Brain Topography (2019) 32:808–824
https://doi.org/10.1007/s10548-019-00723-x

ORIGINAL PAPER

Cross-Species Investigation on Resting State Electroencephalogram

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Received: 21 January 2019 / Accepted: 26 June 2019 / Published online: 4 July 2019

Abstract

Resting state electroencephalography (EEG) during eyes-closed and eyes-open conditions is widely used to evaluate brain states of healthy populations and brain dysfunctions in clinical conditions. Although several results have been obtained by measuring these brain activities in humans, it remains unclear whether the same results can be replicated in animals, i.e., whether the physiological properties revealed by these findings are phylogenetically conserved across species. In the present study, we describe a paradigm for recording resting state EEG activities during eyes-closed and eyes-open conditions from rats, and investigated the differences between eyes-closed and eyes-open conditions for humans and rats. We found that compared to the eyes-open condition, human EEG spectral amplitude in the eyes-closed condition was significantly higher at 8–12 Hz and 18–22 Hz in the occipital region, but significantly lower at 18–22 Hz and 30–100 Hz in the frontal region. In contrast, rat EEG spectral amplitude was significantly higher in the eyes-closed condition than in the eyes-open condition at 1–4 Hz, 8–12 Hz, and 13–17 Hz in the frontal-central region. In both species, the 1/f-like power spectrum scaling of resting state EEG activities was significantly higher in the eyes-closed condition than in the eyes-open condition at parietal-occipital and frontal regions. These results provided a neurophysiological basis for future translational studies from experimental animal findings to human psychophysiology, since the validity of such translation critically relies on a well-established experimental paradigm and a carefully-examined signal characteristic to bridge the gaps across different species.

Keywords Electroencephalogram (EEG) · Resting state · Power spectra · 1/f characteristic · Across-species comparison

Introduction

Resting state Electroencephalogram (EEG), i.e., spontaneous EEG in the wakefulness and relaxed state without performing any specific task in eyes-closed and eyes-open conditions (Michels et al. 2013), has been extensively studied and widely used to evaluate the states of human brain (Lomas et al. 2015; Keune et al. 2017). It is well known that the transition of the resting state from the eyes-closed condition to the eyes-open condition is associated with visible changes in spontaneous EEG oscillations, such as the decreased amplitude of occipital alpha oscillations (8–13 Hz), as revealed in the first EEG study performed by Berger (1929). These changes in resting state EEG, which have been considered as the reorganization of cortical oscillations in response to external and/or internal stimuli (Barry et al. 2007), reflect modulations of intrinsic brain functions and have been popularly used as neurophysiological indicators of brain dysfunctions in various clinical applications (Babiloni et al. 2010; Michel and Koenig 2018).

Handling Editor: Micah M. Murray

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10548-019-00723-x) contains supplementary material, which is available to authorized users.

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The comparison of EEG activities between the eyes-closed and eyes-open conditions is normally achieved using statistical analyses on power spectra across a wide range of frequencies (including five typical frequency bands: delta, 1–4 Hz; theta, 4–7 Hz; alpha, 7–12 Hz; beta, 12–30 Hz; and gamma, 30–100 Hz). Compared to the eyes-closed condition, healthy human subjects normally exhibit smaller amplitude of alpha oscillations and greater amplitude of gamma oscillations in the eyes-open condition (Barry et al. 2007; Miraglia et al. 2016). The difference of resting state EEG oscillations between the eyes-closed and eyes-open conditions is abnormal in clinical situations, thus reflecting cortical dysfunctions in many diseases, e.g., Parkinson's disease (Teramoto et al. 2016), Alzheimer's disease (Neto et al. 2015; Wang et al. 2017), schizophrenia (Narayanan et al. 2014; White and Siegel 2016), and attention-deficit/hyperactivity disorder (Woltering et al. 2012).

In addition to the power spectra, the 1/f-like power spectrum scaling (f means frequency) has been demonstrated as an important alternative to evaluate intrinsic brain functions from resting state EEG, thus providing a useful linkage between the large-scale brain activity and the behavior (Buzsáki 2006). The so-called 1/f-like scaling is a ubiquitous feature of complex biological and physical systems, irrespective of the source of the complexity. In such scaling, the power spectrum of spontaneous EEG activities is dominated by an inverse power ("power" as in "exponent") law: $P \propto f^{-\alpha}$, resulting in an inverse linear relationship between log frequency and log power. By comparing features of power-law dynamics between eyes-closed and eyes-open conditions in humans, previous studies have demonstrated that the 1/f-like scaling of spontaneous EEG activity could reflect the inter-individual variability of brain functions at resting state (Pritchard 1992; Lei et al. 2015).

Although the comparison of EEG activities between eyes-closed and eyes-open conditions has been well studied in previous human investigations (Barry et al. 2007; Tangermann et al. 2012; Barry and De Blasio 2017), it remains unclear whether the same or similar results could be observed in animals (e.g., in rats). This investigation is important as animal models have been extensively used to investigate the pathological and psychophysiological mechanisms of human diseases (Khanna et al. 2015). Specifically, characterizing features of spontaneous EEG activity during eyes-closed and eyes-open conditions through cross-species studies is highly needed, as it could provide a solid basis for the translation of experimental results from animals to humans (Hu and Iannetti 2019).

To achieve this goal, we firstly established a recording paradigm for collecting resting state EEG data during eyes-closed and eyes-open conditions from rats. Then, we compared the recorded EEG activities and investigated the characteristic differences between eyes-closed and eyes-open conditions for humans and rats, in terms of power spectra and 1/f-like scaling. Finally, we evaluated the similarity and difference of these characteristics between species, and discussed the translational value of these findings.

Materials and Methods

Experiment 1: Human EEG

Subjects

Thirty healthy subjects (17 females) aged 22.0 ± 2.6 years (mean $\pm$ SD, range = 19–30 years) participated in the human EEG recording experiment. All subjects gave their written informed consent and were paid for their participation. The local ethics committee approved the experiment procedures.

Experimental Paradigm and EEG Recording

Subjects were seated in a comfortable chair in a silent, temperature-controlled room. The EEG experiment consisted of two sessions (Fig. 1, top panel): eyes-closed and eyes-open. During eyes-closed session, subjects were instructed to close their eyes, keep relaxed but not sleep for 5 min. During eyes-open session, subjects were instructed to stare at a fixation point on the screen and keep relaxed for 5 min. The order of conducting eyes-closed and eyes-open sessions was counterbalanced between subjects. EEG data were recorded utilizing 64 Ag–AgCl electrodes placed on the scalp according to the International 10–20 system (Brain Products GmbH; pass band: 0.01–100 Hz; sampling rate: 1000 Hz). Nose was used as the recording reference, and the impedances of all electrodes were kept lower than 10 kΩ. Electro-oculographic (EOG) signals were simultaneously recorded using two surface electrodes to monitor ocular movements and eye blinks.

EEG Preprocessing

EEG data were processed using EEGLAB (Delorme and Makeig 2004), an open source toolbox running in the MATLAB (Mathworks, USA) environment. Continuous EEG data were first bandpass filtered from 1 to 100 Hz, and then notch filtered from 49 to 51 Hz. Artifacts of eye-blinks and movements were removed using an independent component analysis algorithm (Delorme and Makeig 2004). In all datasets, these independent components had a large EOG electrode contribution and a frontal scalp distribution. Please note that 200-s EEG data in the middle of each recording session were selected for subsequent analyses.

