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Research Paper

Association between resting-state brain network topological organization and creative ability: Evidence from a multiple linear regression model

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ABSTRACT

Previous studies have indicated a tight linkage between resting-state functional connectivity of the human brain and creative ability. This study aimed to further investigate the association between the topological organization of resting-state brain networks and creativity. Therefore, we acquired resting-state fMRI data from 22 high-creativity participants and 22 low-creativity participants (as determined by their Torrance Tests of Creative Thinking scores). We then constructed functional brain networks for each participant and assessed group differences in network topological properties before exploring the relationships between respective network topological properties and creative ability. We identified an optimized organization of intrinsic brain networks in both groups. However, compared with low-creativity participants, high-creativity participants exhibited increased global efficiency and substantially decreased path length, suggesting increased efficiency of information transmission across brain networks in creative individuals. Using a multiple linear regression model, we further demonstrated that regional functional integration properties (i.e., the betweenness centrality and global efficiency) of brain networks, particularly the default mode network (DMN) and sensorimotor network (SMN), significantly predicted the individual differences in creative ability. Furthermore, the associations between network regional properties and creative performance were creativity-level dependent, where the difference in the resource control component may be important in explaining individual difference in creative performance. These findings provide novel insights into the neural substrate of creativity and may facilitate objective identification of creative ability.

1. Introduction

Creativity is commonly defined as the generation of novel and original ideas in a divergent and manifold manner, which is the basis of human civilization and culture development (Guilford, 1950). A growing body of neuroimaging research has demonstrated that an individual's creative ability is highly related to patterns of resting-state functional connectivity. For example, higher creativity measured by tests of divergent thinking is associated with resting-state functional connectivity (RSFC) between the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC), both key nodes of the default mode network (DMN) (Takeuchi et al., 2012). Similarly, Beaty et al. found greater RSFC between the left inferior frontal gyrus (IFG) and the entire default mode network in a high creativity group (Beaty et al., 2014). Furthermore, research also suggests that increased RSFC between the mPFC and the middle temporal gyrus (mTG), which are both located in the DMN, might be crucial to creativity, and that mPFC − mTG connectivity can be improved by cognitive stimulation (Wei et al., 2013). All of these studies suggest the importance of increased functional interactions among distributed regions thought to underlie creativity. Nevertheless, the architecture of these large-scale functional networks contributing to creativity remain unclear.

Many previous studies have demonstrated that the intrinsic activity of brain regions are complexly interconnected when individuals are in a resting state, forming functional networks (Bullmore & Sporns, 2009; van den Heuvel & Hulshoff Pol, 2010). The topological architecture of resting-state networks can be depicted and explored using a graph-based network analysis approach, which has shown that these networks

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are organized in a "small-world" and "scale-free" way (Bullmore & Sporns, 2009). These properties not only ensure that the human brain efficiently transmits information but is also robust in the face of an attack (Watts & Strogatz, 1998; Barabási & Albert, 1999). Of note, high clustering and high efficiency in a small-world architecture contribute to cognitive functions that require either segregated or integrated information processing. On one hand, segregated processes, such as visual processes, benefit from highly clustered connections; on the other hand, integrated processes, such as executive functions, benefit from high global efficiency of information transferred across the whole network (Tononi, Sporns, & Edelman, 1994; Tononi & Sporns, 2003; Bullmore & Sporns, 2012). Recent studies have demonstrated that creativity is highly dependent on functional integration (Dietrich & Kanso, 2010; Wu et al., 2015); however, as yet few studies have investigated how the topological characteristics of resting-state functional networks contribute to creative ability. More importantly, previous research has shown that brain network properties are tightly associated with an individual's cognitive abilities, such as level of intelligence (van den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009), working memory (Langer, von Bastian, Wirz, Oberauer, & Jäncke, 2013) and attentional capacity (Markett et al., 2014). Given that these cognitive abilities are all important components of creativity, it is essential to investigate the relation between creativity and the multiple brain networks which have been linked with creative performance (Beaty, Benedek, Barry Kaufman, & Silvia, 2015; Beaty, Benedek, Silvia, & Schacter, 2016), including the DMN which underpins spontaneous imagination and self-generated thought (Andrews-Hanna, 2012; Andrews-Hanna, Smallwood, & Spreng, 2014) and the executive control network (ECN) which is related to working memory, inhibition, integration, and switching (Seeley et al., 2007). Therefore, the complexity of creativity and the wide involvement of multiple brain networks both converged to suggest the rationality of the network perspective in creativity studies.

