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Enhanced brain small-worldness after sleep deprivation: a compensatory effect

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SUMMARY

Sleep deprivation has a variable impact on extrinsic activities during multiple cognitive tasks, especially on mood and emotion processing. There is also a trait-like individual vulnerability or compensatory effect in cognition. Previous studies have elucidated the altered functional connectivity after sleep deprivation. However, it remains unclear whether the small-world properties of resting-state network are sensitive to sleep deprivation. A small-world network is a type of graph that combines a high local connectivity as well as a few long-range connections, which ensures a higher information-processing efficiency at a low cost. The complex network of the brain can be described as a small-world network, in which a node is a brain region and an edge is present when there is a functional correlation between two nodes. Here, we investigated the topological properties of the human brain networks of 22 healthy subjects under sufficient sleep and sleep-deprived conditions. Specifically, small-worldness is utilized to quantify the small-world property, by comparing the clustering coefficient and path length of a given network to an equivalent random network with same degree distribution. After sufficient sleep, the brain networks showed the property of small-worldness. Compared with the resting state under sufficient sleep, the small-world property was significantly enhanced in the sleep deprivation condition, suggesting a possible compensatory adaptation of the human brain. Specifically, the altered measurements were correlated with the neuroticism of subjects, indicating that individuals with low-levels of neuroticism are more resilient to sleep deprivation.

INTRODUCTION

As a consequence of modern lifestyles and occupations, many people experience fewer hours of sleep or even sleep loss. Task-related functional magnetic resonance imaging (fMRI) has revealed that sleep deprivation (SD) could lead to a variety of cognitive deficits, including poorer attention, learning, memory and decision-making (Goel *et al.*, 2009; Gujar *et al.*, 2011; Tomasi *et al.*, 2009). Specifically, an increasing number of studies are highlighting the labile affective imbalance imposed by SD. SD leads to a more disturbed mood and an amplified subjective rating of emotional materials (Gujar *et al.*, 2011; Yoo *et al.*, 2007; Zohar *et al.*, 2005). Furthermore, the key role of the medial prefrontal cortex (mPFC)–amygdala circuit was well documented when reacting to affective stimuli after SD (Yoo *et al.*, 2007). However, the perplexing antidepressant benefit of SD on patients with depression intimated a latent individual difference in the underlying brain mechanism of the sleep–emotion interaction, especially with respect to the influence of neuroticism (Gillin *et al.*, 2001). Highly neurotic individuals are more susceptible to dysthymic disorders like depression (Jorm *et al.*, 2000), and are also more likely to have poor sleep habits.

It has been confirmed that several consistent neural networks exist in resting state, including the default mode network, fronto-parietal network, occipital network, sensorimotor network, etc., whose cooperation and competition support various cognitive tasks (Smith *et al.*, 2009). In addition, the spontaneous activities of resting-state networks are associated with specific personality traits, and their spatial patterns can be altered by psychiatric/neurological illnesses (Lei *et al.*, 2013). The reported regions disrupted by sleep disorders covered certain resting-state networks, especially the fronto-parietal network, occipital network and sensorimotor network (Goel *et al*., 2009). This suggests that some resting-state networks may be sensitive to SD and related to cognitive impairments (Tomasi *et al*., 2009). A recent investigation reported a decrease in functional connectivity among the default mode network and its anti-correlated network during a visual attention task (De Havas *et al*., 2012). More attention should therefore be paid to reveal the possible alteration of resting-state brain connectivity after SD.

Recently, wide application of graph theory has shown that brain activity can be investigated from the perspective of connectivity between brain regions. A small-world network is a type of graph that combines small average shortest path length and large clustering coefficient, which ensures a higher information-processing efficiency at a low cost (Bullmore and Sporns, 2009). A small-world network has the advantages of both extreme topologies: a high local connectivity (seen in a lattice network, not in a random network); as well as a few long-range connections that ensured global integration (seen in a random, not in a lattice network) (Fig. 1). Many empirical graphs, such as social networks, gene networks, the connectivity of the Internet and the collaboration graph of film actors, are well-modelled by small-world networks. Specifically, small-worldness is utilized to quantify the small-world property, by comparing clustering coefficient and path length of a given network with an equivalent random network with same degree distribution. Previous studies have revealed that brain network exhibits the property of small-world during normal wakefulness and sleep (Ferri *et al*., 2008). SD tends to result in a disrupted electroencephalogram (EEG) network (Koenis *et al*., 2013), but it remains to be explored how SD impacts upon the topological properties of brain functional networks based on fMRI signal.

In order to investigate the effect of SD on brain functional networks, we compared the topological properties of participants' brain networks in a resting state after normal sleep and a resting state after 34 h of SD. Based on the evidence of the cognitive deficits and neural disruptions, we expected that the brain functional network would be disturbed after SD, and the small-worldness would decrease. Taking into account the perplexing emotional reactivity after SD, we further explored the relationship between the altered topological brain network properties and individuals' emotional instability.

MATERIALS AND METHODS

Participants

Twenty-two healthy subjects whose ages ranged between 18 and 24 years (mean = 21.1 years, SD = 1.9, females = 9) participated in this study. All participants had no history of psychiatric or neurological illness as confirmed by a psychiatric clinical assessment. Subjects were excluded if they used any long-term medication. It was confirmed that they all had good sleep habits and normal sleep–wake rhythms with sleep durations of no <7 h each night in the past month according to the Pittsburgh Sleep Quality Index (Buysse *et al*., 1989). Written informed consent was obtained after participants were given a detailed explanation of the study protocol. The study was approved by the Ethics Committee of Southwest University, and all procedures involved were in accordance with the sixth revision of the Declaration of Helsinki.