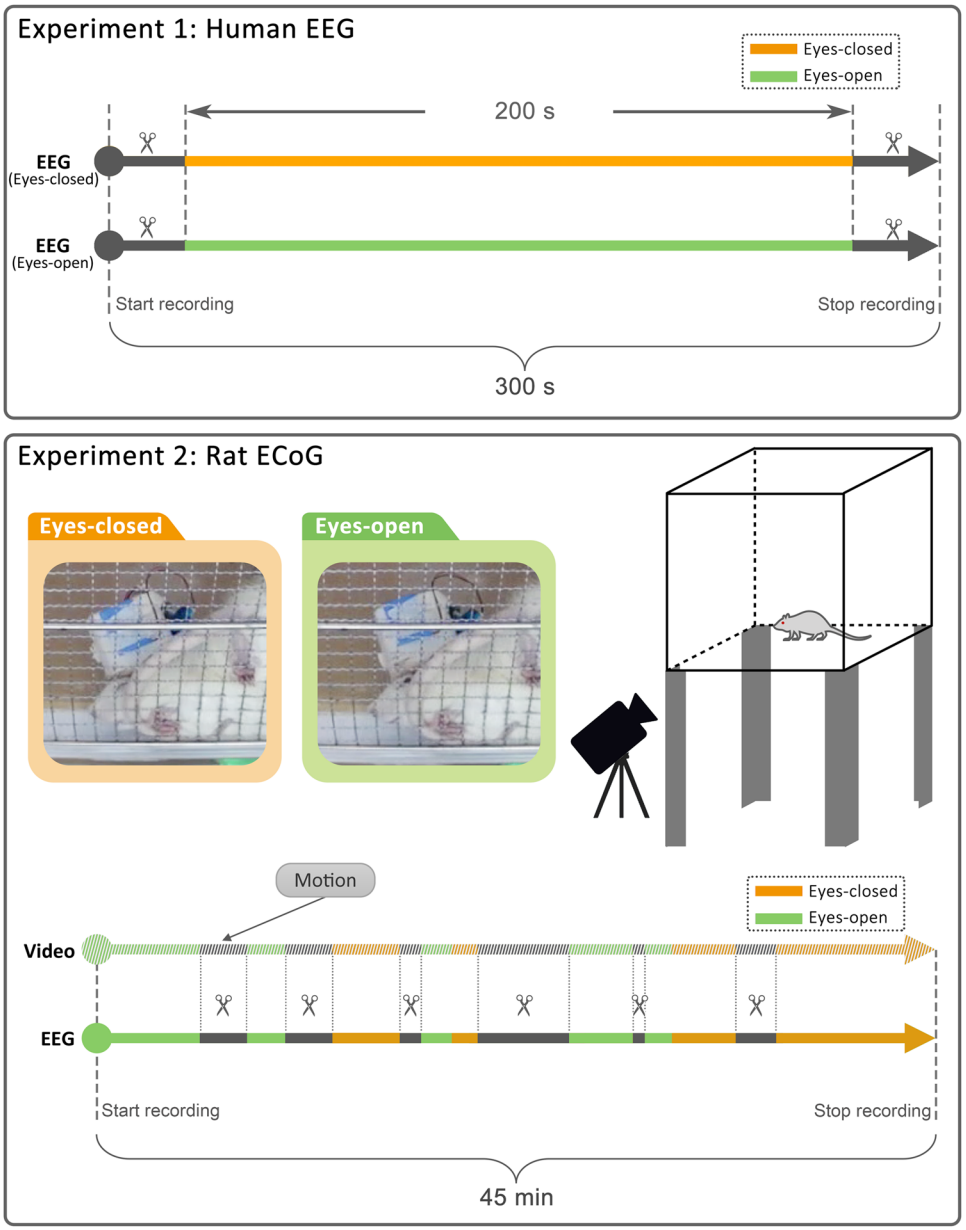


Fig. 1 Paradigms of human and rat experiments. For the human experiment (Experiment 1, top), 300-s EEG data were collected for both eyes-closed and eyes-open conditions, and 200-s EEG data in the middle of the recording session were selected for subsequent analysis. For the rat experiment (Experiment 2, bottom), 45-min ECoG data were collected with simultaneously video recording. After removing the data contained motion artifacts and the sleeping-like data, ECoG data belonging to eyes-closed and eyes-open conditions were manually determined based on the video information

Power Spectra Analyses

For each subject and experimental condition, EEG signals were transformed to the frequency domain using a fast Fourier transform, yielding an EEG spectrum ranging from 1 to 100 Hz. Group-level average spectra were obtained for eyes-closed and eyes-open conditions respectively. We divided all tested frequencies into five bands (Barry et al. 2007), including delta (1–4 Hz), theta (4–7 Hz), alpha (7–12 Hz), beta (12–30 Hz), and gamma bands (30–100 Hz). Scalp topographies of spectral amplitude at each frequency band were calculated in eyes-closed and eyes-open conditions respectively.

To compare the spectral amplitude differences between eyes-closed and eyes-open conditions, a point-by-point paired-sample t test was performed for each frequency point and electrode. It yielded a frequency course of P values representing the significance level of the difference between the two conditions for each electrode. To account for the multiple comparisons, a false discovery rate (FDR) procedure was performed to correct the P values.

Spontaneous EEG activity can be characterized by scale-free dynamics, whose frequency spectra follow a power-law distribution. Thus, for each subject and each electrode, resting state EEG spectra were fitted with a power-law function $P \propto f^{-\alpha}$ using the least-square estimation in the frequency

range of 1–100 Hz. After taking logarithm, the power-law function could be written as $log_{10}(P) \propto -\alpha \cdot log_{10}(f)$, and α is the absolute value of the slope of the linear fit in the log frequency by log power plot. The slope values between eyes-closed and eyes-open conditions were compared using a point-by-point paired-sample t test for each electrode. To account for the multiple comparisons, an FDR procedure was performed to correct the P values.

Connectivity Analysis

To estimate the connectivity between pairs of electrodes for each subject and experimental condition, we used the weighted phase lag index (WPLI, ranging from 0 to 1), which has been widely adopted in EEG/ECoG connectivity studies (Vinck et al. 2011; Lau et al. 2012; Hardmeier et al. 2014). Please note that WPLI has been demonstrated to resistant to the effects of volume conduction, as WPLI would not overestimate the phase lag values due to volume conduction effects of uncorrelated noise sources (Ortiz et al. 2012). In addition, WPLI is less sensitive to noise than other connectivity measures (e.g., phase lag index), thus revealing a more reliable relationship with true phase consistency. In the present study, the WPLI values (debias mode) between pairs of electrodes were calculated using the FieldTrip Toolbox (Oostenveld et al. 2011), for each frequency band and experimental condition. A point-by-point paired-sample t test was performed to compare the difference of WPLI values between eyes-closed and eyes-open conditions for each pair of electrodes and each frequency band. To account for the multiple comparisons, an FDR procedure was performed to correct the P values.

Experiment 2: Rat ECoG

Subjects

The experiment was conducted on eight adult male Sprague–Dawley rats weighing 300–400 g. Rats were fed ad libitum with water and food, and were housed in separate cages under temperature- and humidity-controlled conditions. They were kept in a 12 h day/night cycle (lights on from 19:00 to 7:00). All experimental procedures adhered to the guidelines for animal experimentation.

Surgical Procedures

Prior to the surgery, rats were anesthetized with isoflurane at a concentration of 5% (v/v) with an air flow rate of 0.5 L/min in an induction chamber. During the surgery, rat head was fixed using a stereotaxic apparatus and anesthetized via an anesthetic mask at a concentration of 2% (v/v) with an air flow rate of 0.5 L/min. After the dorsal aspect of the scalp was shaved, the skull was exposed by a midline incision. As previously described (Xia et al. 2016; Jin et al. 2018), sixteen holes were drilled on the skull, at defined locations on the stereotaxic reference system (Shaw et al. 2001). Stainless steel screws (diameter = 1 mm) were inserted into the holes, without penetrating the underlying dura mater. Fourteen screws acted as active electrodes, and their coordinates in respect to the bregma were as follows (in mm; positive X and Y axis values indicate right and anterior locations, respectively). FL1: X = − 1.5, Y = 4.5; FR1: X = 1.5, Y = 4.5; FL2: X = − 1.5, Y = 1.5; FR2: X = 1.5, Y = 1.5; LFL: X = − 4.5, Y = 0; RFR: X = 4.5, Y = 0; PL1: X = − 1.5, Y = − 1.5; PR1: X = 1.5, Y = − 1.5; LPL: X = − 4.5, Y = − 3; RPR: X = 4.5, Y = − 3; PL2: X = − 1.5, Y = − 4.5; PR2: X = 1.5, Y = − 4.5; OL: X = − 3, Y = − 7; OR: X = 3, Y = − 7. The reference and ground electrodes were placed on the midline, 2 mm and 4 mm caudally to the Lambda (Hu et al. 2015), respectively. The wires from each electrode were held together with a connector module fixed on the scalp with dental cement. To prevent post-surgical infections, rats were injected with penicillin (60,000 U, i.p.) immediately after the surgery. Following the surgery, rats were kept in individual cages for at least 7 days before the collection of ECoG data.

Experimental Paradigm and ECoG Recording

During the ECoG data collection, rats were placed into a plastic chamber (length × width × height: 30 × 30 × 30 cm^3), within which they could move freely. ECoG cables were connected to the wireless amplifier (Multi Channel System MCS Gmbh, Germany). Before the data collection, rats were placed in the same plastic cage for at least four slots of 1 h each, to familiarize them with the recording environment. ECoG data were simultaneously collected with rats' behaviors (movements, eyes open or closed) that were recorded using video for 45 min (Fig. 1, bottom panel). Such ECoG recording procedure was repeated three times in three days for each rat.