The current study aimed to investigate the relationships between the topological attributes of resting-state brain networks and individual differences in creativity. We used the Torrance Tests of Creative Thinking (TTCT) to identify high-creativity (n = 22) and low-creativity (n = 22) groups (HG and LG, respectively) from one hundred and eighty participants. Resting-state fMRI data were collected from HG and LG participants, and network analyses based on graph theory were implemented to measure the architectural properties of resting-state functional networks. These network properties were compared between the two groups, and within each group, associations between network topological attributes and behavioral performance were computed using multiple linear regression models.

2. Materials and methods

2.1. Participants

One hundred and eighty healthy volunteers (age = 18.88 ± 1.05 years, 85 males), which are all students enrolled at South China Normal University (Guangzhou, China), participated in the behavioral assessment; the results of this assessment were used to identify 22 high-creativity and 22 low-creativity individuals according to the TTCT scores distribution (see below for a detailed description of this process), a method used in previous studies (Carlsson, Wendt, & Risberg, 2000; Villarreal et al., 2013; Beaty et al., 2014). The HG and LG individuals were well-matched with respect to age, gender, and intelligence (see Results). These 44 participants, who completed a resting-state fMRI scan, were all right-handed, with no history of neurological or psychiatric problems. Exclusion criteria included an implant, device, or object in the body. All participants provided written informed consent, and the protocol was approved by the Research Ethics Review Board of South China Normal University.

2.2. Behavioral assessment

The TTCT-figural version was used to identify high-creativity and low-creativity individuals. The TTCT is widely used to measure key aspects of creativity, such as divergent thinking. The TTCT has high validity with respect to the measurement of divergent thinking (Kim, 2008) and is more predictive of creative achievements in different fields than other divergent thinking tests (Kim, 2005). The TTCT-figural version consists of three tasks: The first task requires participants to imagine a picture or story based on an egg-shaped line figure; the second task instructs participants to draw interesting things based on 10 unfinished pictures; and the third task instructs participants to draw different objects by adding lines to 30 parallel lines. All tasks require participants to imagine and draw novel answers as quickly as possible. The TTCT total creativity score is based on scores for the following dimensions of the creative process (each summed across all three tasks): 1) Fluency is measured by the number of relevant responses and is related to the ability to produce many alternatives. 2) Flexibility is measured by the number of categories that relevant responses can be assigned to (according to specific criteria) and reflects the ability to change perspective. 3) Originality is based on the degree of the ideas produced that differ from others, and is measured by the number of uncommon ideas generated (based on normative data) (De Souza et al., 2010). Consistent with previous studies (Takeuchi et al., 2012; Wei et al., 2013), our analysis only used the total creativity score. There is a high association among the subscales in the TTCT; thus, each subscale could not provide meaningfully different information (Heausler & Thompson, 1988), and some have argued that independent interpretations of TTCT subscores should be avoided (Treffinger, 1985).

Intelligence is associated with divergent thinking (Nusbaum & Silvia, 2011; Benedek, Franz, Heene, & Neubauer, 2012; Benedek, Jauk, Sommer, Arendasy, & Neubauer, 2014; Silvia & Beaty, 2012); thus, we also assessed intelligence using the Raven's Standard Progressive Matrices (RSPM)-Chinese version. This version of RSPM has good split-half reliability (0.95), and good test-retest reliabilities (0.82 and 0.79 over intervals of 15 days and 30 days, respectively).

