang et al., 2016a, 2018b), significant lfSSBR was evoked at the fundamental frequency (0.05 Hz) of task. Following these studies (Wang et al., 2014, 2015, 2016b), a narrow band of 0.048–0.052 Hz around the fundamental frequency was filtered using the finite-impulse response (FIR) filter (Omidvarnia et al., 2016). This frequency band contained task-specific brain activities and avoided non-task noises in other frequency bands (Wang et al., 2016a, 2018b). However, it is largely unclear whether there is particular neural mechanism responsible for such a narrow band fMRI signals, although significant psychophysiological effects have been documented in narrow frequency bands in the low frequency range (Yordanova et al., 2011; Yaesoubi et al., 2015; Zhang et al., 2015; Domenico et al., 2016; Gutierrez-Barragan et al., 2019). Recently, the neurophysiological mechanism of narrow band fMRI signals has been gradually uncovered (Li et al., 2015; Lewis et al., 2016; Mitra et al., 2018). The narrow frequency band we studied here may further help to clarify the neurophysiological mechanism of narrow band fMRI signals. Besides, the same analysis was performed using wider bands such as 0.04–0.07 Hz (Glerean et al., 2012) and 0.01–0.1 Hz (Huang et al., 2017) to evaluate how the choice of frequency range can affect the results and conclusions.

We then divided the gray matter into 246 regions of interest (ROIs) using the Brainnetome Atlas (Fan et al., 2016; Wang et al., 2019). These regions were segregated by the similarity of functional connections and were thought to be functional homogeneous within region and heterogeneous among regions, providing functionally meaningful division of brain regions. Signal in each of the 246 ROIs was extracted and used for further analyses.

Local phase calculation

Following previous studies (Mormann et al., 2000; Palva et al., 2005; Glerean et al., 2012; Stam and van Straaten, 2012; Omidvarnia et al., 2016; Huang et al., 2017), we calculated the instantaneous phase course in each of the 246 ROIs using Hilbert Transform (HT). Unlike the traditional General Linear Model, HT does not require the time domain signals to be stationary, thus is suitable for analyzing fMRI signals (Laird et al., 2002; Huang et al., 2017). The HT approach can be explained with the analytic signal concept. The analytical signal $z(t)$ is complex with $f(t)$ a real time course and $H[f(t)]$ the Hilbert transform of this time course. In other words, $z(t) = f(t) + iH[f(t)]$. We obtained the instantaneous phase $\theta(t)$ by computing the inverse tangent of the ratio of the imaginary and real signals (Eq. (1)):

$$\theta(t) = \arctan \frac{H[f(t)]}{f(t)} \qquad (1)$$

Instantaneous phases of 300 time points were obtained in each brain region. After that, the first and last 10 time points were removed to avoid border effects inherent to the HT, leaving 280 time points (Ponce-Alvarez et al., 2015). Instantaneous phases of resting state were calculated in the same way.

Inter-regional phase synchronization

Inter-regional phase synchronization is a key mechanism in coding the representation of stimuli or memories which has been investigated extensively during resting state and task state using the fMRI technique (Kitzbichler et al., 2009; Omidvarnia et al., 2016; Huang et al., 2017). Huang and colleagues (Huang et al., 2017) verified the reliability of the phase synchronization analysis in blood oxygen level dependent (BOLD) signal by comparing it with several other methods such as the Kuramoto FC, Hilbert phase-based FC, and Hilbert amplitude-based FC. Results showed that phase synchronization shared very similar pattern with FC analyses. On the other hand, phase synchronization in fMRI signals has been demonstrated to uncover novel characteristics of brain function than the traditional Pearson's correlation-based FC (Yaesoubi et al., 2015; Gutierrez-Barragan et al., 2019). In fact, the Pearson's correlation-based FC (traditional FC) and phase coherence are non-linearly changed along the phase lag between two sinusoidal signals (see Fig. 1). Therefore, these indices provide complementary evidence for us to understand functional networks. The non-linear relationship among traditional FC, phase coherence, and phase lag suits well with sinusoidal fMRI signals during lfSSBR (Wang et al., 2016a, 2018b). However, in other situations, the fMRI signals are often non-sinusoidal waves (Cole and Voytek, 2017) and are made up of multiple frequencies (Yaesoubi et al., 2015; Yang et al., 2018) which makes the relationship among these indices extremely complex. A better understanding of
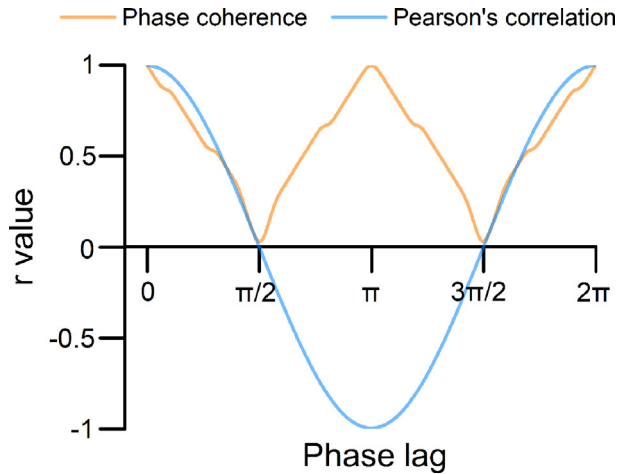
Fig. 1. The relationship between phase lag, phase coherence, and Pearson's correlation in standard sinusoidal signals.

brain function could be achieved by systematic research on the relationship among these indices under diverse situations, which is beyond the topic of the present study. Here we only compared our main results of phase lag and phase coherence with traditional FC to evaluate their relationships under the particular situation.

The phase lag and phase coherence indices were used to investigate the nonlinear functional relationship between each pair of the 246 ROIs. Let $\theta_x(t)$ and $\theta_y(t)$ be the instantaneous phase of two time series, respectively. Phase lag between two signals ($|\varphi_{xy}|$) is defined by Eq. (2):

$$\left|\varphi_{x,y}\right| = \left|n\theta_x(t) - m\theta_y(t)\right| < const \qquad (2)$$

where n and m are integers determined by the ratio of two frequency bands. We restricted $n = m = 1$ because the two signals are in the same frequency band (Palva et al., 2005).

Based on phase lag, phase synchronization for two signals was measured by computing the mean phase coherence R_{xy} according to Eq. (3):

$$R_{x,y} = \sqrt{\left\langle \cos\left(\theta_x(t) - \theta_y(t)\right)\right\rangle^2 + \left\langle \sin\left(\theta_x(t) - \theta_y(t)\right)\right\rangle^2} \qquad (3)$$

where $< >$ denotes the mean value. R_{xy} ranges between 0 and 1 ($0 <= R_{xy} <= 1$). $R_{x,y} = 1$ represents no random phase lag between two signals, whereas $R_{x,y} = 0$ manifests a uniform distribution of phase lag between the two signals.

Statistic analysis

We computed the mean phase lag and mean phase coherence across 280 time points for each pair of ROIs. Task effects on the mean phase lag and mean phase coherence were assessed with paired-samples t-test between signals of task state and resting state. To get a finer inspection of point-by-point phase lag modulated by the task, phase lags at each of the ten time points in each trial of the task state were extracted and averaged across trials. The phase lag of resting state was

obtained using the same event timings as the task state and averaged across pseudo trials. The latter served as the baseline and was compared with the phase lag at each time point of task state using paired-samples t-tests. Multiple comparisons were corrected with the false discovery rate (FDR) method ($q < 0.05$). Brain maps were visualized with the BrainNet Viewer software (https://www.nitrc.org/projects/bnv) (Xia et al., 2013). Furthermore, brain-behavioral relationship was measured with Pearson's correlation between phase synchronization indices and the mean and SD of RT. The mean phase lag of 10 time points in one trial was deemed to phase lag of that trial or trial-level phase lag. The trial-level phase lag, mean phase lag and mean phase coherence of 280 time points were recruited for correlation analysis. The correlation analysis was limited to edges with significant task effect and results were corrected with FDR method ($q < 0.05$). Significant edges with $-0.2 < r < 0.2$ were excluded because of the small effect size.