ECoG Preprocessing and Power Spectra Analyses

According to the recorded video, we discarded ECoG data when rats were moving and the sleeping-like ECoG data (Yuan et al. 2017; Luppi et al. 2017; Sánchez-López et al. 2018). Specifically, the sleeping-like data were identified when the rats huddled up and relaxed onto the ground (Sánchez-López et al. 2018). Representative examples showing rats in eyes-closed, eyes-open, and sleeping-like conditions are provided in Supplementary videos 1, 2, and 3, respectively. To demonstrate that the sleeping-like ECoG data were correctly identified from the eyes-closed condition, we adopted the EEG index (iEEG: delta power/(sigma power * theta power)), which is widely used to monitor the

sleeping-like behavior (Luppi et al. 2017). Please note that delta, sigma, and theta powers were estimated from the EEG data at 1–4 Hz, 11–15 Hz, and 4–7 Hz, respectively. When rats were in waking state, iEEG would be lower than that when rats were in non-rapid eye movement sleeping state (Luppi et al. 2017). As demonstrated in Supplementary Fig. 1, iEEG was significantly larger in the sleeping-like condition than in the eyes-closed condition (eyes-closed: 0.33 ± 0.012; sleeping-like: 0.38 ± 0.012; $P = 0.006$, independent-sample t test), which suggested the correctness of our condition classification for rats. In addition, the ECoG data with uncertainty in the condition classification were discarded from the following analyses. The remaining ECoG data were segmented based on the video information, assigned to eyes-closed or eyes-open conditions accordingly (Fig. 1, bottom panel). Other preprocessing procedures and power spectra analyses were identical to Experiment 1.

Results

Experiment 1: Human EEG

The grand average human EEG spectra and the scalp topographies of spectral amplitudes within the five typical frequency bands (delta, theta, alpha, beta, and gamma) for eyes-closed and eyes-open conditions, as well as their differences, were showed in Fig. 2. Human EEG spectra in both eyes-closed and eyes-open conditions showed a dominant spectral peak around 10 Hz, whose scalp topography was maximal over the occipital region. The differential EEG spectra between eyes-closed and eyes-open conditions showed that (1) spectral amplitudes were larger in the eyes-closed condition than in the eyes-open condition at lower frequencies (e.g., alpha and beta bands); and (2) spectral amplitudes were smaller in the eyes-closed condition than in the eyes-open condition at higher frequencies (e.g., gamma band).

As revealed by statistical analyses, there were three distinct frequency intervals exhibiting significant differences between eyes-closed and eyes-open conditions (Fig. 3, top panels): (1) at 8–12 Hz for almost all regions; (2) at 18–22 Hz for frontal and occipital regions; and (3) at 30–100 Hz for frontal regions (Fig. 3, middle panel). Specifically, relative to the eyes-open condition, EEG spectra in the eyes-closed condition showed a greater amplitude (1) at parietal-occipital region (P7, P5, P3, Pz, P2, P4, P6, P8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2) within 8–12 Hz (eyes-closed: 1.4 ± 0.1 μV; eyes-open: 0.75 ± 0.06 μV; $P < 0.001$), and (2) at occipital region (PO7, PO3, POz, PO4, PO8, O1, Oz, O2) within 18–22 Hz (eyes-closed: 0.48 ± 0.02 μV; eyes-open: 0.39 ± 0.02 μV; $P = 0.003$), but exhibited a smaller amplitude (1) at frontal region (AF7, AF3, F5, F3, FP2, AF4, AF8, F4, F6, F8, FT8, FT10) within 18–22 Hz (eyes-closed: 0.26 ± 0.01 μV; eyes-open: 0.33 ± 0.02 μV; $P = 0.003$), and (2) at frontal region (FPz, FP2, AF7, AF3, AFz, AF4, AF8) within 30–100 Hz (eyes-closed: 0.13 ± 0.01 μV; eyes-open: 0.19 ± 0.01 μV; $P < 0.001$).

The slopes of the linear fit (1/f characteristic) of human EEG spectra in eyes-closed and eyes-open conditions were summarized in the left part of Fig. 4. For both conditions, scalp topographies for the slope of the linear fit displayed a negative maximum at parietal-occipital regions. Statistical comparisons revealed that the absolute value of the slope (α value) was significantly larger in the eyes-closed condition than in the eyes-open condition at parietal-occipital (eyes-closed: 1.2 ± 0.04; eyes-open: 1.06 ± 0.03; $P = 0.007$) and frontal (eyes-closed: 1.15 ± 0.04; eyes-open: 0.96 ± 0.04; $P < 0.001$) regions.

As showed in Fig. 5, significant differences of WPLI values between eyes-closed and eyes-open conditions were observed in theta, alpha, and beta frequency bands. Compared to the eyes-closed condition, WPLI values at alpha frequency band were significantly smaller in the eyes-open condition for almost all pairs of electrodes. In addition, WPLI values at theta and beta frequency bands were significantly smaller in the eyes-open condition than in the eyes-closed condition for the pairs of electrodes, in which one electrode was situated at the occipital region (the position and the name of the indexed electrodes for humans are displayed in the top panel of Supplementary Fig. 2).

Experiment 2: Rat ECoG

The grand average rat ECoG spectra and the scalp topographies of spectral amplitudes within the five typical frequency bands (delta, theta, alpha, beta, and gamma) for eyes-closed and eyes-open conditions, as well as their differences, were showed in Fig. 6. Differences of spectral amplitudes between the two conditions revealed that spectral amplitudes in the eyes-closed condition were larger than eyes-open condition at lower frequencies, especially in the delta and alpha bands at the frontal-central region.

As revealed by statistical analyses, there were three distinct frequency intervals exhibiting significant differences between eyes-closed and eyes-open conditions (Fig. 7, top panels): (1) at 1–4 Hz for frontal and parietal regions; (2) at 8–12 Hz for frontal-central and parietal regions; (3) at 13–17 Hz for right frontal region (Fig. 7, middle panel). Specifically, relative to the eyes-open condition, ECoG spectra in the eyes-closed condition showed a greater amplitude (1) at central region (FL2, FR2, PL1, PR1) within 1–4 Hz (eyes-closed: 13.4 ± 0.70 μV; eyes-open: 9.6 ± 0.52 μV; $P < 0.001$); (2) at frontal-central region (FL1, FR1, FL2, FR2) within 8–12 Hz (eyes-closed: 5.9 ± 0.34 μV; eyes-open: 4.6 ± 0.23 μV; $P = 0.002$); and (3) at right frontal-central region (FR1, FL2, FR2, RFR, PR1) within 13–17 Hz