Experiment procedure

Participants visited the lab three times. During their first visit, they were informed of the whole study procedure, and completed questionnaires about their mental health and sleep habits. They were asked to keep to their normal sleep habits until the end of the experiment, verified by a sleep dairy. Participants returned to the lab weekly for two fMRI scan sessions, one after normal sleep (NS session) and one

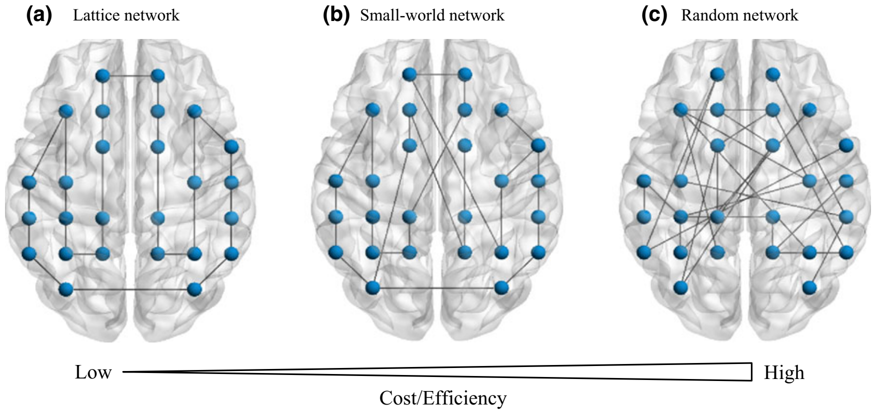

Figure 1. Structure of lattice, small-world and random networks. All networks have 26 nodes and 26 connections with nodes arranged on a slice of brain. (a) Lattice network, each node connects its two nearest-neighbours. (b) Small-world network. Most connections are among neighbouring nodes, but some connections go to distant nodes to create short-cuts across the network. (c) Random network. Small-world network combines the advantages of lattice network and random network, which ensures a high information efficiency procession at a low cost.

after SD (SD session). The order of the two sessions was counterbalanced.

On each experimental day, participants got up as usual. For the NS session, scans took place at 15:00 hours. During the whole experimental procedure, participants continued their usual daily activities on non-scanning days, but vigorous physical activities were not permitted 1 day before scanning. For the SD session, participants were monitored in the lab from 08:00 hours on Day 1 until scanning at 17:00 hours on Day 2 to ensure about 34 h of SD (exact data: mean = 33.54 h, SD = 2.5). Participants were permitted to engage in non-strenuous activities, including reading, Internet surfing and occasional short walking. Participants had to refrain from medications, alcohol and caffeine intake 3 days prior to each scanning.

Psychometric testing

Every participant completed a self-report questionnaire, the Eysenck Personality Questionnaire-Revised, Short Scale for Chinese (EPQ-RSC; Eysenck and Eysenck, 1994; Qian *et al*., 2000). The EPQ-RSC contains three dimensions: neuroticism; extraversion; and psychoticism. We were only concerned with subjects' neuroticism, which reflects an individual's emotional imbalance in daily life. The overall mean score of neuroticism was 11.28 (SD = 2.49). Before each scanning session, subject's sleepiness and mood were assessed by a questionnaire including the Stanford Sleepiness Scale, and the Positive and Negative Affect Scale.

Resting-state fMRI acquisition

A high-resolution T1-weighted structural volume was acquired using a 3T Siemens Trio scanner. The 3D spoiled gradient recalled sequence used the following parameters: thickness = 1 mm (no gap), TR = 8.5 ms, TE = 3.4 ms, FOV = 240×240 mm^2, flip angle = 12 ° and a matrix of 512×512. The high-resolution T1-weighted structural volume provided an anatomical reference for the functional scan. Subsequently, 200 functional volumes were scanned, using an EPI sequence with the following parameters: TR = 1500 ms, TE = 29 ms, flip angle = 90 °, acquisition matrix = 64×64, in-plane resolution = 3.0×3.0 mm^2, FOV = 192×192 mm^2, axial slices = 25, thickness/gap = 5/0.5 mm. Slice acquisition was performed interleaved. All subjects were scanned for 5 min, and no specific instructions were given except to relax and hold still. Head movements were minimized by using a cushioned head fixation device.

Functional magnetic resonance imaging data preprocessing

All the data were preprocessed with the SPM8 (http://www.fil.ion.ucl.ac.uk/spm). The first six volumes were discarded. After slice-timing correction and head motion correction, the remaining images were spatially normalized to the standard Montreal Neurological Institute (MNI) template with a resampling voxel size of $3 \times 3 \times 3$ mm^3 and smoothed with a 6-mm full-width at half-maximum Gaussian kernel. No subjects were excluded because all the head motions were <2 mm or 2 °.

Anatomical parcellation and estimation of the interregional correlations

The data were segmented into 160 regions of interest (ROIs; Dosenbach *et al*., 2010), which could be partitioned into six networks: default mode network; cingulo-opercular network; fronto-parietal network; occipital network; sensorimotor network; and cerebellum network. The representative time series of each ROI was obtained by averaging the time series over all voxels in the 5-mm radius sphere at the MNI location. Then each region's mean time series was corrected for the effect of head movement, the ventricular signal, the white matter signal and the global mean signal by linear regression. After linear detrending, the residuals of these regressions were used.