RESULTS

Behavioral results

Because the first 20 and last 10 time points were removed during the preprocessing and phase calculation of imaging data, three trials corresponding to these time points were deleted in behavioral data. Twenty-eight trials remained for each subject. The accuracy of performance was extremely high with only two error responses out of 672 trials in all 24 subjects. The mean RT ranged from 432.43 ms to 894.27 ms with the SD ranging from 64.64 to 208.05 ms for different subjects. The group mean RT was 662.91 ms ± 133.56 ms (mean ± SD).

The modulation of inter-regional phase lag by the task

Fig. 2 shows the phase in the right inferior frontal gyrus (ID: R61 in the template (Fan et al., 2016); Fig. 2A) and right fusiform gyrus (R33; Fig. 2B), and phase lag between these two regions (Fig. 2C) during task state and resting state in one subject. Lower mean phase lag could be observed during task state than during resting state.

Further analysis shows task effect on mean phase lag of 280 time points in two systems (Fig. 3). One is the face processing system which is defined previously as the core (the occipital face area, fusiform face area, posterior superior temporal sulcus) and extended (the insula, amygdala, thalamus, hippocampus, anterior cingulate cortex, dorsal and ventral lateral frontal cortices, precuneus, and superior and inferior parietal lobes) face areas (Gauthier et al., 2000; Haxby et al., 2000; Gao et al., 2018). Mean phase lag in this system was decreased during task state than during resting state. Another includes links between the face processing system and frontoparietal regions (the medial frontal cortex, right inferior frontal gyrus, superior parietal lobe, precentral gyrus) (Spreng et al., 2010). Phase lag in this system was increased during face recognition (Fig. 3C). The
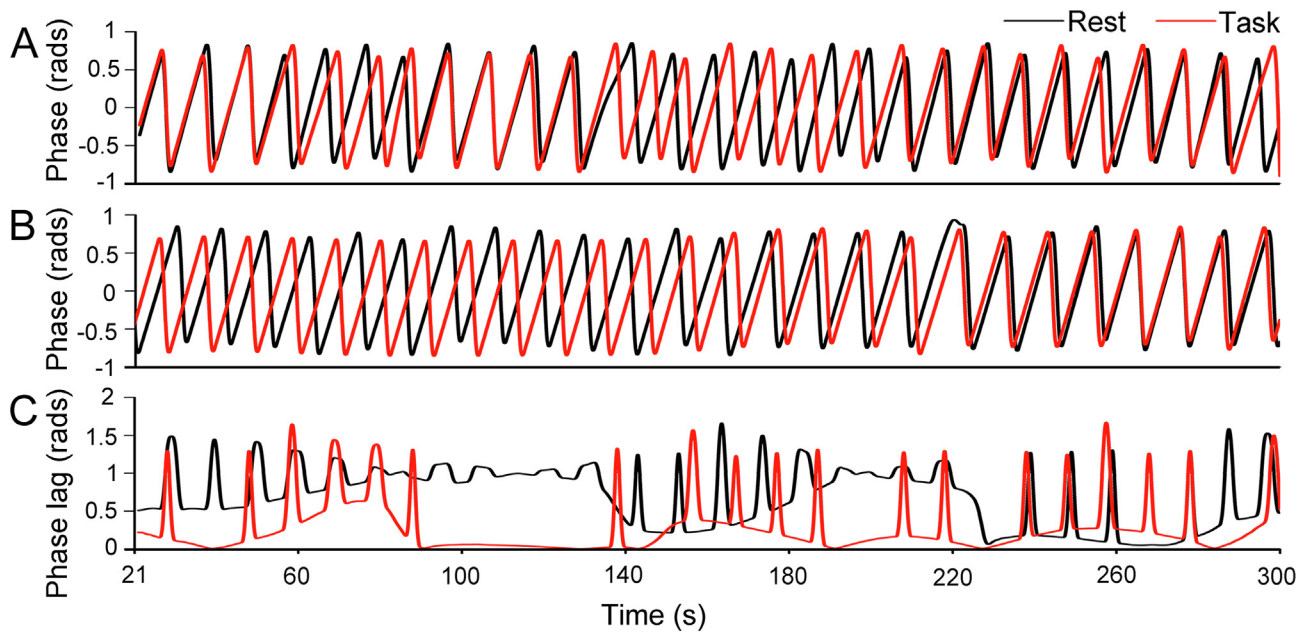
Fig. 2. Local phase (A, B) of the right inferior frontal gyrus and fusiform gyrus and inter-regional phase lag (C) between these two regions across time from one subject.
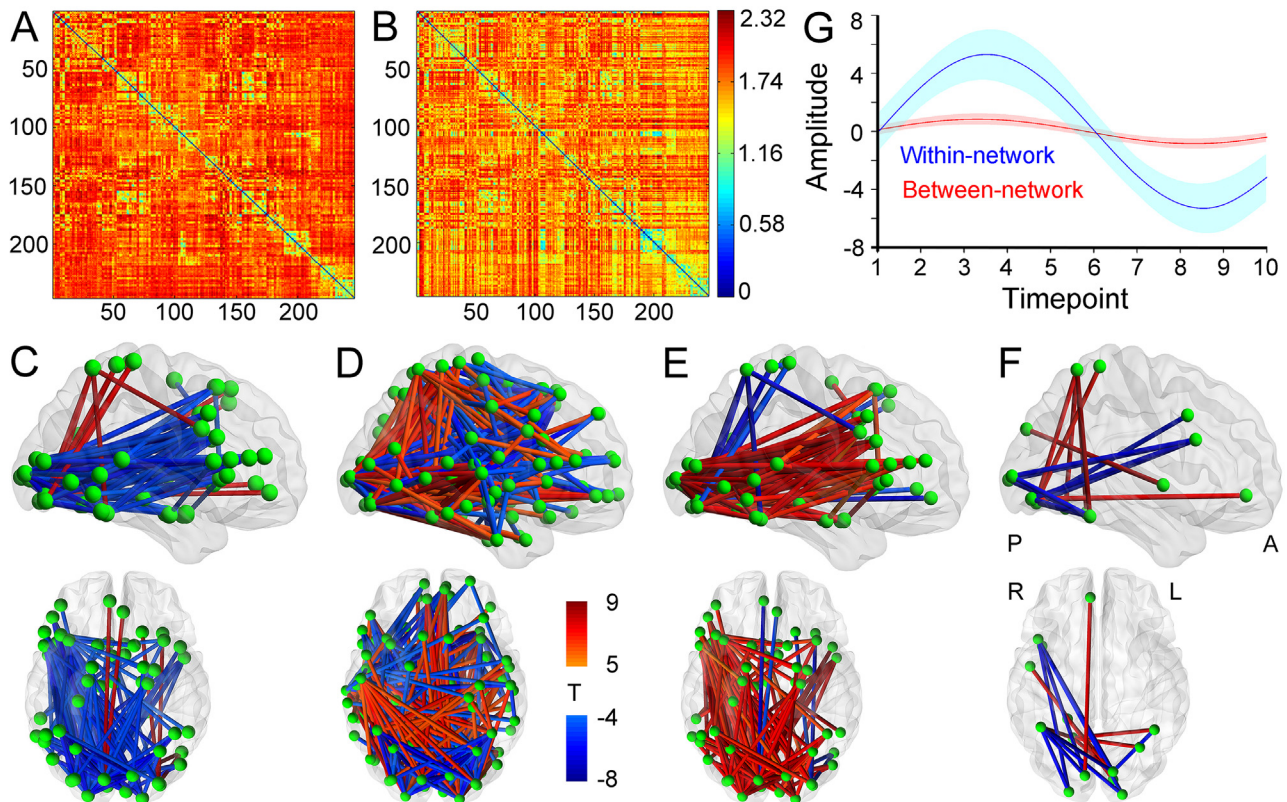