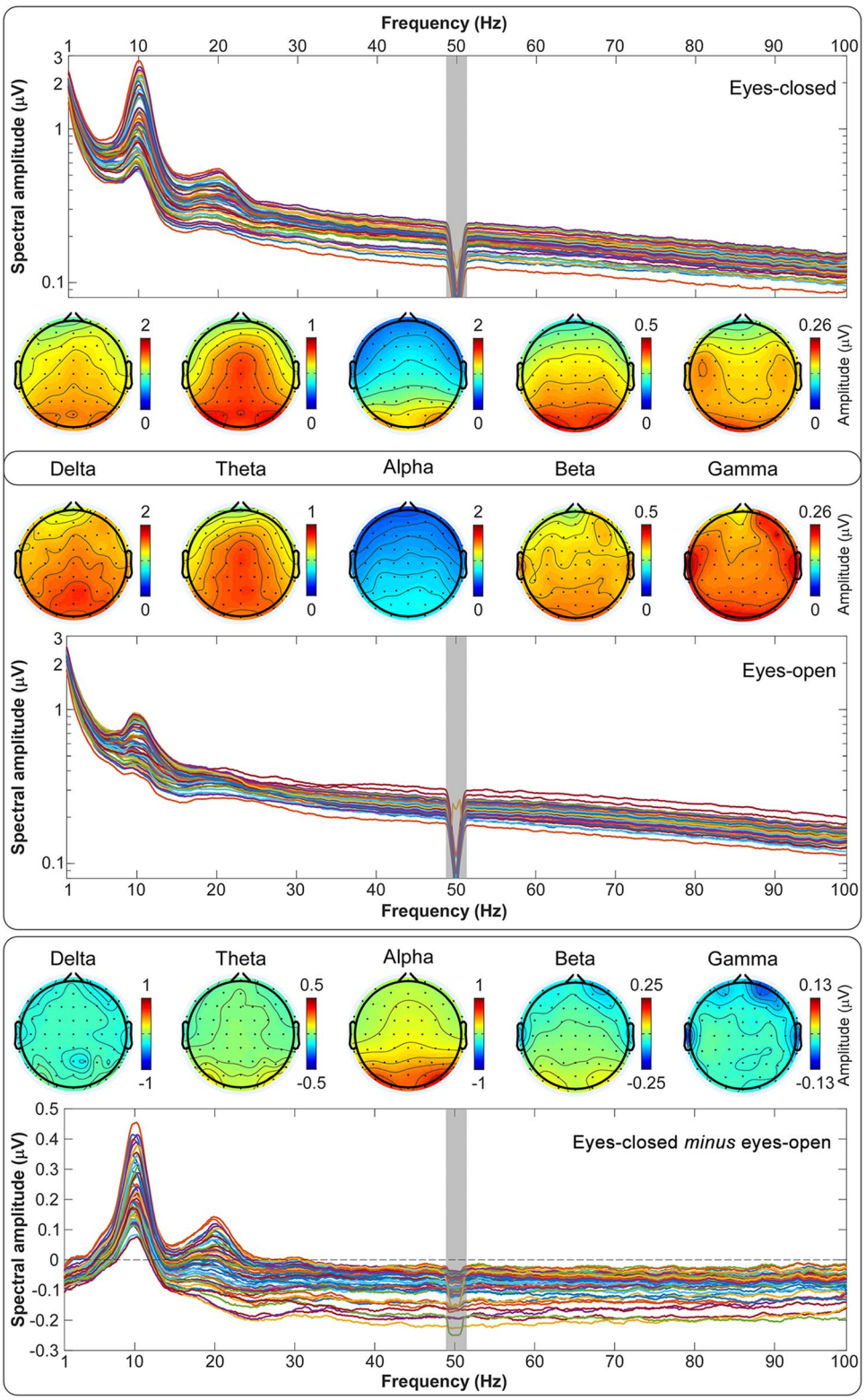


Fig. 2 Human EEG spectra and scalp topographies in eyes-closed and eyes-open conditions. EEG data were collected from 30 subjects. Signals from different electrodes are plotted in different colors and superimposed. Scalp topographies are displayed at five typical frequency bands, i.e., delta (1–4 Hz), theta (4–7 Hz), alpha (7–12 Hz), beta (12–30 Hz), and gamma (30–100 Hz) bands. While EEG spectra and scalp topographies in eyes-closed and eyes-open conditions are showed in the top panel, their differences are showed in the bottom panel. Please note that spectral amplitudes were higher in the eyes-closed condition than in the eyes-open condition at lower frequencies (e.g., alpha and lower beta bands) in the occipital region. In contrast, spectral amplitudes were lower in the eyes-closed condition than in the eyes-open condition at higher frequencies (e.g., higher beta and gamma bands) in the frontal region (Color figure online)

(eyes-closed: 3.9 ± 0.14 μV; eyes-open: 3.2 ± 0.13 μV; $P = 0.003$).

The slopes of the linear fit (1/f characteristic) of rat ECoG spectra in eyes-closed and eyes-open conditions were summarized in the right part of Fig. 4. For both conditions, scalp topographies for the slope of the linear fit displayed a negative maximum at parietal-occipital regions. Statistical comparisons revealed that the absolute

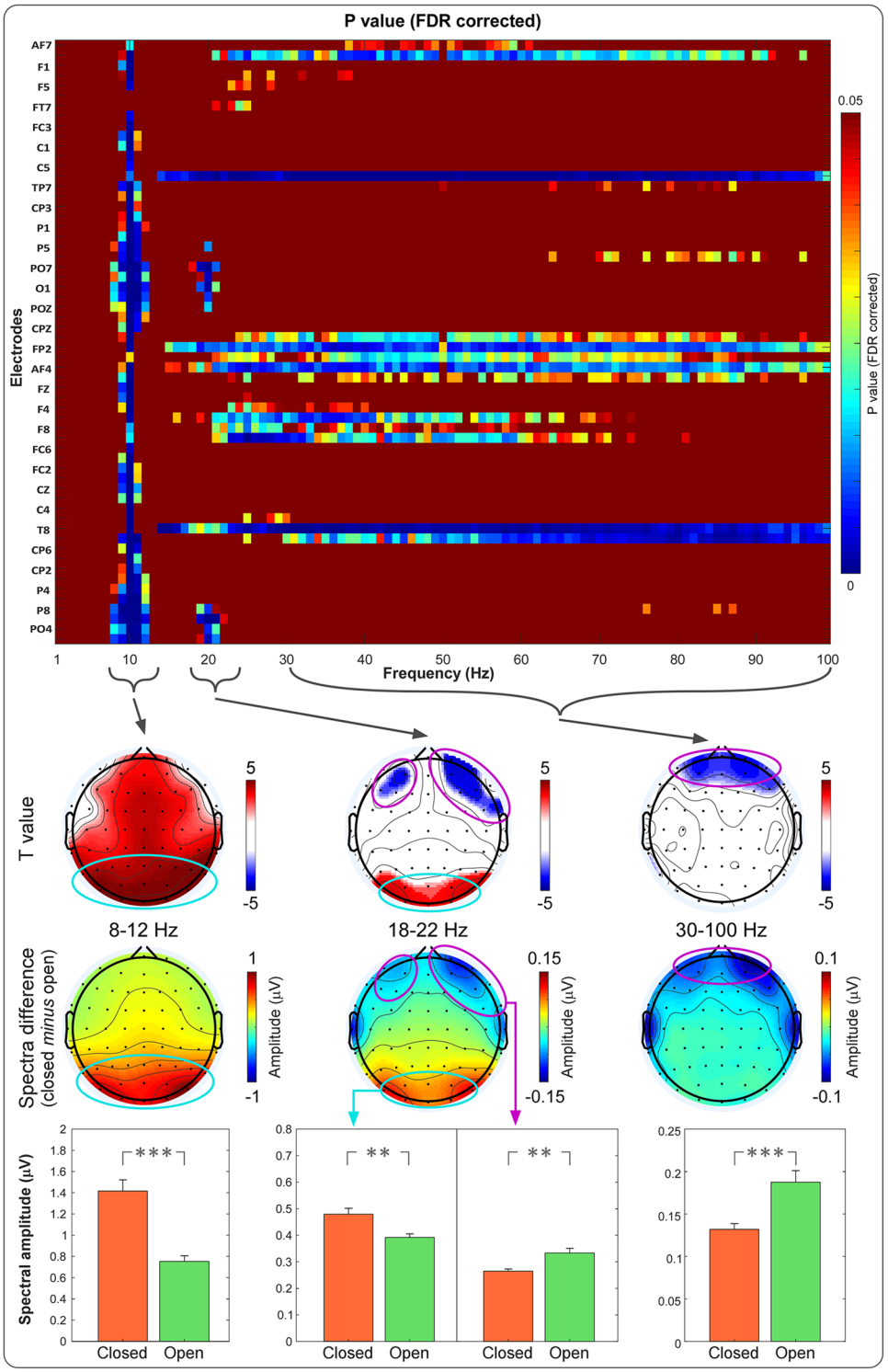


Fig. 3 Statistical comparison of human EEG spectra between eyes-closed and eyes-open conditions. The frequency-electrode map displaying the statistical P values (FDR corrected) exhibited distinct patterns of significance at three different frequencies (i.e., 8–12 Hz, 18–22 Hz, and 30–100 Hz; top panel). Scalp topographies of statistical T values (significant regions are color-coded) and spectral differences (eyes-closed minus eyes-open) at these frequencies (middle panel) showed that (1) spectral amplitudes were significantly higher in the eyes-closed condition than in the eyes-open condition at 8–12 Hz and 18–22 Hz in the occipital region, and (2) spectral amplitudes were significantly lower in the eyes-closed condition than in the eyes-open condition at 18–22 Hz and 30–100 Hz in the frontal region. To better visualization the significant difference, we summarized and displayed the spectral amplitudes at the identified frequencies in their respectively significant regions (bottom panel) (Color figure online)

value of the slope (α value) was significantly larger in the eyes-closed condition than in the eyes-open condition at parietal-occipital (eyes-closed: 1.96 ± 0.02; eyes-open: 1.79 ± 0.03; $P < 0.001$) and frontal (eyes-closed: 1.86 ± 0.02; eyes-open: 1.66 ± 0.03; $P < 0.001$) regions.