The Pearson correlation coefficients were calculated for each pair of regions to measure the functional connectivity, and then a 160×160 correlation matrix was obtained for each subject. A Fisher's r-to-z transformation was performed to improve the normality of the matrix (Liu *et al*., 2008).

Graph theoretical analysis

A threshold T (Fisher's r-to-z) was applied to construct a binary network. If the absolute z_{ij} (edge) between a pair of brain regions, i and j, exceeded a given threshold T, the edge was assumed to exist; otherwise it was assumed not to exist (the degree threshold K was also used to construct the binary brain network (Van Wijk *et al*., 2010), which can be found in Data S1). The main measurements (Table 1) of the topological properties were calculated using Brain Connectivity Toolbox (http://www.brain-connectivity-toolbox.net; Rubinov and Sporns, 2010).

Statistical analysis

Unless otherwise specified, all the statistical analyses were performed in MATLAB (Math Works, Natick, MA, USA). In order to explore the differential impact of SD on the positive and negative correlations, we first defined a positive correlation as the type of connection whose correlation coefficient was significantly greater than zero ($P < 0.05$) in the NS condition, and a negative correlation as a connection whose correlation coefficient was significantly less than zero ($P < 0.05$).

Paired *t*-tests were performed on K_p, E_{corr}, C_p, L_p, γ, λ, σ, E_{global} and E_{local} to compare the differences between NS and SD sessions ($P < 0.05$, uncorrected). If any statistically significant change was found, the distribution of the brain regions was investigated.

The relationship between the topological properties of the functional brain networks and psychometric data (scores on

Table 1 Complex network measurements and their meaning in the brain functional network

Character	*Meaning*
z_{ij}	*z*-score of Fisher r-to-z transform of correlation coefficients
k_p	Degree of connectivity that evaluates the level of sparseness of a network
E_{corr}	Mean *z*-score of a brain functional network
C_p	The absolute clustering coefficient that measures the extent of a local cluster of the network
L_p	The shortest absolute path length that measures the extent of average connectivity of the network
γ	The ratio of the clustering coefficients between real and random networks
λ	The ratio of the path length between real and random networks
σ	Scalar quantitative measurement of the small-worldness of a network
E_{global}	A measure of the global efficiency of parallel information transfer in the network
E_{local}	A measure of the information exchange of each subgraph and the fault tolerance of the network

Table 2 Sleepiness and moods of subjects in NS session and SD session

	NS session	*SD session*	P
Sleepiness	2.36 ± 0.85	3.14 ± 1.13	<0.001
Positive affect	33.64 ± 4.34	28.05 ± 6.22	<0.001
Negative affect	17.45 ± 5.54	17.23 ± 6.1	0.0804

NS, normal sleep; SD, sleep deprivation.

neuroticism, sleepiness and mood scales) was evaluated using Spearman's Rank correlation coefficient. The age and gender of participants were included as covariates to obtain comparable results. The Bonferroni correction was employed when performing multiple statistical tests simultaneously in these six topological properties.

RESULTS

Psychometric results

Subjects reported a higher sleepiness rating after SD (2.35 versus 3.14, paired *t*-test, $P < 0.001$; Table 2). At the same time, there was a significant reduction in positive affect (33.64 versus 28.05, paired *t*-test, $P < 0.001$; Table 2). However, the negative affect was not significantly changed ($P = 0.0804$).

Direct comparisons between the NS and SD sessions

In both sessions, 160 ROIs were organized into six modules, corresponding to the default mode network, cingulo-opercular network, fronto-parietal network, occipital network, sensorimotor network and cerebellum network (Fig. 2). For the separate impact of SD on different correlations, we found that the strength of the average positive functional connectivity tended to increase after SD, and the negative correlation was significantly less suppressed (Fig. 3).

Altered topological properties of brain functional networks after SD

We investigated the topological properties of brain functional networks as a function of *T* to avoid the influence of threshold selection. We selected the range of $0.14 \leq T \leq 0.29$, ensuring the resulting networks had a lower global efficiency and a larger local efficiency compared with random networks (Bullmore and Sporns, 2009). In addition, the maximum thresholds used assured that each network was fully connected (Liu *et al*., 2008). Then we repeated the full

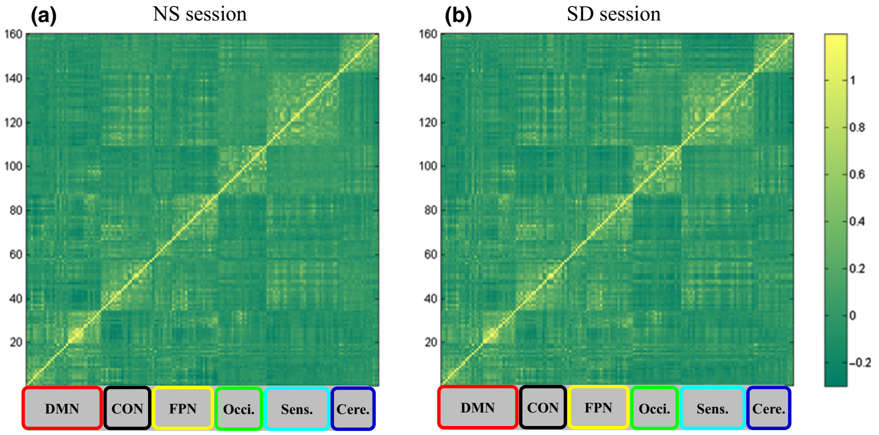

Figure 2. Mean *z*-score matrices for (a) normal sleep (NS) session and (b) sleep deprivation (SD) session. The *x*-axis corresponds to the default mode network (DMN), cingulo-opercular network (CON), fronto-parietal network (FPN), occipital network (Occi.), sensorimotor network (Sens.) and cerebellum network (Cere.); the *y*-axis corresponds to the regions used in Dosenbach's work, and each entry indicates the mean strength of the functional connectivity between each pair of brain regions. The *z*-score of the functional connectivity is indicated with a coloured bar.