Fig. 3. Inter-regional phase lag and traditional functional connectivity are modulated by the task. Panel A and panel B show phase lags during resting state and task state between each pair of the 246 regions. Phase lags are shorter during task state than during resting state among regions in the face processing system and are longer between the face processing system and frontoparietal network (C). Global signal regression introduces some longer phase lags during task state (D). The Pearson's correlation analysis shows opposite results to phase lag analysis (E). Task effect on phase lag is mainly limited in the core face areas at a wider frequency band (0.04–0.07 Hz; F). The time courses of BOLD signals for within-network nodes (blue) and between-network nodes (red; G). Results are corrected with FDR method ($q < 0.05$). P: Posterior; A: Anterior; R: Right; L: Left. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

opposite reorganization of inter-regional relationships in these two systems supports the cognitive-related modularization (DeSalvo et al., 2014). Being different from traditional FC, the GSR introduced many enlarged phase lags for long distant links, indicating the non-linear relationship between phase lag and traditional FC (Fig. 3D).

In order to clarify the relationship between phase lag and traditional FC, we further calculated Pearson's correlation within these two systems and observed opposite changes of phase lag and FC (Fig. 3E). Considering the sinusoidal waveform of lfSSBR (Wang et al., 2016a, 2018b), the model in Fig. 1 suits well with the current result. Specifically, one can expect opposite relationship between FC and phase lag since the phase lags for both task state and resting state are shorter than pi (see Fig. 3A, B). However, it should be cautious to explain these results in other situations with unstable and non-sinusoidal fMRI signals (Cole and Voytek, 2017).

We further calculated phase lags at 0.04–0.07 Hz and 0.01–0.1 Hz frequency bands to evaluate how the frequency band affects task-specific brain activities. Significant task effect was observed only at 0.04–0.07 Hz band. Limited links appeared mainly in the core face areas (Fig. 3F). These results demonstrated that task-related brain activities are limited to a narrow frequency band during lfSSBR.

To clarify the meaning of phase lag, we extracted the time courses of BOLD signal for nodes within the face processing system and between face processing system and frontoparietal regions and averaged them across trials. As shown in Fig. 3G, the amplitude of nodes within the face processing system is higher than that between the face processing system and frontoparietal regions. This is in line with the fact in electrophysiological studies that tighter phase-locking would produce higher peak (Luck, 2005), indicating that the phase lag was shorter in the face processing system than that between the face processing system and frontoparietal regions.

Point-by-point analysis shows significant task effect on phase lag primarily at time points of 1, 2, 5, 6, 7 (see Fig. 4). These time points are at the ascending and descending phases of the BOLD signal (Wang et al., 2016a), indicating the phase-dependent modulation of inter-regional phase lag by the task. Interestingly, we extracted inter-regional phase lag based on each node in Fig. 3 and found that phase lag was shorter at the ascending, descending, and peak phases of the temporal BOLD signal both during task state and during resting state (see Fig. 5). At these phases inter-regional phase lag was shorter during task state than during resting state [all $t(23) > 7.69$, $p < 8.25e\text{-}8$; paired-sample t test]. However, phase lag was comparable between task state
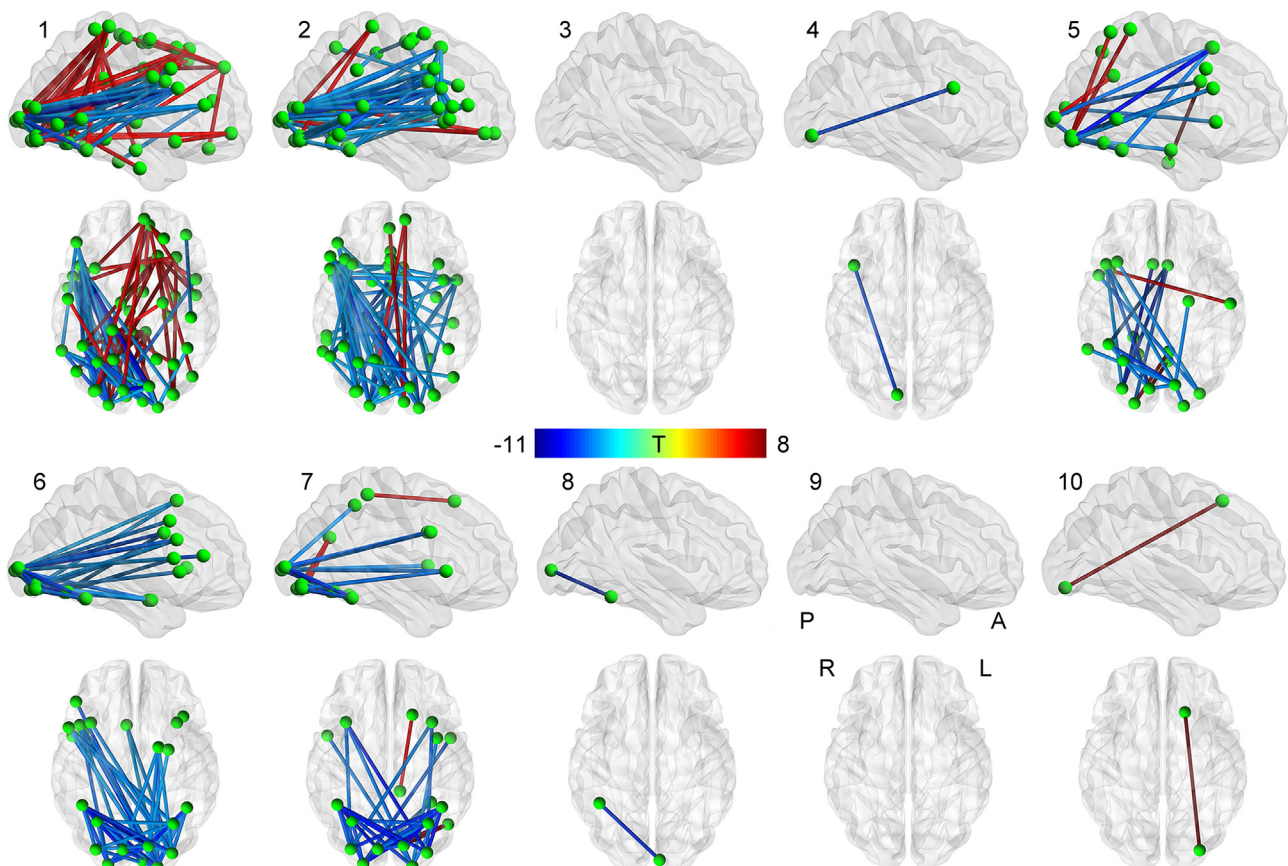