As showed in Fig. 8, significant differences of WPLI values between eyes-closed and eyes-open conditions were observed in delta and beta frequency bands. Compared to the eyes-closed condition, WPLI values were significantly smaller in the eyes-open condition at delta frequency band

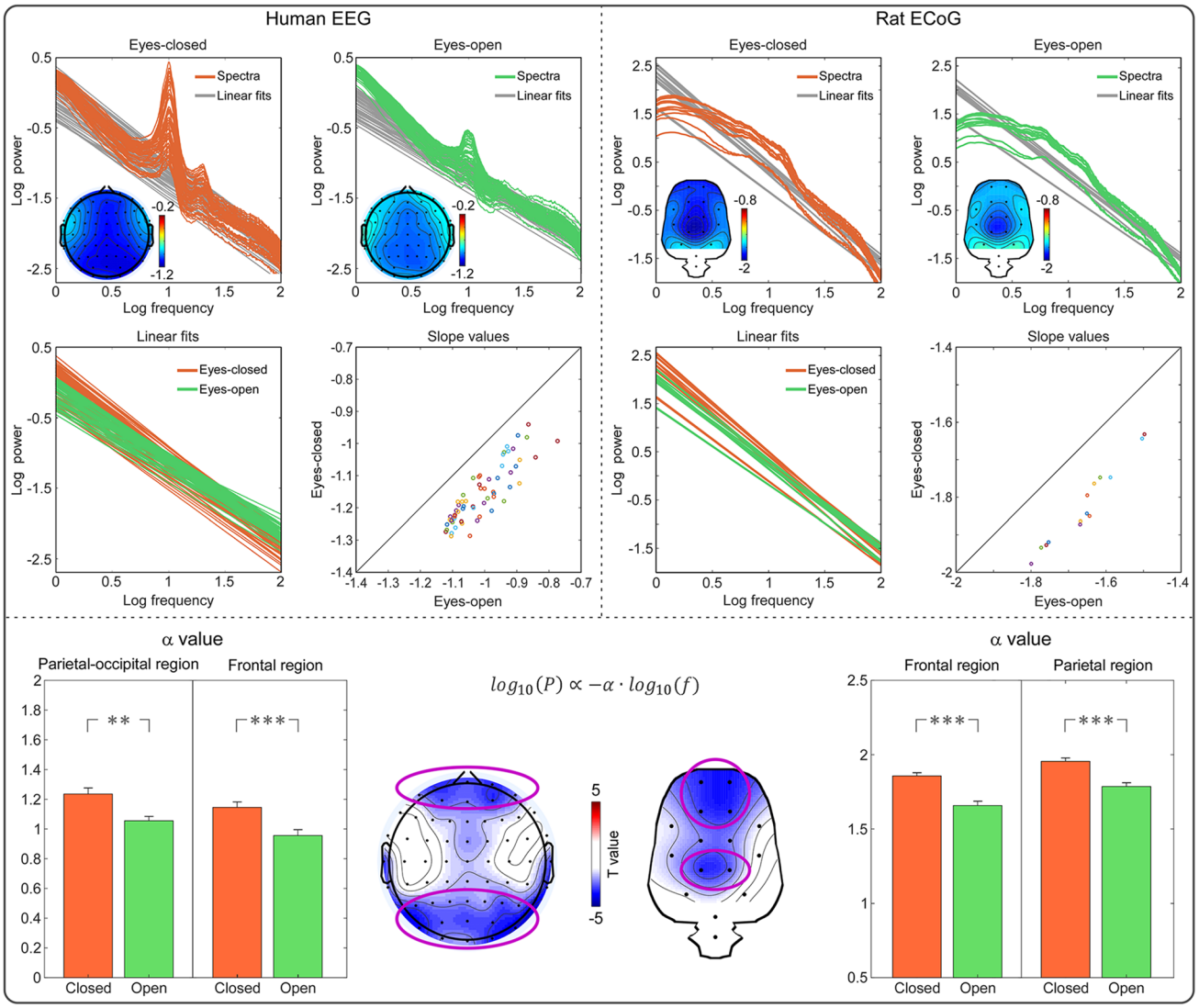


Fig. 4 The 1/f characteristic of human EEG and rat ECoG spectra in eyes-closed and eyes-open conditions. EEG spectra (displayed in log frequency by log power strategies; marked in orange and green in eyes-closed and eyes-open conditions respectively) and their linear fits (marked in grey for both conditions) of all electrodes are showed in the top panel. Note that scalp topographies of the slope of the linear fit (i.e., the 1/f characteristic) displayed a negative maximum at parietal–occipital regions for both conditions and both species. To better visualization the difference of the slope between eyes-closed and eyes-open conditions, we displayed the linear fits (middle panel: first and third columns) and their slope values (middle panel: second and fourth columns) of all electrodes in the same plots. Statistical comparisons revealed that absolute value of the slope (i.e., the α value) was significantly larger in the eyes-closed condition than in the eyes-open condition at two distinct regions (parietal–occipital and frontal regions) for both species (T values in the significant regions are color-coded; bottom panel). To better visualization the significant difference, we summarized the slope values in their respectively significant regions for both species (bottom panel) (Color figure online)

for some pairs of electrodes around the central region (e.g., PL1 and FL2, PL1 and LPL). In addition, WPLI values were significantly larger in the eyes-open condition than in the eyes-closed condition at beta frequency band for the pairs of electrodes, in which one electrode was situated at the parieto-occipital region (e.g., PL2) (The position and the name of the indexed electrodes for rats are displayed in the bottom panel of Supplementary Fig. 2).

Discussion

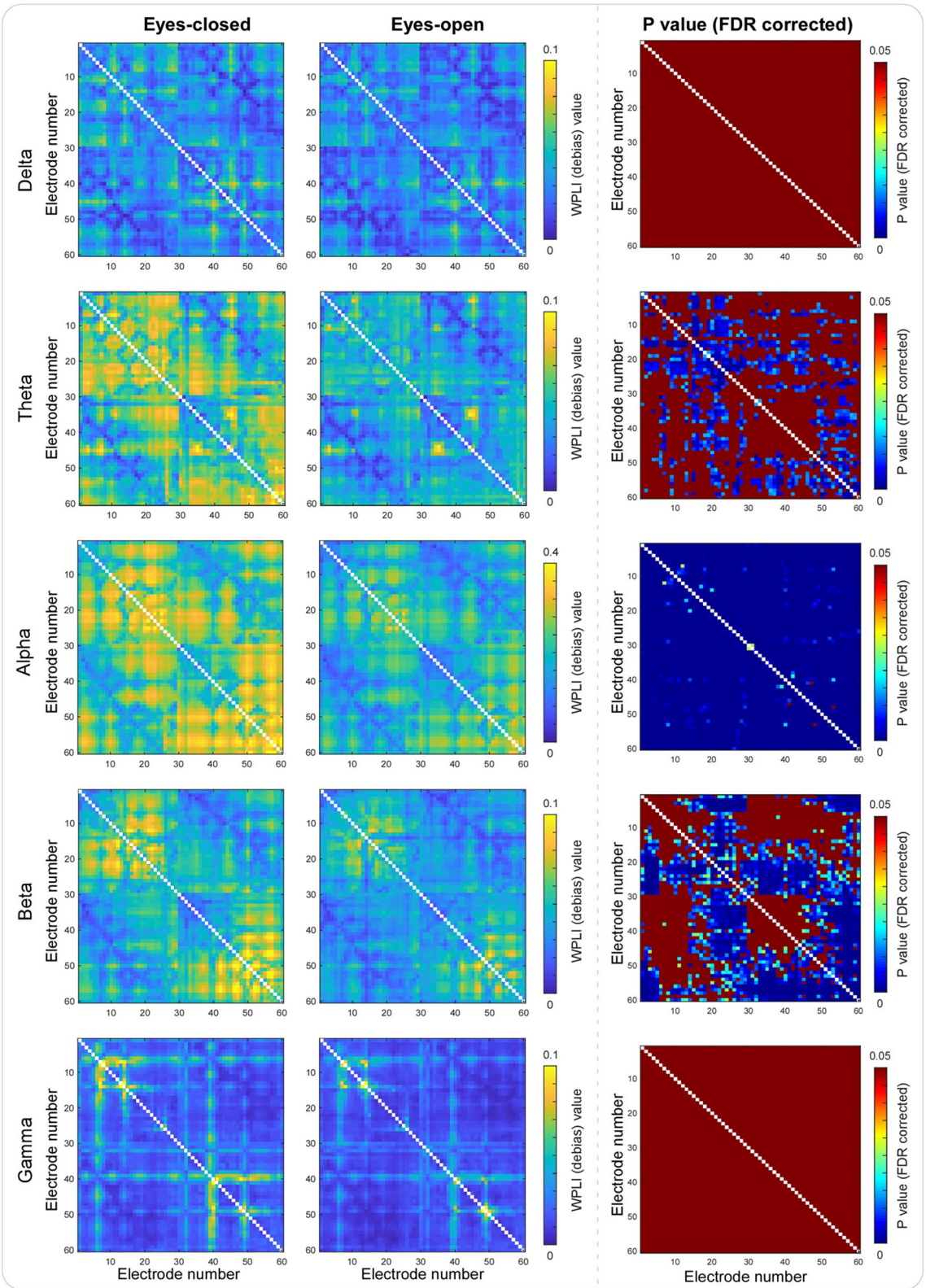
In the present study, we have established the recording paradigm for collecting resting state EEG activities during eyes-closed and eyes-open conditions from rats. Comparing EEG activities between the two conditions for humans and rats, we obtained three main findings. First, power

spectra analyses revealed that compared to the eyes-open condition, human EEG spectral amplitudes in the eyes-closed condition were significantly higher at 8–12 Hz and 18–22 Hz in the occipital region, but significantly lower at 18–22 Hz and 30–100 Hz in the frontal region (Fig. 3). Second, rat ECoG spectral amplitudes were significantly higher in the eyes-closed condition than in the eyes-open condition at 1–4 Hz, 8–12 Hz, and 13–17 Hz in the frontal-central region (Fig. 7). Third, the 1/f-like power spectrum scaling analyses showed that the absolute slope values of the linear fits were significantly higher in the eyes-closed condition than in the eyes-open condition at parietal-occipital and frontal regions for both species (Fig. 4). These results illustrated the cross-species similarity and difference in resting state EEG during eyes-closed and eyes-open conditions, which provided the neurophysiological basis for future translational studies from animal findings to human psychophysiology.