analysis for each value of T in the range, with increments of 0.01.

We first compared the differences of K_p, E_{corr}, C_p and L_p of the brain networks between the NS and SD sessions. Over the whole range of threshold values, the values of K_p were significantly higher in the SD session (Fig. 4a), indicating more regions were connected to each region. For most values of T, E_{corr} was significantly stronger after SD (Fig. 4b), and C_p in the SD session was significantly higher (Fig. 4c). For all values of T, values of L_p were significantly shorter after SD (Fig. 4d). The results showed that the adjacent regions were closer connected to a certain region, and the communication paths of a certain region to any other regions across the whole brain were shorter after SD.

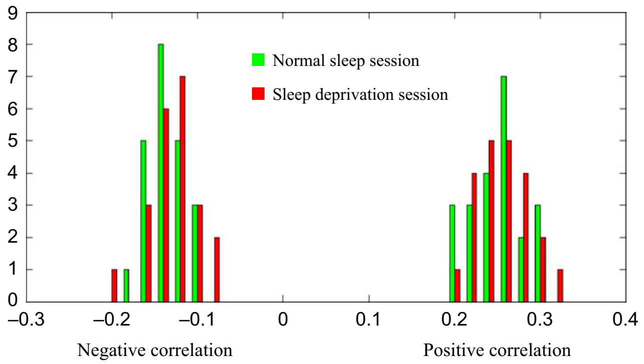

Figure 3. The distribution of negative (left) and positive (right) connectivity in NS session (green) and SD session (red). There was a significant increase in negative correlation after SD compared with NS condition.

The higher C_p and shorter L_p indicated a more optimal network after SD, which was further confirmed by the measurements of γ, λ and σ. The small-world attribute was evident in the brain networks in both sessions, but it was higher in the SD condition (Fig. 5). This indicated that the small-worldness of the functional brain network was enhanced after SD.

In addition, the speed of information transfer in the brain was also measured by calculating global efficiency and local efficiency. Compared with the normal resting state, SD resulted in a higher global efficiency (Fig. 6a). The local efficiency was also significantly increased after SD for most values of T (Fig. 6b). We conducted a complementary analysis based on the degree of connectivity in the range of 27 and 51 (Liu *et al.*, 2008), which yielded comparable results (see Figs S1–S3 in the Supplementary materials).

Distribution of the altered regions in the brain

In order to investigate the networks vulnerable to SD, we used a paired *t*-test to detect statistical differences in topological properties between the SD and NS sessions for each brain region. Because all thresholds exhibited a similar