Fig. 4. Phase lag difference between task state and resting state. Arabic numerals show the time point from stimulus onset. Task effect appears mainly at the 1st, 2nd, 5th, 6th, and 7th time points, corresponding to the ascending and descending phases of original BOLD signal.
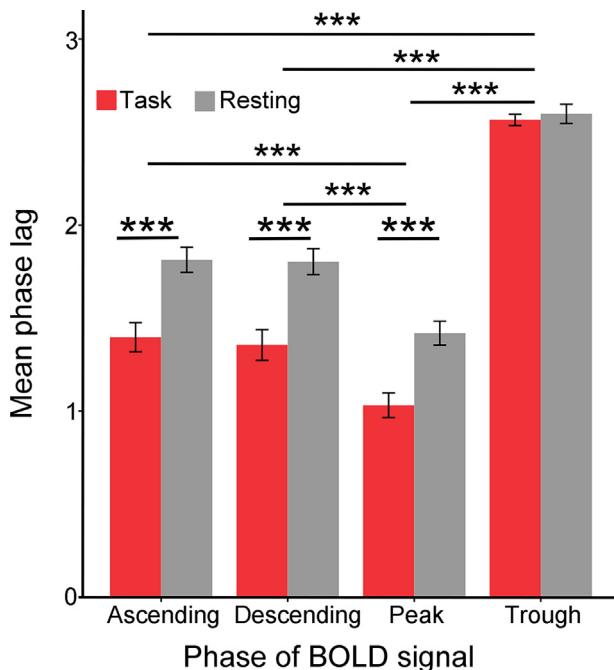
Fig. 5. The relationship between local phase of temporal BOLD signal and inter-regional phase lag. The task reduces inter-regional phase lag at the ascending, descending, and peak of the temporal BOLD signal in the infra-slow frequency range. *** represents $p < 0.0001$.

and resting state at the trough of the temporal BOLD signal [$t (23) = 1.04$, $p = 0.31$; paired-sample t test]. These findings suggest that inter-regional phase lag was phase-dependent even during the resting state and further support the phase-dependent modulation of phase lag by the task.

The modulation of inter-regional phase coherence by the task

Phase coherence within the face processing system and between face processing system and motor regions was significantly increased during task state (Fig. 6C) than during resting state, suggesting higher level of inter-regional phase-locking during face recognition. By regressing out GS, links with significant increased phase coherence during task state were much fewer than those without GSR. Significant task effect was primarily located in the core face areas (Fig. 6D), indicating that GSR diminished task-related phase coherence.

We further calculated phase coherences at 0.04–0.07 Hz and 0.01–0.1 Hz frequency bands to evaluate how the frequency band affects task-specific brain activities. Significant task effect was observed only at 0.04–0.07 Hz band. Limited links appeared mainly in the core face areas (Fig. 6E). These results suggested that task-related brain activities are limited to a narrow frequency band during lfSSBR.

In order to clarify the relationship between phase coherence and traditional FC, we further computed Pearson's correlation between these regions and

observed increased correlation during task state than during resting state (Fig. 6F). As shown in Figs. 3G and 5, the lfSSBR has sinusoidal waveform with inter-regional phase lag primarily shorter than pi/2. One can expect from the model in Fig. 1 that both phase coherence and Pearson's correlation coefficient should be increased when phase lag is shortened. This could explain the similar results for phase coherence and FC. However, it should be cautious to explain these results in other situations with non-sinusoidal and unstable fMRI signals (Cole and Voytek, 2017).

Brain-behavior relationship

We did not find significant correlation between the mean phase lag/mean phase coherence and the mean and SD of RT at the subject level for both task state and resting state data. By contrast, at the trial level, there were significantly positive correlation between RT and phase lag (Fig. 7). Fig. 7A shows the correlation between RT and phase lag during task state, indicating that shorter phase lags between these regions are associated with faster performance. Fig. 7B shows the correlation between RT and the difference of phase lag between task state and resting state, suggesting that the more reduced phase lags by the task the faster cognitive performance. In order to clarify the relationship between phase lag and time delay, we split trials into two equal parts of long RTs and short RTs for each subject and computed BOLD curves for both types of trials in the $AmygR21$, $CunR51$, $PrGR66$, and $OcGR41$, respectively. The time delay was calculated based on latencies of the curve peaks. Although there was no significant time delay between any pair of the BOLD time courses (measured with paired-samples t-test, ps > 0.22), the mean peak latency of BOLD curve in the Cun_{R51} is 0.311 s later than that in the $Amyg_{R21}$, while that in the PrG_{R66} is 0.104 s later than that in the OcG_{R41} for trials with short RTs. For trials with long RTs, the mean peak latency of BOLD curve in the $Amyg_{R21}$ is 0.104 s later than that in the Cun_{R51}, while that in the PrG_{R66} is the same as that in the OcG_{R41}. We further computed time delays between trials with long RTs and those with short RTs in the same region. The time delays ($trial_{long\ RTs}$-$trial_{short\ RTs}$) is 0.416 s, 0.00 s, 0.104 s, and 0.208 s in the $Amyg_{R21}$, Cun_{R51}, PrG_{R66}, and OcG_{R41}, respectively (see Fig. 7C). Therefore, the inter-regional time delays were mainly caused by delayed time in the $Amyg_{R21}$ and OcG_{R41} during trials with long RTs than during trials with short RTs. These two regions are responsible for rapid emotional detection and visual information coding of faces (Hung et al., 2010; Wang et al., 2018a). These results link phase lag and time delay and suggest that rapid emotional detection and visual coding are essential for fast reaction in the task.

DISCUSSION

We investigated the phase synchronization of infra-slow frequency neural fluctuations during a face recognition task. We observed that phase lags were reduced within
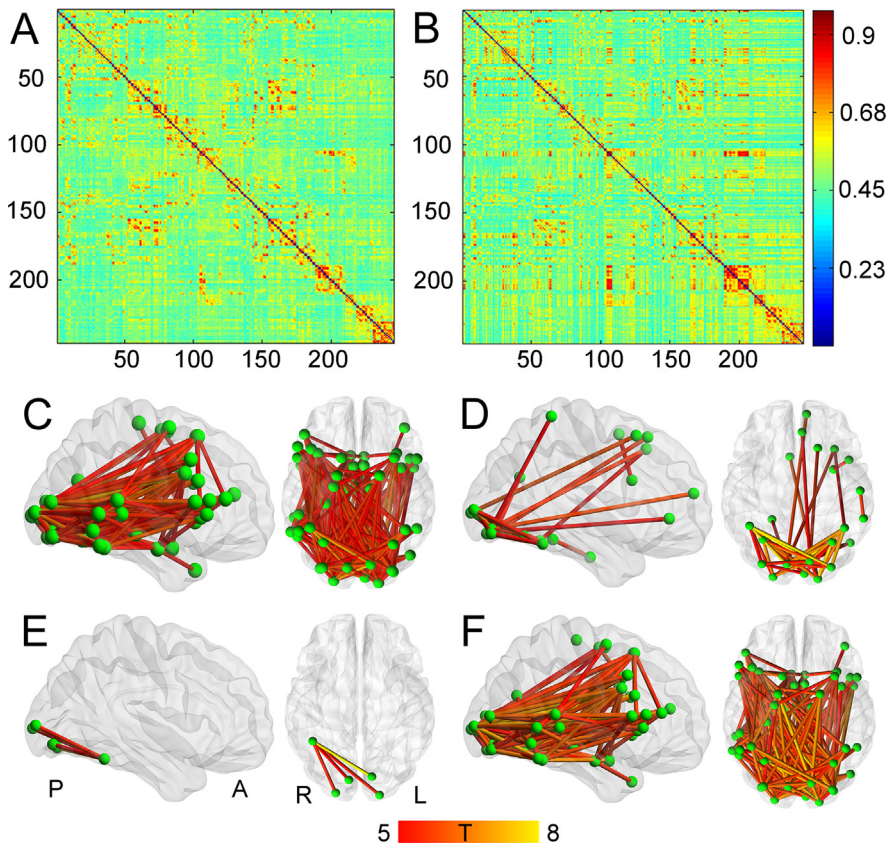
Fig. 6. Inter-regional phase coherence and traditional functional connectivity are modulated by the task. Panel A and panel B show phase coherences during resting state and task state between each pair of the 246 regions. Phase coherences among regions in the face processing system and between the face processing system and motor cortex are greater during task state than during resting state (C). Global signal regression dramatically reduces phase coherence with significant task effect primarily remaining in the core face areas (D). Task effect on phase coherence is mainly limited in the core face areas at a wider frequency band (0.04–0.07 Hz; E). Pearson's correlation coefficients are also higher during task state than during resting state (F) which is much similar to phase coherence.