Even both human EEG and rat ECoG spectral amplitudes at low frequencies were significantly higher in the eyes-closed condition than in the eyes-open condition, cross-species differences of such comparison existed: enhanced amplitudes were observed at 8–22 Hz in the occipital region for humans (Fig. 3), but at 1–17 Hz in the frontal-central region for rats (Fig. 7). In line with previous human studies, we observed that occipital alpha oscillations were the dominant component in resting state EEG in the eyes-closed condition, and the amplitude of this component was greatly decreased in the eyes-open condition (Lopes and Storm 1977; Bazanova 2012). This decrease, or named desynchronization, of occipital alpha oscillations has been functionally linked to the activation of the visual system (Volavka et al. 1967; Härdle et al. 1984), and the functional regulation of mesencephalic-medial thalamic network (Goldman et al. 2002; Moosmann et al. 2003; Feige et al. 2005). In contrast, the decrease of alpha oscillations due to eyes-close was not observed in the occipital region for rats, but in the frontal-central region, underlying which is dominated by the primary somatosensory cortices (e.g., Barrel cortex of the facial whiskers). This cross-species difference of brain regions could be related to the different sensory sensitivities between humans and rats: (1) mainly relying on visual information to detect the changes of the external environment, humans showed large desynchronization of occipital alpha oscillations from the eyes-closed condition to the eyes-open condition (Gale et al. 1971; Feige et al. 2005; Diamant 2008; Schaeffel 2009); (2) Instead of vision (Burn 2008), rats largely rely on the tactile sensation (e.g., the facial whiskers) (Petersen 2007) to explore environmental information, thus exhibiting significant desynchronization of alpha oscillations at the frontal-central region from the eyes-closed condition to the eyes-open condition. This reasoning is supported by the fact that individuals were normally in a relaxed state with less interaction with the environment in the eyes-closed condition, while their arousal level was increased to detect the changes of the environment using their sensory systems (not limited to the visual system) in the eyes-open condition (Boĭtsova and Dan'ko 2010). Please note that our statement was partly based on the inference of EEG sources according to the observed scalp topographies. To provide evidence to support this statement, we have estimated the current source density (CSD) for rat ECoG data (please refer to Supplementary Fig. 3 for details), since CSD topographies could be used to identify the neuronal generator patterns contributing to the scalp-recorded EEG signal (Tenke and Kayser 2012). We observed that the CSD topography difference between eyes-closed and eyes-open conditions was maximal at central and frontal regions (especially for alpha oscillations). The observation is similar to the findings in Fig. 6, which could serve as additional evidence to support our statement. Notably, we are fully aware that the inference of EEG sources based the scalp topography without performing the source estimation is problematic. In addition, the cross-species difference was observed in frequencies showing significant changes of spectral amplitudes from the eyes-closed condition to the eyes-open condition: 8–22 Hz for humans and 1–17 Hz for rats, and such difference could be arising from the different size of the brain between humans and rats (Buzsáki et al. 2013; Klimesch 2013; Peng et al. 2018).

Besides, cross-species difference in EEG power spectra was also observed in the amplitude modulation of gamma oscillations: compared to the eyes-closed condition, increase, or named synchronization, of gamma oscillations (30–100 Hz) in the frontal region was observed in the eyes-open condition for humans (Fig. 3), but not for rats (Fig. 7). This observation is consistent with previous human studies (Wyckoff et al. 2015; Miraglia et al. 2016; Schoenberg et al. 2018), and has been functionally linked to the binding of perception in the human brain (Chen et al. 2008). Indeed, we observed a trend of synchronization of gamma oscillations in the eyes-open condition relative to the eyes-closed condition in rats (Fig. 6). However, such synchronization was not statistically significant, which could be caused by the fact that the sample size in experiment 2 (rat ECoG experiment) is too small to ensure a high signal-to-noise ratio for gamma oscillations.

Please note that the amplitude of EEG oscillations (e.g., alpha oscillations) varies with time elapsed from the beginning of the data collection (Lim et al. 2013; Hu et al. 2014), and it is possible that this time-varying effect could influence our results on the comparison of resting state EEG activities between the eyes-closed condition and the eyes-open condition. To clarify this issue, we assessed the relationship between the amplitude of alpha oscillations and time, by dividing the EEG data into three sections,



i.e., early, middle, and late sections. For both species, the amplitudes of alpha oscillations between sections were compared using a one-way repeated-measures ANOVA for eyes-closed and eyes-open conditions, and their difference, respectively. As demonstrated in Supplementary Figs. 4 and 5, no between-section difference was observed

◂**Fig. 5** Human EEG connectivity (WPLI values) in eyes-closed and eye-open conditions. The WPLI values (debias mode), calculated between pairs of electrodes in eyes-closed and eyes-open conditions at five typical frequency bands, i.e., delta (1–4 Hz), theta (4–7 Hz), alpha (7–12 Hz), beta (12–30 Hz), and gamma (30–100 Hz) bands, are showed in the left panel. Statistical comparisons of WPLI values between eyes-closed and eyes-open conditions for each pair of electrodes and each frequency band are showed in the right panel (P values are FDR corrected). The WPLI values were significantly smaller in the eyes-open condition than in the eyes-closed condition for almost all pairs of electrodes at alpha frequency band (the third row in the right panel). In addition, the WPLI values were significantly smaller in the eyes-open condition than in the eyes-closed condition at theta and beta frequency bands for the pairs of electrodes, in which one electrode was situated at the occipital region (the second and fourth rows in the right panel)

in the amplitudes of alpha oscillations for all comparisons and both species. This result indicated that the comparison of resting state EEG activities between the eyes-closed condition and the eyes-open condition would be robust to the time-varying effect of EEG oscillations.

Importantly, the 1/f-like scaling (i.e., the slope value of the linear fit) of resting state EEG power spectra was significantly higher in the eyes-closed condition than in the eyes-open condition at parietal–occipital and frontal regions for both humans and rats. This result is in line with the observation that compared to the eyes-open condition, spectral amplitudes were increased at low frequencies but decreased at high frequencies in the eyes-closed condition (Fig. 4). Theoretically, the smaller the absolute value of the slope (e.g., 0), the more stochastic the EEG signal (i.e., the signal is not autocorrelated and the power spectrum of the signal is flat) (Pritchard 1992). In contrast, the larger the absolute value of the slope (e.g., 2), the more periodic the EEG signal (i.e., the signal is highly autocorrelated). In our study, we observed that the α values (i.e., the absolute values of the slopes) of the linear fits were larger than 0 and smaller than 2. This observation is consistent with previous studies (Pritchard 1992; Linkenkaer-Hansen et al. 2001; Miller et al. 2009), indicating that EEG signals of both humans and rats manifest 1/f-like power spectrum scaling. In addition, the α values of the linear fits were significantly larger in the eyes-closed condition than the eyes-open condition for both species. This finding indicated that EEG signals in the eyes-closed condition were more autocorrelated (i.e., the system is more deterministic) than the eyes-open condition (Pritchard 1992). In contrast, the system turned to be more stochastic in the eyes-open condition (Lei et al. 2013), which would be important to ensure that the brain is in a vigilant state to respond to any changes in the environment (Jung et al. 1997; Falahpour et al. 2018). It is very interesting that the difference of the 1/f-like scaling between the eyes-closed condition and the eyes-open condition was commonly observed at parietal–occipital and frontal regions for both humans and rats, and the functional meaning of this cross-species similarity needs further investigation.

However, the 1/f characteristic of human EEG and rat ECoG could not be directly comparable since the EEG recorded from the scalp does not have the same power spectrum as the ECoG recorded directly from the surface of the cortex (Buzsáki et al. 2012), and the high-frequency part of cortex ECoG has more power than scalp EEG (Graimann et al. 2002). For this reason, we did not directly compare the 1/f characteristic between humans and rats, but assessed the difference of the 1/f characteristic between the eyes-closed condition and the eyes-open condition for both humans and rats.