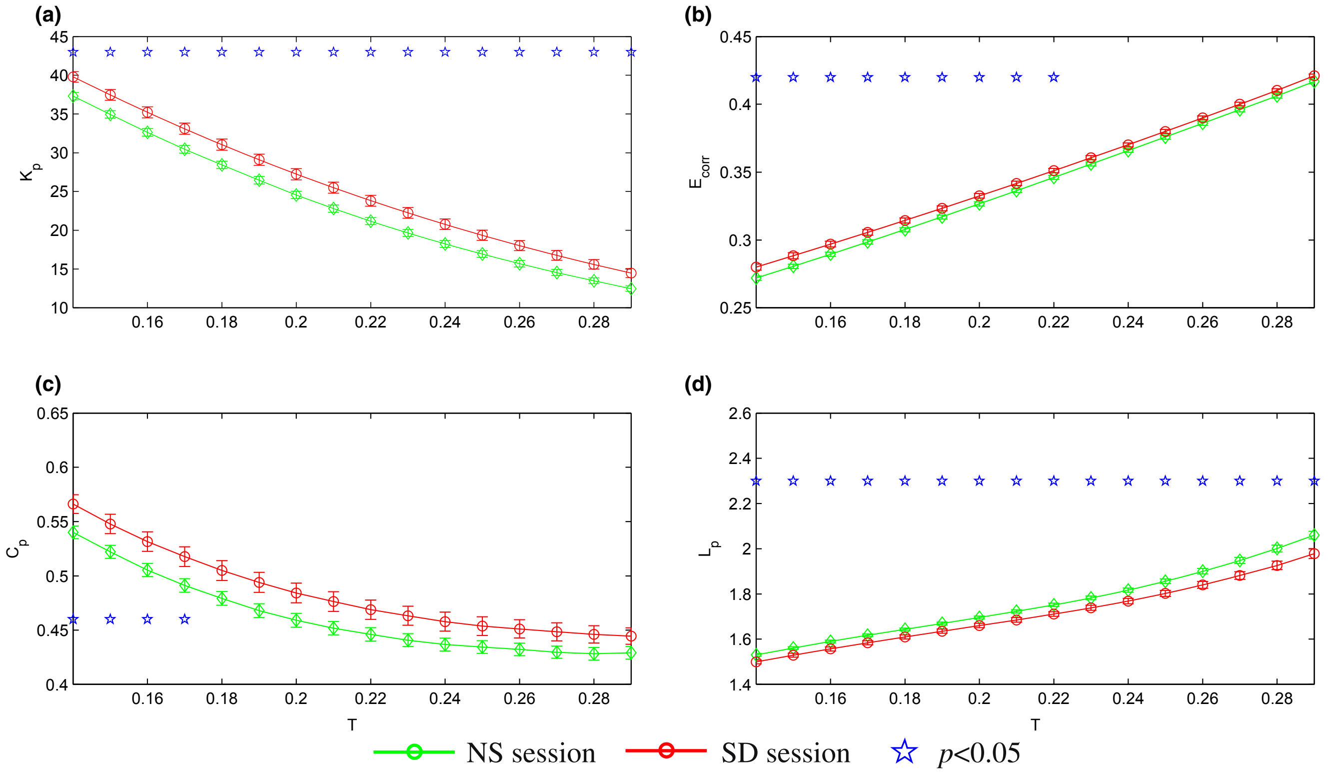

Figure 4. (a) K_p and (b) e_{corr}, (c) C_p and (d) L_p (with error bars) of normal sleep (NS) session (green) and sleep deprivation (SD) session (red) as a function of threshold T. Blue stars indicate where the difference between the two sessions is significant ($P < 0.05$).

trend, we have chosen to report a typical threshold ($T = 0.28$; Fig. 7). We found that topological properties tended to significantly alter in the less-advanced occipital network (occupying for the biggest fraction for K_p, C_p, L_p and E_{global}) and sensorimotor network (the second largest for K_p, E_{corr}, L_p and E_{global}). For the high-order networks, the fronto-parietal network exhibited the largest alteration in E_{local}, reflecting its selective sensitivity for local information exchange.

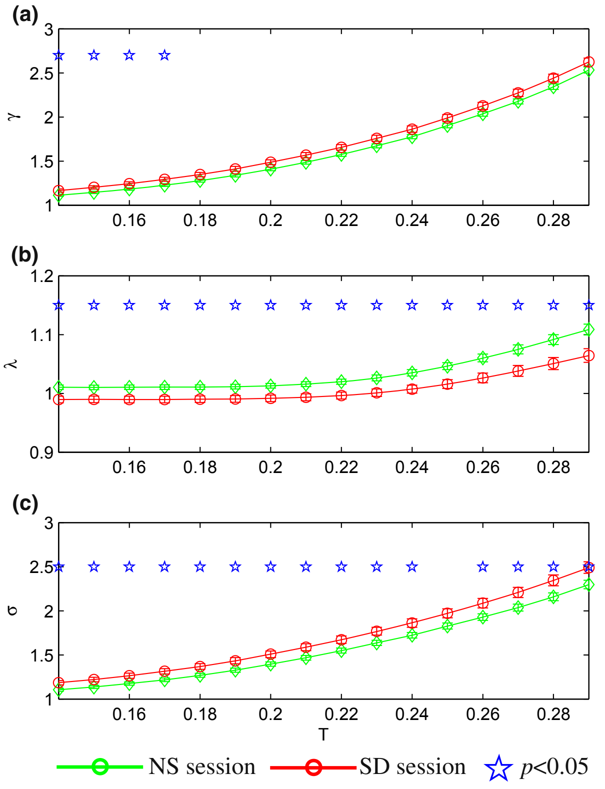

Figure 5. (a) γ, (b) λ, (c) σ (with error bar) for normal sleep (NS) session (green) and sleep deprivation (SD) session (red) as a function of threshold *T*. Blue stars indicate where the difference between the two sessions is significant ($P < 0.05$).

Relationship between the altered topological measures and neuroticism

As shown in Fig. 8, the altered topological measures were significantly correlated with neuroticism after SD (correlation analysis revealed no significant relationship between the topological measures and the alteration of sleepiness, or mood after SD). E_{corr}, C_p, E_{global} and E_{local} were negatively correlated, whereas L_p was positively correlated with neuroticism ($P < 0.05$, uncorrected). After adjustment for multiple comparisons, results confirmed the significant correlation between E_{corr} and neuroticism (smaller than $0.05/6 = 0.00833$, Bonferroni corrected).

DISCUSSION

In this study, the influence of SD on the topological properties of brain networks was investigated using resting-state fMRI. In the SD condition, the negative functional connectivity was significantly less suppressed, indicating a global decrease in inhibition. Contrary to our expectations, the small-world property was significantly enhanced, which may represent a compensatory effect of the brain's functional network. Furthermore, the alteration of the topological measurements was correlated with subjects' neuroticism scores. The results revealed the dynamic and adaptive mechanisms of brain functional networks, which may help to explain why multiple cognitive deficits occur after SD, especially emotional instability.