the face processing system and were increased between the face processing system and frontoparietal network. Inter-regional phase coherence was increased in the face processing system and motor system. Furthermore, phase lags between the amygdala and visual cortex and between visual cortex and motor cortex were positively related to RT. Both phase lag and phase coherence were non-linearly associated with traditional FC, indicating that phase synchronization could provide novel information for us to understand inter-regional relationship beyond traditional FC. These findings highlighted the essential role of particular phase lag in the infra-slow frequency range on information communication and cognition.

Inter-regional phase lag in the infra-slow frequency range is modulated by the task

Phase synchronization is an important mechanism of information communication between neuronal assemblies. The binding-by-synchronization hypothesis suggests that adjacent neurons can establish a functional assembly by the synchronization of action potentials (Singer, 1999). The communication-through-coherence hypothesis further argues that two sets of neurons can effectively communicate when their oscillations are coherent (Fries, 2015). Recently, the synchronized gating hypothesis stresses the role of the phase synchronization of low frequency neural fluctuations in gating the coherence of high frequency neural oscillations (Florin and Baillet, 2015). These hypotheses are primarily based on electrophysiological evidence, highlighting the role of phase synchronization in information communication. However, the mechanism of phase synchronization in the infra-slow frequency range has rarely been investigated (Monto et al., 2008; Glerean et al., 2012; Omidvarnia et al., 2016). In this frequency band, the default mode network and task positive network are anti-correlated (Fox et al., 2005; Kelly et al., 2008; Abbas et al., 2019). In other words, the phase lag between these two networks is around π. Furthermore, different temporal lags have been determined across voxels in the gray matter which are sensitive to brain states and neuropathological features (Mitra et al., 2015a,b, 2017). It is still unknown that whether and how the phase lag or temporal lag in the infra-slow frequency range determines cognition.

In the current study, we observed shorter phase lags within the face processing system and longer phase lags between the face processing system and frontoparietal network during face recognition than during resting state. These findings suggest that inter-regional phase relationship was reorganized during face recognition in which the face processing system and frontoparietal network are separated into two modular. This is in line with the opinion that task-specific modular could be established by different cognitive processes (DeSalvo et al., 2014; Di and Biswal, 2019). Specifically, brain regions in the face processing system are more strongly connected to each other to complete the particular face recognition task and are more loosely connected to the frontoparietal control network to be disengaged from externally-oriented attention (Chun et al., 2010; Wang et al., 2018c).

Furthermore, inter-regional phase lag was modulated by the task at the ascending and descending phases of the sinusoidal-like BOLD signal. This phase-dependent modulation has been revealed in local functional connectivity density and EEG fluctuations (Monto et al., 2008; Wang et al., 2016a), suggesting that the phase of infra-slow fluctuations is essential for inter-regional infor-
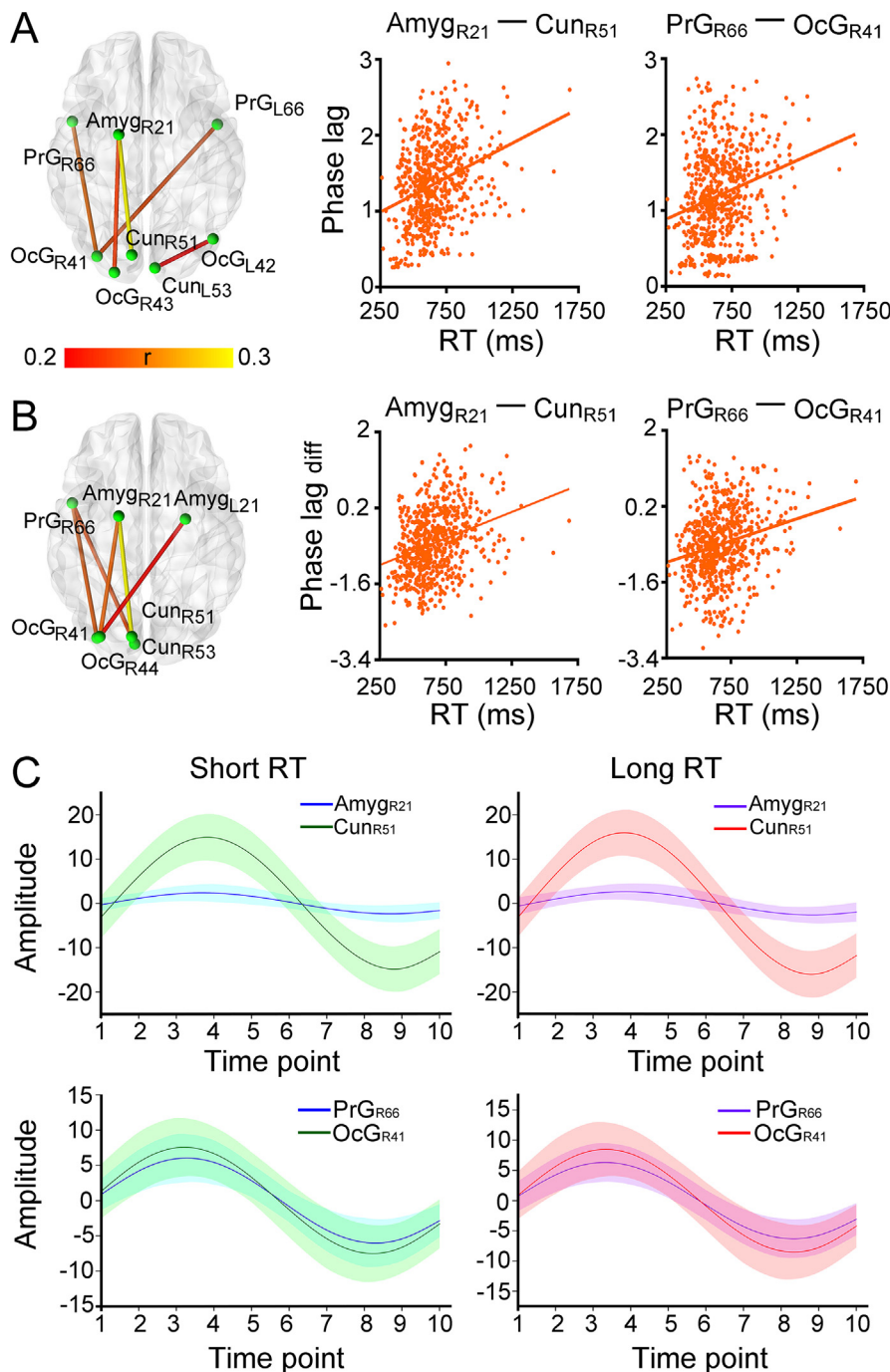
Fig. 7. The relationship between phase lag and reaction time. Panel A and panel B show positive correlation between RT and phase lag during task state and positive correlation between RT and phase lag difference between task state and resting state. Panel C shows the time courses of BOLD signals in relevant regions for trials with short RT and long RT, respectively. Amyg: Amygdala; Cun: Cuneus; OcG: Occipital gyrus; PrG: Precentral gyrus; L: Left; R: Right; RT: Reaction time. R21, L66, et al. are the labels in the 246 template.