To sum up, the comparison of resting state EEG activities between the eyes-closed condition and the eyes-open condition yielded distinct findings when different features (i.e., power spectra and 1/f-like scaling) were used to assess the cross-species similarity and difference. The changes of spectral amplitudes between the eyes-closed condition and the eyes-open condition were quite different between humans and rats: significant changes were observed at different frequencies and brain regions. This observation indicated that power spectra would be sensitive to detect the cross-species difference in resting state EEG activities. In contrast, the changes of the 1/f characteristic between the eyes-closed condition and the eyes-open condition were quite similar between humans and rats: significant differences of similar spatial pattern were observed. This observation suggested that the properties of scale-free dynamics might be phylogenetically conserved, at least between humans and rats, and that the 1/f characteristic would be robust across species to assess the modulation of brain states from resting state EEG activities. Clearly, our findings indicated that cautions should be made when performing translational studies from animal EEG findings to human psychophysiology. The validity of such translations critically relies on a well-established experimental paradigm and a carefully-examined signal characteristic to bridge the gaps across different species.

Notably, there are several limitations of our study. First, there is a clear anatomical difference between humans and rats. This difference could result in different spatial configuration of the detected features, thus influencing our results on the across-species comparison of resting state EEG activities. In addition, the anatomical difference, along with the differences in density, location, and montage of the mounted electrodes, could lead to distinct connectivity patterns between humans and rats (Figs. 5, 8). Second, during the experiment, humans were instructed to keep voluntarily

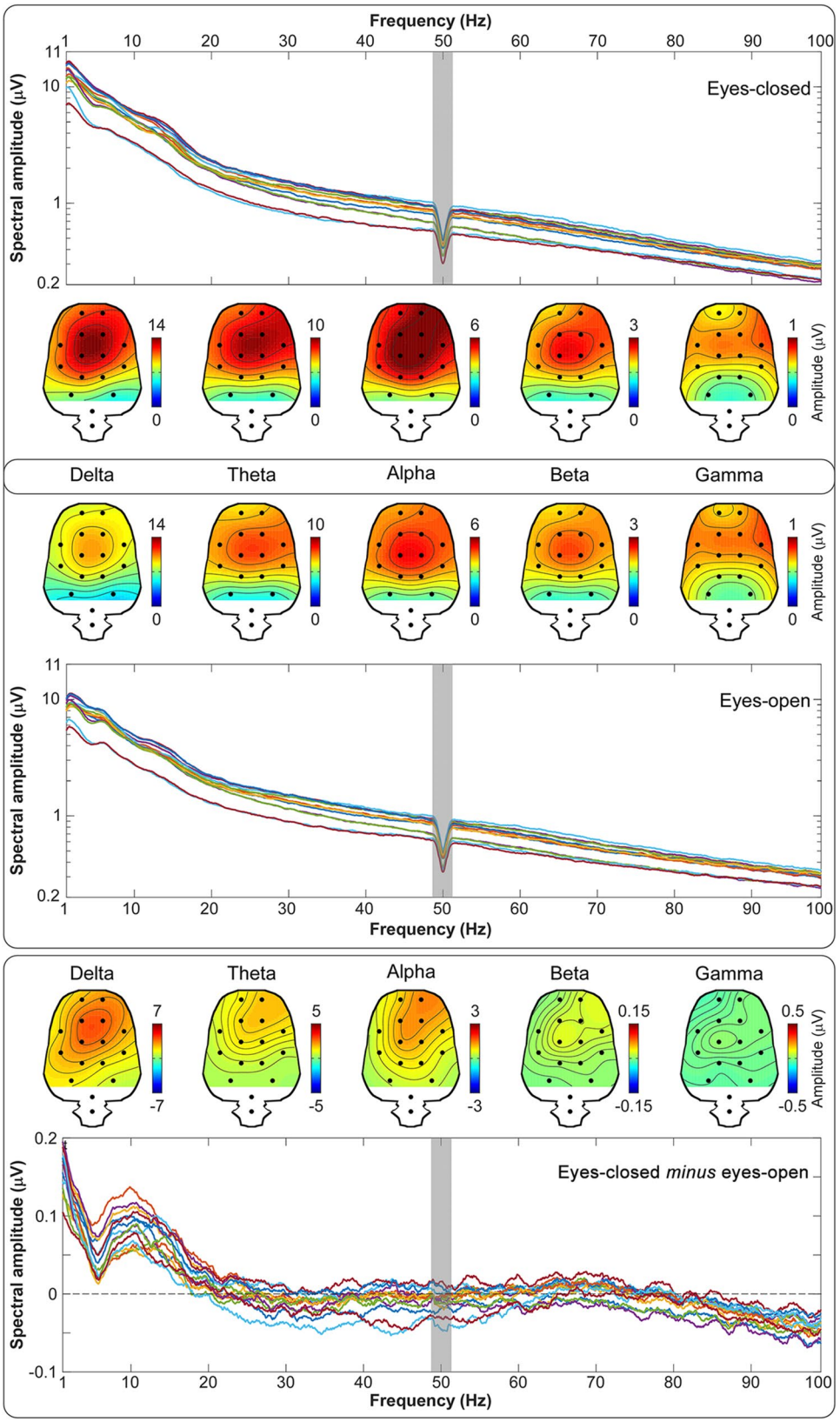


Fig. 6 Rat ECoG spectra and scalp topographies in eyes-closed and eyes-open conditions. ECoG data were collected from 8 subjects. Signals from different electrodes are plotted in different colors and superimposed. Scalp topographies are displayed at five typical frequency bands, i.e., delta (1–4 Hz), theta (4–7 Hz), alpha (7–12 Hz), beta (12–30 Hz), and gamma (30–100 Hz) bands. While ECoG spectra and scalp topographies in eyes-closed and eyes-open conditions are showed in the top panel, their differences are showed in the bottom panel. Please note that spectral amplitudes were higher in the eyes-closed condition than in the eyes-open condition at lower frequencies (e.g., delta band in the central region and alpha band in the frontal region). Spectral amplitudes were slightly lower in the eyes-closed condition than in the eyes-open condition at higher gamma frequencies (Color figure online)