Decreased anti-correlation after SD

The human brain is a dynamically and optimally organized functional network to facilitate efficient information process-

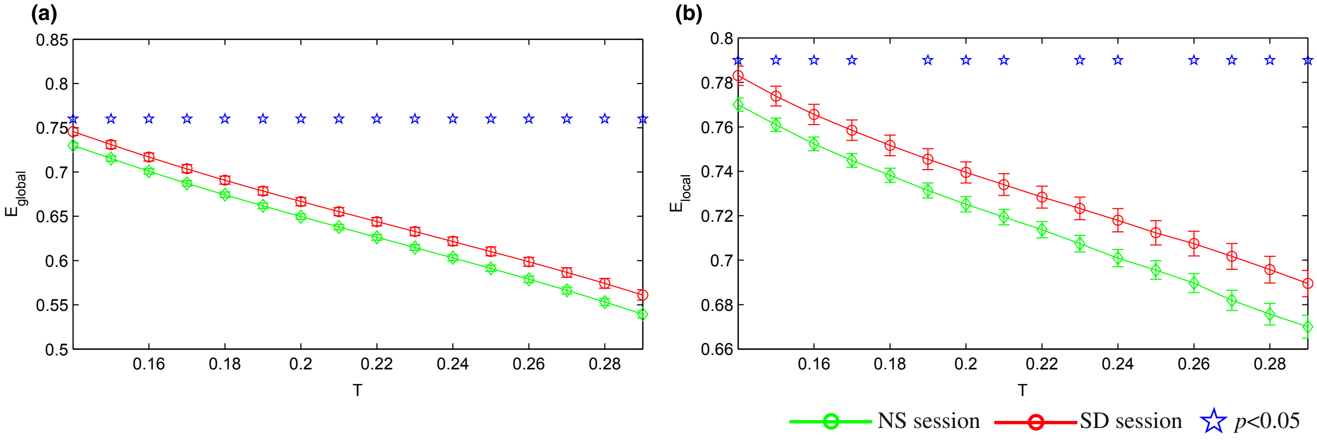

Figure 6. (a) E_{global} and (b) E_{local} (with error bar) for normal sleep (NS) session (green) and sleep deprivation (SD) session (red) as a function of threshold *T*. Blue stars indicate where the difference between the two sessions is significant ($P < 0.05$).

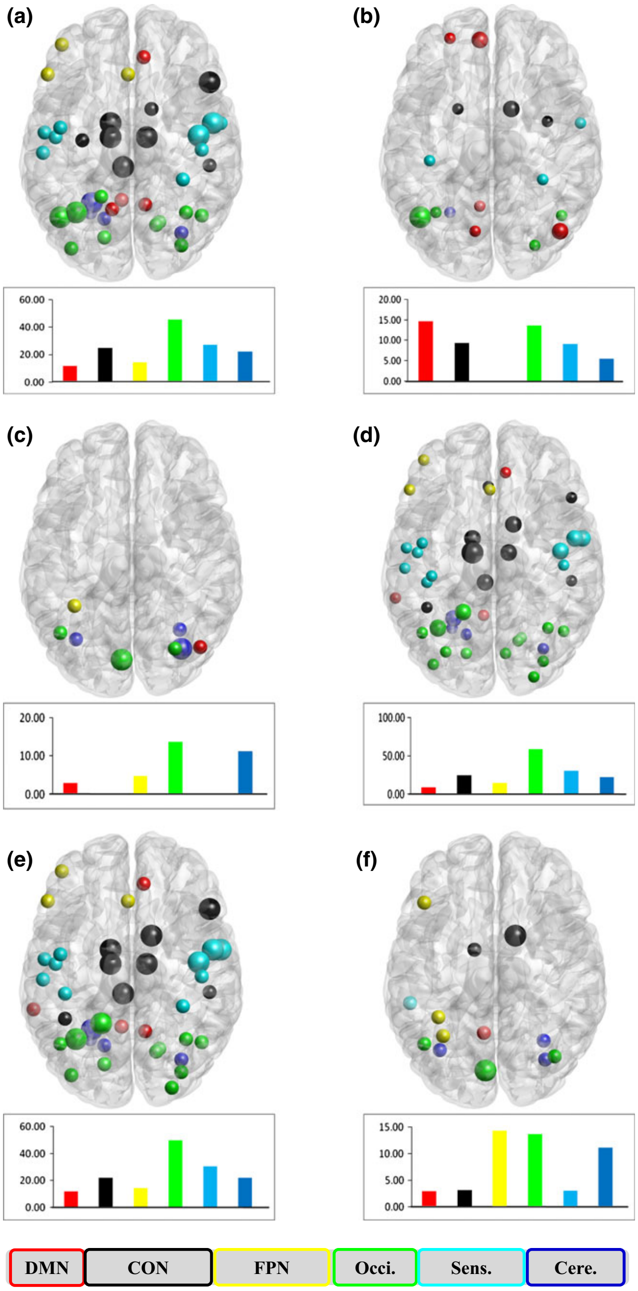

Figure 7. Distribution of brain regions where topological properties [(a) K_p, (b) E_{corr}, (c) C_p, (d) L_p, (e) E_{global} and (f) E_{local}] altered significantly between SD and NS sessions for $T = 0.28$. Top: spheres indicate the significant altered areas, and the size of the sphere indicates the significant level of the differences ($P < 0.05$, $P < 0.01$ or $P < 0.001$). Bottom: the histogram showed the percentage of aberrant ROIs ($P < 0.05$) in each resting-state network [red: default mode network (DMN); black: cingulo-opercular network (CON); yellow: fronto-parietal network (FPN); green: occipital network (Occi.); cyan: sensorimotor network (Sens.); blue: cerebellum network (Cere.)].

ing, which is characterized by small-worldness (Bullmore and Sporns, 2009). This feature was also replicated during SD and sufficient sleep in our study. Though the functional module patterns were maintained after SD, the negative functional connectivity was significantly less suppressed, indicating a global decrease in inhibition. As a weakened anti-correlation between the default mode network and its anti-correlated network after SD was reported before (De Havas *et al*., 2012), our result extended this phenomenon to the whole brain. This decrease may be the reason behind cognitive deficits occurring after SD. It is recommended that further studies should be conducted to explore the links between decreases in brain inhibition and cognitive performances.