that inter-regional phase relationship is determined by the phase of local temporal signal (illustrated in Fig. 5). Specifically, the ascending and descending phases of infra-slow fluctuations gate information communication (Monto et al., 2008; Wang et al., 2016a). In contrast, the peak and trough have been demonstrated to matter in the higher frequency range (> 1 Hz) (Hyafil et al., 2015; Züst et al., 2019). In addition, many other differences have been reported between infra-slow frequency and higher frequency fluctuations (Chan et al., 2015; Dash et al., 2018; Wang et al., 2018c, Watson, 2018). For instance, the direction of information flow in the infra-slow frequency range is opposite to that in higher frequency range (Mitra et al., 2018). These differences suggest that there are different mechanisms supporting infra-slow and higher frequency fluctuations where the phase-dependent information communication is one of them.

Inter-regional phase coherence in the infra-slow frequency range is modulated by the task

Inter-regional phase coherence in higher frequency range (> 1 Hz) has been suggested to be a basic mechanism of information communication and cognition (Siegel et al., 2012; Fries, 2015; Deco and Kringelbach, 2016; Maris et al., 2016). Dynamic phase coherence in the infra-slow and higher frequency ranges could capture different brain states (Mormann et al., 2000; Yaesoubi et al., 2015). However, cognitive-related phase coherence in the infra-slow frequency range has not been uncovered.

In the present study, we observed increased phase coherence in the face processing system, indicating stronger phase-locking among task-specific regions during face recognition than during resting state. This is the first time finding cognitive-related modulation of inter-regional phase coherence in the infra-slow frequency range. This finding suggests that infra-slow frequency phase coherence itself can be cognitive-related, besides improving information communication by gating interactions of cognitive-related neural oscillations in higher frequency bands (Florin and Baillet, 2015). Similar results between phase

mation communication. Although instantaneous phase has been shown to be modulated in task activated regions (Laird et al., 2002), this phase-dependent modulation could not be explained by traditional task activation because the peak point of hemodynamic response function often appears at 4–8 seconds after stimuli presentation (Wang et al., 2016a). Instead, these findings suggest

coherence and traditional FC suggest that phase coherence is an effective index of inter-regional relationship. It's worth noting that the relationship between phase coherence and traditional FC depends on the range of phase lag (see Fig. 1) and the waveform of brain signals (Cole and Voytek, 2017). The relationship between phase lag, phase coherence, and traditional FC, therefore, warrants systematic investigations.

Phase lag and phase coherence are sensitive to global signal and frequency band

The global signal has been demonstrated to convey important information about inter-regional relationship especially the anti-correlation relationship (Murphy and Fox, 2017). Here we observed enlarged phase lag and weakened phase coherence with GSR. These effects are in accord with previous findings that GSR may remove some phase lag information especially the long cycle durations that extend across regions which are important for phase coherence (Zhang et al., 2019). Furthermore, different phases of GS drive particular network configurations which may contribute to phase-dependent inter-regional relationship (Gutierrez-Barragan et al., 2019). Therefore, the findings from data without GSR were used as mainly results here. However, the GSR should be considered according to specific situations (Murphy and Fox, 2017; Zhang et al., 2019).

We also observed significant task effect in fewer links at 0.04–0.07 Hz but no task effect at 0.01–0.1 Hz. As the frequency band gets wider, effective task-related information may be overrode by task-unrelated noises (Norcia et al., 2015). This is why SSBR should be limited in a very narrow frequency band (Silberstein, 1995; Vialatte et al., 2010; Wang et al., 2014). However, that does not mean these task-unrelated noises are meaningless since frequency-specific effects have been widely documented in fMRI studies (He et al., 2016; Wang et al., 2018c, Lou et al., 2019). To clarify their neural mechanisms, future studies should test frequency-specific inter-regional phase lag and phase coherence at multiple different frequency bands both during resting state and during various task states.

Behavioral association of inter-regional phase lag

High frequency phase synchronization is essential to cognitive performance (Fries, 2015; Clouter et al., 2017). However, it is still unknown whether and how the infra-slow frequency phase synchronization is associated with the efficiency of cognition. In the current study, we observed positive correlations between RT and phase lag in two circuits. The first circuit links the amygdala and visual cortex which is responsible for rapid detection of visual emotion information (Brosch and Wieser, 2011; Wang et al., 2013), while the second circuit connects the visual cortex and motor cortex relating to the stimulus-reaction system (Dassonville et al., 2001; Wang et al., 2014). Time delay analysis of regional BOLD signals further suggests that the amygdala and lateral occipital cortex play the leading role in these two circuits. Positive correlations between RT and phase lag in these

two circuits suggest that the RT is determined by the speed of both visual information detection and visual-motor connection. Shorter phase lag in these circuits implies faster information communication which further leading to faster response. Therefore, inter-regional phase lag could serve as an effective indicator of information communication and cognitive efficiency. These results argue that inter-regional phase delay or time delay should vary dynamically and flexibly to adapt ever-changing environmental stimuli and cognitive activities.

Limitations

We revealed the essential role of phase synchronization in the infra-slow frequency range to cognition, some limitations remain. First, frequency specificity is a vital characteristic of low frequency neural activities and functional connections (Zuo et al., 2010; Thompson and Fransson, 2015; Wang et al., 2018c, 2019). It cannot be determined whether phase lag is frequency-dependent because only one narrow frequency band was investigated here. Second, it seems that inter-regional phase lag in the infra-slow frequency range is not directly related to fast neuronal information transmission (Hillebrand et al., 2016). The significance of phase lag in this frequency range is largely unclear, thus warranting further investigations. Third, many edges in the face processing system are related to task performance. Future studies could clarify how are these brain regions collaborate to support the optimal performance with multivariate pattern analysis.

In summary, phase synchronization in the infra-slow frequency range plays essential role in cognition. Inter-regional phase lags were reorganized in different systems to particular non-zero delays respectively to facilitate a specific cognitive processing. Inter-regional phase coherence was enhanced in the cognitive processing system, showing stronger phase-locking in the infra-slow frequency range during cognition. Furthermore, behavioral performance was determined by phase lags in key circuits of information communication. Overall, inter-regional phase synchronization in the infra-slow frequency range is a key mechanism of information communication and cognitive performance.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Abbas A, Belloy M, Kashyap A, Billings J, Nezafati M, Schumacher EH, Keilholz S (2019) Quasi-periodic patterns contribute to functional connectivity in the brain. NeuroImage 191:193–204.

Aladjalova N (1957) Infra-slow rhythmic oscillations of the steady potential of the cerebral cortex. Nature 179:957–959.

Bonnefond M, Jensen O (2015) Gamma activity coupled to alpha phase as a mechanism for top-down controlled gating. PLoS ONE 10 e0128667.

Brosch T, Wieser MJ (2011) The (non)automaticity of amygdala responses to threat: on the issue of fast signals and slow measures. J Neurosci 31:14451–14452.

Busch NA, Dubois J, VanRullen R (2009) The phase of ongoing EEG oscillations predicts visual perception. J Neurosci 29:7869–7876.

Canavier CC (2015) Phase-resetting as a tool of information transmission. Curr Opin Neurobiol 31:206–213.