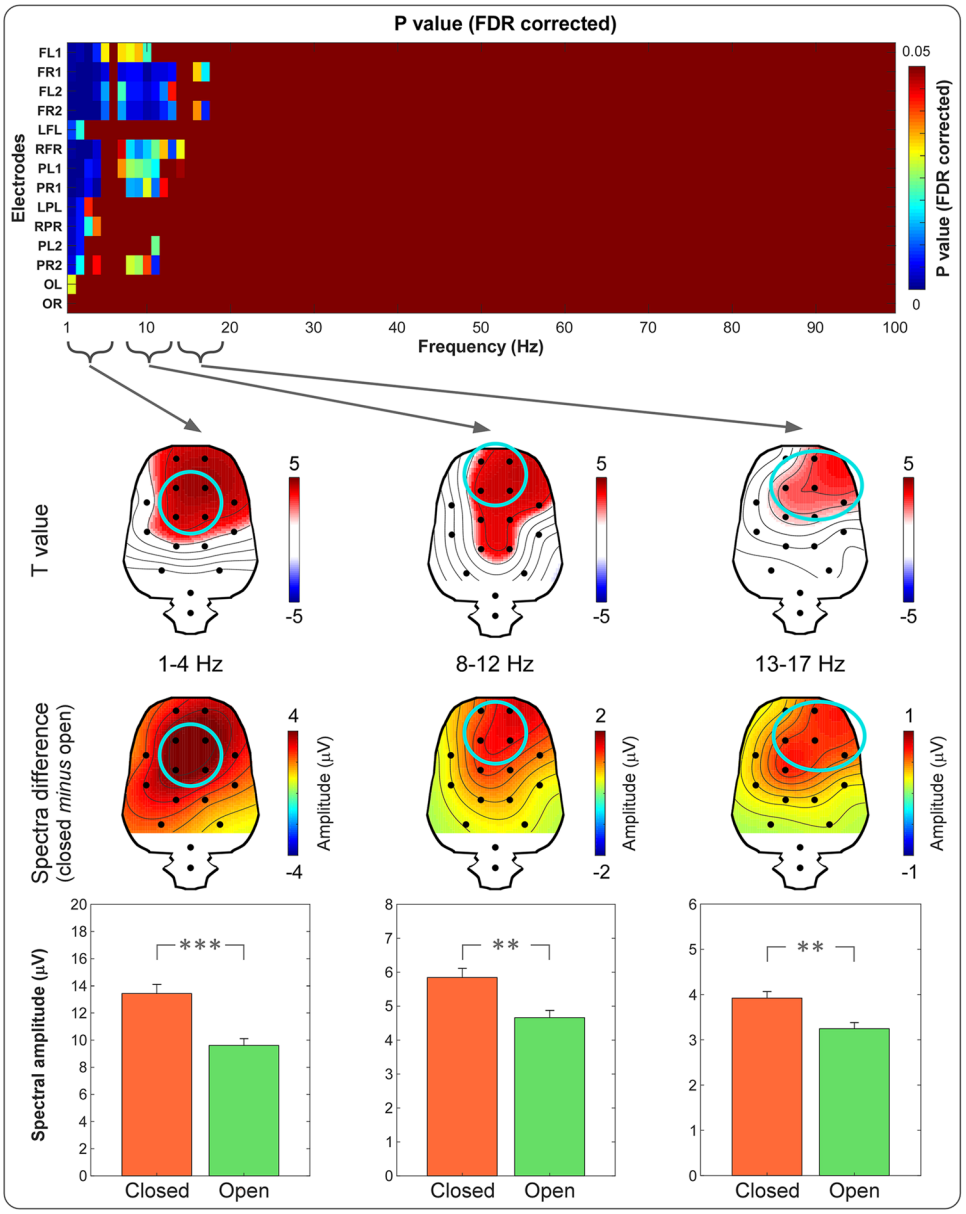
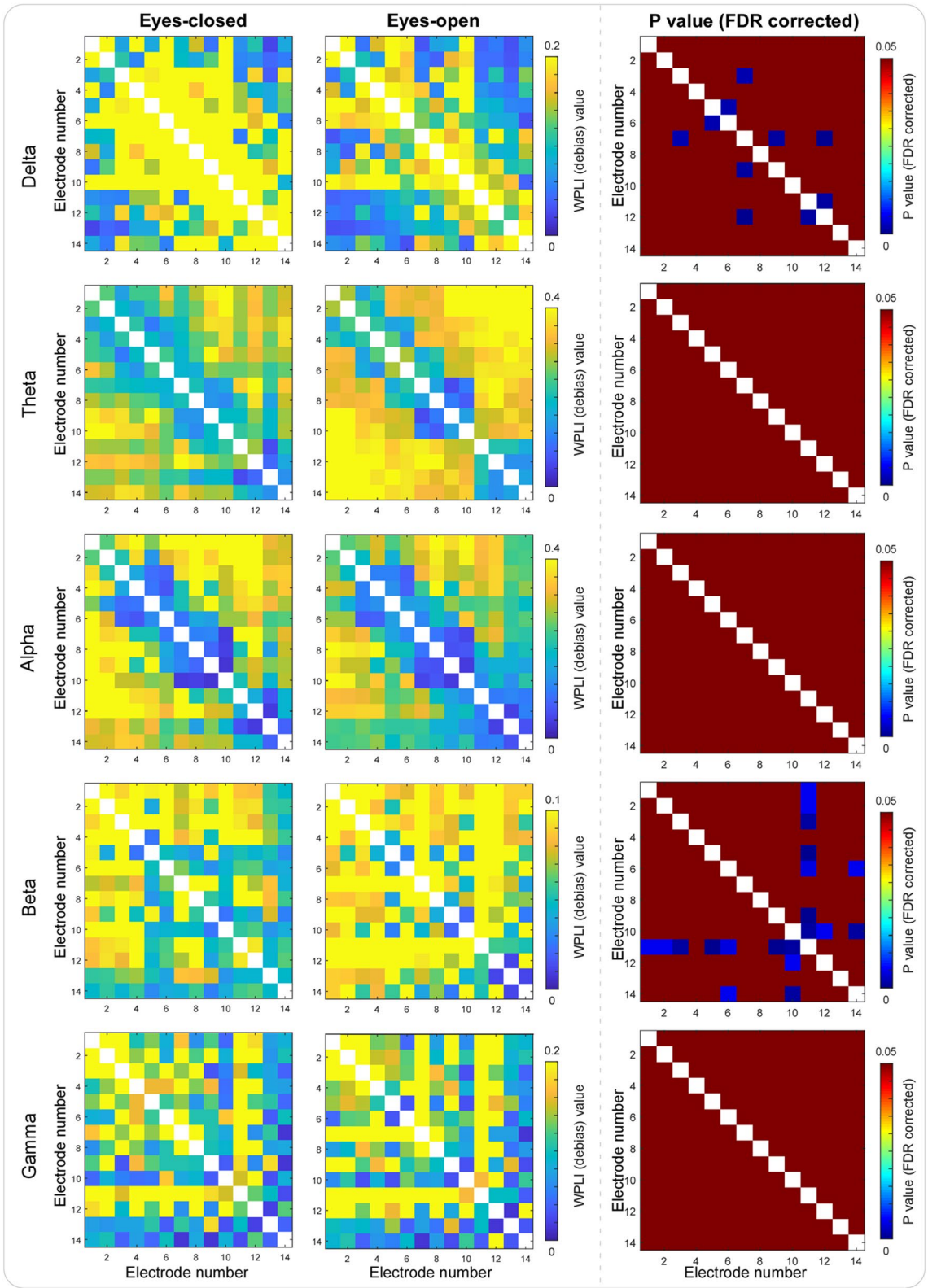


Fig. 7 Statistical comparison of rat ECoG spectra between eyes-closed and eyes-open conditions. The frequency-electrode map displaying the statistical P values (FDR corrected) exhibited distinct patterns of significance at three different frequencies (i.e., 1–4 Hz, 8–12 Hz, and 13–17 Hz; top panel). Scalp topographies of statistical T values (significant regions are color-coded) and spectral differences (eyes-closed minus eyes-open) at these frequencies (middle panel) showed that spectral amplitudes were significantly higher in the eyes-closed condition than in the eyes-open condition at 1–4 Hz, 8–12 Hz, and 13–17 Hz in the frontal–central regions. To better visualization the significant difference, we summarized and displayed the spectral amplitudes at the identified frequencies in their respectively significant regions (bottom panel) (Color figure online)

their eyes closed or open, while rats were keeping their eyes closed or open spontaneously. This difference would result in different patterns of the recorded data, i.e., continuous for human EEG data and fragmented for rat ECoG data, which would also influence our statistical results for the across-species comparisons. Third, the choice of EEG reference is one of the most critical but unsolved issues in EEG studies, and impacts many EEG measures, including the amplitude, power spectrum, and temporal structure of EEG recordings (Yao et al. 2005). Therefore, the choice of EEG reference would affect the scalp topographies of power spectra both in humans and rats, thus impacting our findings related to the comparisons between species. To provide an intuitive illustration of such impact, we provided the results of power spectra using the average reference (Supplementary Figs. 6 and 7). While the scalp topographies in eyes-closed and eye-open conditions were influenced by re-referencing, their differences (eyes-closed minus eyes-open) were similarly distributed, regardless of the choice of reference. This similarity indicated that, even non-negligible, the choice of EEG reference does not impact much on our findings about


Eyes-closed
Eyes-open
P value (FDR corrected)
Delta
Theta
Alpha
Beta
Gamma
Electrode number
WPLI (debias) value
P value (FDR corrected)
0.2
0.4
0.1
0.05
0

◂**Fig. 8** Rat ECoG connectivity (WPLI values) in eyes-closed and eye-open conditions. The WPLI values (debias mode), calculated between pairs of electrodes in eyes-closed and eyes-open conditions at five typical frequency bands, i.e., delta (1–4 Hz), theta (4–7 Hz), alpha (7–12 Hz), beta (12–30 Hz), and gamma (30–100 Hz) bands, are showed in the left panel. Statistical comparisons of WPLI values between eyes-closed and eyes-open conditions for each pair of electrodes and each frequency band are showed in the right panel (P values are FDR corrected). The WPLI values were significantly smaller in the eyes-open condition than in the eyes-closed condition at delta frequency band for some pairs of electrodes around the central region (the first row in the right panel). In addition, WPLI values were significantly larger in the eyes-open condition than in the eyes-closed condition at beta frequency band for the pairs of electrodes, in which one electrode was situated at the parieto-occipital region (the fourth row in the right panel)

the differences of EEG spectral amplitudes between eyes-closed and eyes-open conditions.

Acknowledgements This work was supported by the National Natural Science Foundation of China (Nos. 31671141, 31822025), the Informatization Special Project of Chinese Academy of Sciences (No. XXH13506-306), and the Scientific Foundation project of Institute of Psychology, Chinese Academy of Sciences (No. Y6CX021008). The funders had no role in study design, data collection, data analysis, decision to publish, or preparation of the manuscript. The authors have declared that no competing interests exist.

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