Enhanced small-worldness after SD: a compensatory effect

A previous study showed that the small-worldness of EEG brain network was stronger during sleep (Ferri *et al*., 2008). It seems that the network should be disrupted when sleep is prevented. A following study confirmed that SD would result in a more random network in the alpha band and a more ordered network in the gamma band (Koenis *et al*., 2013). Conversely, our results showed an enhanced small-worldness after SD based on the blood oxygen level-dependent (BOLD) signal, presenting a more efficient organization of the brain network. Some researchers have suggested that the BOLD signal is related to the local field potentials (Logothetis, 2008). However, the relationship between the electrophysiological activities and the BOLD signal is still unclear. The disrupted EEG networks after SD were frequency specific, and it is hard to infer how the fMRI network would change in the same condition. We suspect that the enhanced small-worldness on the BOLD signal may reflect a dynamic optimizing of blood oxygen metabolism under the condition of SD. But the efficiency of underlying electrophysiological activities may not increase as the BOLD signal does. Moreover, task-related fMRI studies confirmed the existence of this potential self-adjusting process. Some studies have highlighted that increasing cerebral activation can promote verbal learning after SD (Drummond *et al*., 2000), and this compensatory effect could increase to facilitate more difficult tasks (Chee and Chuah, 2008; Drummond *et al*., 2004). More importantly, resilient subjects exhibited an increase in the activation of their fronto-parietal areas during an attention task after SD, highlighting individual differences in cerebral compensation (Chee and Tan, 2010). In the same manner as additional activation, the enhanced small-worldness after SD could be a reflection of the adaptive mechanisms of brain networks under conditions of diminished processing resources due to insufficient sleep.

Selective effect on occipital, sensorimotor and fronto-parietal networks

In our study, altered regions were detected across the whole brain after SD. Most of these regions were scattered in less-advanced networks. The occipital network had the largest alterations, which were similar to the abnormal regions in a visual task after SD (Kong *et al*., 2011). The changed

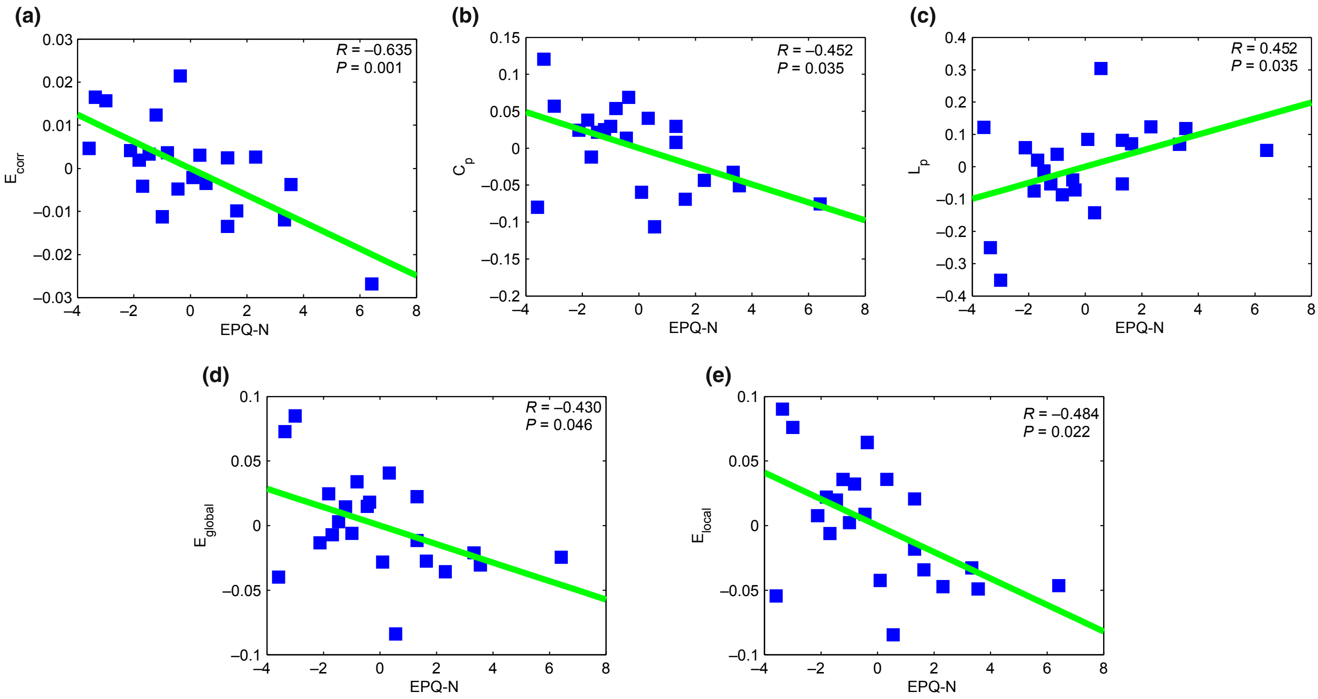

Figure 8. Scatter plots with trend line showing the altered topological properties (ΔE_{corr}, ΔC_{p}, ΔL_{p}, $\Delta E_{\mathrm{global}}$, $\Delta E_{\mathrm{local}}$) of the brain functional networks ($\Delta X = X_{\mathrm{SD\ session}} - X_{\mathrm{NS\ session}}$; blue squares) for $T = 0.28$ as a function of nervousness after SD.