Chan AW, Mohajerani MH, LeDue JM, Wang YT, Murphy TH (2015) Mesoscale infraslow spontaneous membrane potential fluctuations recapitulate high-frequency activity cortical motifs. Nat Commun 6:7738.

Chun MM, Golomb JD, Turkbrowne NB (2010) A taxonomy of external and internal attention. Annu Rev Psychol 62:73–101.

Clouter A, Shapiro KL, Hanslmayr S (2017) Theta phase synchronization is the glue that binds human associative memory. Curr Biol 27:3143–3148.

Cole SR, Voytek B (2017) Brain oscillations and the importance of waveform shape. Trends Cognitive Sci 21:137–149.

Cottereau B, Lorenceau J, Gramfort A, Clerc M, Thirion B, Baillet S (2011) Phase delays within visual cortex shape the response to steady-state visual stimulation. NeuroImage 54:1919–1929.

Dash MB, Ajayi S, Folsom L, Gold PE, Korol DL (2018) Spontaneous infraslow fluctuations modulate hippocampal EPSP-PS coupling. eNeuro 5. e0403-0417.2017.

Dassonville P, Lewis SM, Zhu XH, Ugurbil K, Kim SG, Ashe J (2001) The effect of stimulus-response compatibility on cortical motor activation. Neuroimage 13:1–14.

Deco G, Kringelbach ML (2016) Metastability and coherence: extending the communication through coherence hypothesis using a whole-brain computational perspective. Trends Neurosci 39:125–135.

DeSalvo MN, Douw L, Takaya S, Liu H, Stufflebeam SM (2014) Task-dependent reorganization of functional connectivity networks during visual semantic decision making. Brain Behav 4:877–885.

Di X, Biswal BB (2019) Toward task connectomics: examining whole-brain task modulated connectivity in different task domains. Cereb Cortex 29:1572–1583.

Domenico MD, Sasai S, Arenas A (2016) Mapping multiplex hubs in human functional brain networks. Front Neurosci 10:1–14.

Fan L, Li H, Zhuo J, Zhang Y, Wang J, Chen L, Yang Z, Chu C, Xie S, Laird AR, Fox PT, Eickhoff SB, Yu C, Jiang T (2016) The human brainnetome atlas: a new brain atlas based on connectional architecture. Cereb Cortex 26:3508–3526.

Florin E, Baillet S (2015) The brain's resting-state activity is shaped by synchronized cross-frequency coupling of neural oscillations. NeuroImage 111:26–35.

Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks. PNAS 102:9673–9678.

Fries P (2015) Rhythms for cognition: communication through coherence. Neuron 88:220–235.

Friston KJ, Stephan K, Frackowiak R (1997) Transient phase-locking and dynamic correlations: are they the same thing? Hum Brain Mapp 5:48–57.

Gao X, Gentile F, Rossion B (2018) Fast periodic stimulation (FPS): a highly effective approach in fMRI brain mapping. Brain Struct Funct 223:2433–2454.

Gauthier I, Skudlarski P, Gore JC, Anderson AW (2000) Expertise for cars and birds recruits brain areas involved in face recognition. Nat Neurosci 3:191–197.

Glerean E, Salmi J, Lahnakoski JM, Jääskeläinen IP, Sams M (2012) Functional magnetic resonance imaging phase synchronization as a measure of dynamic functional connectivity. Brain Connect 2:91–101.

Gonzalez-Castillo J, Hoy CW, Handwerker DA, Robinson ME, Buchanan LC, Saad ZS, Bandettini PA (2015) Tracking ongoing cognition in individuals using brief, whole-brain functional connectivity patterns. PNAS 112:8762–8767.

Gutierrez-Barragan D, Basson MA, Panzeri S, Gozzi A (2019) Infraslow state fluctuations govern spontaneous fMRI network dynamics. Curr Biol 29:2295–2306.

Haxby JV, Hoffman EA, Gobbini MI (2000) The distributed human neural system for face perception. Trends Cognitive Sci 4:223–233.

He Z, Cui Q, Zheng J, Duan X, Pang Y, Gao Q, Han S, Long Z, Wang Y, Li J (2016) Frequency-specific alterations in functional connectivity in treatment-resistant and -sensitive major depressive disorder. J Psychiatr Res 82:30–39.

Hillebrand A, Tewarie P, Dellen EV, Yu M, Carbo EWS, Douw L, Gouw AA, Straaten ECWV, Stam CJ (2016) Direction of information flow in large-scale resting-state networks is frequency-dependent. Proc Natl Acad Sci 113:3867–3872.

Huang Z, Zhang J, Longtin A, Dumont G, Duncan NW, Pokorny J, Qin P, Dai R, Ferri F, Weng X (2017) Is there a nonadditive interaction between spontaneous and evoked activity? Phase-dependence and its relation to the temporal structure of scale-free brain activity. Cereb Cortex 27:1037–1059.

Hung Y, Smith ML, Bayle DJ, Mills T, Cheyne D, Taylor MJ (2010) Unattended emotional faces elicit early lateralized amygdala-frontal and fusiform activations. Neuroimage 50:727–733.

Hyafil A, Giraud AL, Fontolan L, Gutkin B (2015) Neural cross-frequency coupling: connecting architectures, mechanisms, and functions. Trends Neurosci 38:725–740.

Kelly AC, Uddin LQ, Biswal BB, Castellanos FX, Milham MP (2008) Competition between functional brain networks mediates behavioral variability. NeuroImage 39:527–537.

Kitzbichler MG, Smith ML, Christensen SR, Bullmore E (2009) Broadband criticality of human brain network synchronization. PLoS Comput Biol 5 e1000314.

Laird AR, Rogers BP, Carew JD, Arfanakis K, Moritz CH, Meyerand ME (2002) Characterizing instantaneous phase relationships in whole-brain fMRI activation data. Hum Brain Mapp 16:71–80.

Lewis LD, Setsompop K, Rosen BR, Polimeni JR (2016) Fast fMRI can detect oscillatory neural activity in humans. Proc Natl Acad Sci 113:e6679–e6685.

Li JM, Bentley WJ, Snyder AZ, Raichle ME, Snyder LH (2015) Functional connectivity arises from a slow rhythmic mechanism. Proc Natl Acad Sci 112:2527–2535.

Lou W, Wang D, Wong A, Chu WCW, Mok VCT, Shi L (2019) Frequency-specific age-related decreased brain network diversity in cognitively healthy elderly: a whole-brain datadriven analysis. Hum Brain Mapp 40:340–351.

Luck SJ (2005) An introduction to the event-related potential technique. Cambridge, Mass.: MIT Press.

Maris E, Fries P, van Ede F (2016) Diverse phase relations among neuronal rhythms and their potential function. Trends Neurosci 39:86–99.

Mitra A, Kraft A, Wright P, Acland B, Snyder AZ, Rosenthal Z, Czerniewski L, Bauer A, Snyder L, Culver J, Lee J-M, Raichle ME (2018) Spontaneous infra-slow brain activity has unique spatiotemporal dynamics and laminar structure. Neuron 98:297–305.

Mitra A, Snyder AZ, Blazey T, Raichle ME (2015a) Lag threads organize the brain's intrinsic activity. PNAS 112:2235–2244.

Mitra A, Snyder AZ, Constantino JN, Raichle ME (2017) The lag structure of intrinsic activity is focally altered in high functioning adults with autism. Cereb Cortex 27:1083–1093.

Mitra A, Snyder AZ, Tagliazucchi E, Laufs H, Raichle ME (2015b) Propagated infra-slow intrinsic brain activity reorganizes across wake and slow wave sleep. Elife 4 e10781.