topological property in the alpha band also implicated the possible aberrant activity in the occipital area – the source of alpha rhythm (Goldman *et al.*, 2002). For the sensorimotor network, a meta-analysis showed its sensitivity to SD, especially the paracentral lobule (Pilcher and Huffcutt, 1996). In addition, regions in the fronto-parietal network took up a large proportion of the altered areas, though it remains uncertain whether less-advanced cognition or the high-order cognition is more susceptible to SD (Waters and Bucks, 2011). The notion that regions in charge of executive function (such as mPFC, cingulate cortex and insula) can be affected by SD has repeatedly been demonstrated. The selective sensitivity to SD of areas belonging to the occipital, sensorimotor and fronto-parietal networks in the task-related fMRI studies was consolidated in the current analysis, which may indicate the possible relationship between altered resting-state brain efficiency and abnormal task activation after SD.

The influence of neuroticism

We found that the altered topological measurements of the brain functional networks after SD were correlated with subjects' neuroticism scores. People with a high level of neuroticism are often irritable and anxious, tend to be weak in emotional regulation, have poor sleep habits and are more susceptible to dysthymic disorders like depression (Jorm *et al.*, 2000). We found that higher neuroticism was related to a smaller change in E_{corr}. This smaller variation of the small-world structure may reflect a poorer compensative function after SD, which may further be related to neuroticism. On the contrary, subjects with lower neuroticism tended to exhibit an additional increased efficiency, and were less vulnerable to SD. By relating brain network properties to personality score, our findings are helpful in understanding the individual's emotional instability after SD. In fact, emotion processing after SD is much more labile (Gujar *et al.*, 2011), and is accompanied by aberrant activities in the amygdala–mPFC circuit and reward network. Normal subjects usually report a worse mood after SD (Zohar *et al.*, 2005), whereas SD seems to have an antidepressant effect on patients with depression (Gillin *et al.*, 2001), which suggests a complicated interaction between individual traits and emotion reactivity after SD. What we have found provides another way to understand the labile nature of emotional imbalances after SD. At the same time, it also provides a new perspective from which to investigate the function of brain networks under a condition of SD, which is different from the traditional analysis of a certain circuit.

Limitations and future directions

It should be noted that this study has some limitations. First, we did not monitor the subjects in the lab the day before the NS session, which may have led to some potentially uncontrolled factors. Second, the use of global signal regressions in pre-processing is still controversial (Fox *et al.*, 2009; Murphy *et al.*, 2009), because the regression may create artifactual negative correlations. In our data, the effect of negative correlations may be exaggerated by this approach. Despite these concerns, this method is still widely used to improve the spatial specificity of functional connectivity maps (Uehara *et al*., 2013). We also repeated our analysis using a component-based noise reduction method (CompCor; Chai *et al*., 2012), and the results confirmed the same effects (data not shown in the paper). Third, behavioural performance data were not obtained in our study. SD typically leads to poorer performance on varied cognitive functions. However, our findings indicate that in some terms, participants may be able to demonstrate better cognitive performance because small-worldness is generally associated with better cognitive performance (Douw *et al*., 2011). This is a counter-intuitive finding. Though our results showed an enhanced effect of small-worldness on the BOLD signal, the cognitive performance would be worse after SD, because the EEG network is disrupted, and the neural activities are directly related to cognitive processes while the BOLD signals are not (Logothetis, 2008). Further investigations based on behavioural information may clarify this question. Last, our results contradicted previous EEG studies. Due to the unclear relationship between EEG and fMRI, it is necessary to address the influence of SD on the functional brain networks with combined EEG–fMRI recoding (Lei *et al*., 2010, 2014).

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AUTHOR CONTRIBUTIONS

HL & XL designed and performed the experiments. HL, YW & XL analysed the data. HL, HL, YW & XL wrote the manuscript.

CONFLICT OF INTEREST

No conflicts of interest declared.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Materials

Figure S1. Topological properties of normal sleep (green) and sleep deprivation (red) session as a function of threshold *K*. (a) strength of functional connectivity, E_{corr}, (b) Mean absolute clustering coefficient, C_p, and (c) absolute path length, L_p. Error bars correspond to standard error of the mean. Blue stars indicate where the difference between the two sessions is significant (paired *t*-test, $P < 0.\ 05$).

Figure S2. (a) γ, (b) λ, (c) σ, for normal sleep session (green dots) and sleep deprivation session (red dots) as a function of threshold *K*. Error bars correspond to standard error of the mean. Blue stars indicate where the difference between the two sessions is significant (paired *t*-test, $P < 0.\ 05$).

Figure S3. (a) Mean global efficiency, E_{global}, and (b) local efficiency, E_{local}, for normal sleep session (green dots) and sleep deprivation session (red dots) as a function of threshold K. Error bars correspond to standard error of the mean. Blue stars indicate where the difference between the two sessions is significant (paired *t*-test, $P < 0.\ 05$).