Monto S, Palva S, Voipio J, Palva JM (2008) Very slow EEG fluctuations predict the dynamics of stimulus detection and oscillation amplitudes in humans. J Neurosci 28:8268–8272.

Mormann F, Lehnertz K, David P, Elger CE (2000) Mean phase coherence as a measure for phase synchronization and its application to the EEG of epilepsy patients. Physica D 144:358–369.

Murphy K, Fox MD (2017) Towards a consensus regarding global signal regression for resting state functional connectivity MRI. NeuroImage 154:169–173.

Norcia AM, Appelbaum LG, Ales JM, Cottereau BR, Rossion B (2015) The steady-state visual evoked potential in vision research: a review. J Vision 15:1–46.

Omidvarnia A, Pedersen M, Walz JM, Vaughan DN, Abbott DF, Jackson GD (2016) Dynamic regional phase synchrony (DRePS): an instantaneous measure of local fMRI connectivity within spatially clustered brain areas. Hum Brain Mapp 37:1970–1985.

Palva JM, Palva S, Kaila K (2005) Phase synchrony among neuronal oscillations in the human cortex. J Neurosci 25:3962–3972.

Ponce-Alvarez A, Deco G, Hagmann P, Romani GL, Mantini D, Corbetta M (2015) Resting-state temporal synchronization networks emerge from connectivity topology and heterogeneity. PLoS Comput Biol 11 e1004100.

Siegel M, Donner TH, Engel AK (2012) Spectral fingerprints of large-scale neuronal interactions. Nat Rev Neurosci 13:121–134.

Silberstein RB (1995) Steady-state visually evoked potentials, brain resonances, and cognitive processes. In: Nunez PL, editor. Neocortical dynamics and human EEG rhythms. New York: Oxford University Press. p. 272–303.

Singer W (1999) Neuronal synchrony: a versatile code for the definition of relations? Neuron 24:49–65.

Spreng RN, Stevens WD, Chamberlain JP, Gilmore AW, Schacter DL (2010) Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. Neuroimage 53:303–317.

Stam CJ, van Straaten EC (2012) Go with the flow: use of a directed phase lag index (dPLI) to characterize patterns of phase relations in a large-scale model of brain dynamics. Neuroimage 62:1415–1428.

Thompson GJ, Riedl V, Grimmer T, Drzezga A, Herman P, Hyder F (2016) The whole-brain "global" signal from resting state fMRI as a potential biomarker of quantitative state changes in glucose metabolism. Brain Connect 6:435–447.

Thompson WH, Fransson P (2015) The frequency dimension of fMRI dynamic connectivity: network connectivity, functional hubs and integration in the resting brain. NeuroImage 121:227–242.

Turchi J, Chang C, Ye FQ, Russ BE, Yu DK, Cortes CR, Monosov IE, Duyn JH, Leopold DA (2018) The basal forebrain regulates global resting-state fMRI fluctuations. Neuron 97:940–952.

Vialatte F-B, Maurice M, Dauwels J, Cichocki A (2010) Steady-state visually evoked potentials: focus on essential paradigms and future perspectives. Prog Neurobiol 90:418–438.

Wang X, Zhu Q, Song Y, Liu J (2018a) Developmental reorganization of the core and extended face networks revealed by global functional connectivity. Cereb Cortex:1–10.

Wang Y-F, Dai G-S, Liu F, Long Z-L, Yan JH, Chen H-F (2015) Steady-state BOLD response to higher-order cognition modulates low frequency neural oscillations. J Cognit Neurosci 27:2406–2415.

Wang Y-F, Liu F, Long Z-L, Duan X-J, Cui Q, Yan JH, Chen H-F (2014) Steady-state BOLD response modulates low frequency neural oscillations. Sci Rep 4:7376.

Wang Y, Chen W, Ye L, Biswal BB, Yang X, Zou Q, Yang P, Yang Q, Wang X, Cui Q, Duan X, Liao W, Chen H (2018b) Multiscale energy reallocation during low-frequency steady-state brain response. Hum Brain Mapp 39:2121–2132.

Wang Y, Liu F, Jing X, Long Z, Chen H (2016a) Phase-dependent alteration of functional connectivity density during face recognition in the infra-slow frequency range. In: Wang R, Pan X, editors. Advances in cognitive neurodynamics (V). Singapore: Springer Singapore. p. 305–310.

Wang Y, Liu F, Li R, Yang Y, Liu T, Chen H (2013) Two-stage processing in automatic detection of emotional intensity: a scalp event-related potential study. NeuroReport 24:818–821.

Wang Y, Wang X, Ye L, Yang Q, Cui Q, He Z, Li L, Yang X, Zou Q, Yang P, Liu D, Chen H (2019) Spatial complexity of brain signal is altered in patients with generalized anxiety disorder. J Affect Disord 246:387–393.

Wang Y, Zhu L, Zou Q, Cui Q, Liao W, Duan X, Biswal B, Chen H (2018c) Frequency dependent hub role of the dorsal and ventral right anterior insula. Neuroimage 165:112–117.

Wang YF, Long Z, Cui Q, Liu F, Jing XJ, Chen H, Guo XN, Yan JH, Chen HF (2016b) Low frequency steady-state brain responses modulate large scale functional networks in a frequency-specific means. Hum Brain Mapp 37:381–394.

Watson BO (2018) Cognitive and physiologic impacts of the infraslow oscillation. Front Syst Neurosci 12.

Wong CW, Olafsson V, Tal O, Liu TT (2013) The amplitude of the resting-state fMRI global signal is related to EEG vigilance measures. Neuroimage 83:983–990.

Xia M, Wang J, He Y (2013) BrainNet Viewer: a network visualization tool for human brain connectomics. PLoS ONE 8 e68910.

Yaesoubi M, Allen EA, Miller RL, Calhoun VD (2015) Dynamic coherence analysis of resting fMRI data to jointly capture state-based phase, frequency, and time-domain information. NeuroImage 120:133–142.

Yan C-G, Zang Y-F (2010) DPARSF: a MATLAB toolbox for "pipeline" data analysis of resting-state fMRI. Front Systems Neurosci 4:1–7.

Yang AC, Tsai SJ, Lin CP, Peng CK, Huang NE (2018) Frequency and amplitude modulation of resting-state fmri signals and their functional relevance in normal aging. Neurobiol Aging 70:59–69.

Yang GJ, Murray JD, Glasser M, Pearlson GD, Krystal JH, Schleifer C, Repovs G, Anticevic A (2017) Altered global signal topography in schizophrenia. Cereb Cortex 27:5156–5169.

Yordanova J, Albrecht B, Uebel H, Kirov R, Banaschewski T, Rothenberger A, Kolev V (2011) Independent oscillatory patterns determine performance fluctuations in children with attention deficit/hyperactivity disorder. Brain 134:1740–1750.

Zhang H, Zhang L, Zang Y (2015) Fluctuation amplitude and local synchronization of brain activity in the ultra-low frequency band: an fMRI investigation of continuous feedback of finger force. Brain Res 1629:104–112.

Zhang J, Magioncalda P, Huang Z, Tan Z, Hu X, Hu Z, Conio B, Amore M, Inglese M, Martino M (2019) Altered global signal topography and its different regional localization in motor cortex and hippocampus in mania and depression. Schizophr Bull 45:902–910.

Zuo X-N, Di Martino A, Kelly C, Shehzad ZE, Gee DG, Klein DF, Castellanos FX, Biswal BB, Milham MP (2010) The oscillating brain: complex and reliable. NeuroImage 49:1432–1445.

Züst MA, Ruch S, Wiest R, Henke K (2019) Implicit vocabulary learning during sleep is bound to slow-wave peaks. Curr Biol 29:541–553.