Participants with TTCT total scores in the top 12% (*n* = 22, 11 males and 11 females) of the total sample were assigned to the high-creativity group, while the participants in the bottom 12% (*n* = 22, 11 males and 11 females) were assigned to the low-creativity group. Of note, we selected 12% as cut-off point for magnifying the difference of creative ability between two groups and minimizing the influence of gender differences on our results (Matud, Rodríguez, & Grande, 2007; Lin, Hsu, Chen, & Wang, 2012).

2.3. MRI acquisition

All MRI data were obtained on a 3 T Siemens Trio Tim MR scanner with a 12-channel phased-array head coil at South China Normal University. The fMRI data were acquired using a gradient-echo echo-planar imaging (EPI) sequence with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 90°, matrix = 64 × 64, field of view (FOV) = 224 × 224 mm^2, thickness/gap = 3.5/0.8 mm, and 32 axial slices covering the whole brain. During resting-state scanning, participants were instructed to keep their eyes closed. Two hundred and forty functional volumes were obtained during the 8-min scan.

In addition, 3D high-resolution structural images were obtained using a 3D T1-weighted MP-RAGE sequence with the following parameters: TR = 1900 ms, TE = 2.52 ms, flip angle = 90°, matrix = 256 × 256, FOV = 230 × 230 mm^2, thickness = 1.0 mm, and 176 sagittal slices.

2.4. Data analysis procedures

2.4.1. Behavioral data analysis

Behavioral data were analyzed using SPSS 17.0 (SPSS Inc., Chicago, IL). Group differences in demographic variables (i.e., age, gender, intelligence, and TTCT total scores) were analyzed using independent-sample *t* tests.

2.4.2. Functional imaging data preprocessing

All MRI data were processed using DPARSF_V2.0 (Yan & Zang, 2010) based on SPM8 (http://www.fil.ion.ucl.ac.uk/spm/). The procedures were as follows: (1) The first 10 vol were removed to allow for scanner stabilization and participant adaptation to the MR environment. (2) Slice timing and realignment were performed to correct for acquisition time delay and head motion. No participant was excluded based on predefined criteria (i.e., head motion in any direction of more than 1 mm or 1°). To assess the influence of the head motion on the functional images (Mowinckel, Espeseth, & Westlye, 2012), we compared the mean absolute value of head translations and head rotations between the two groups. Statistical analyses indicated no significant between-group differences in head motions (all $p > 0.05$). (3) The acquired functional images were spatially normalized. Each participant's structural image was initially coregistered to the mean functional image. The transformed structural image was then segmented into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF) using a unified segmentation algorithm. Finally, the functional brain images were spatially normalized to MNI space using the normalization parameters estimated during unified segmentation. To reduce physiological noise and low frequency drift in the fMRI data, data were band-pass filtered (0.01-0.08 Hz) and a linear trend was also removed. Spatial smoothing (Gaussian kernel full-width at half-maximum = 4 mm) was performed to improve the signal-to-noise ratio. Moreover, we regressed out nuisance covariates, including 24 head motion parameters as well as WM and CSF signal. Of note, the global signal was not regressed out, in line with recommendations arising from recent debates (Fox, Zhang, Snyder, & Raichle, 2009; Murphy, Birn, Handwerker, Jones, & Bandettini, 2009).

2.4.3. Construction of functional brain networks

For each participant, the whole brain was parceled into 160 cortical and sub-cortical regions-of-interest (ROIs) using a functional template derived from a previous study (Dosenbach, Nardos, & Cohen, 2010). Each ROI time series was derived by averaging the time series over all voxels within this region. A 160 × 160 correlation matrix was obtained by calculating Pearson's correlation coefficients for the time courses from every pair of ROIs for each participant. We abandoned all negative edges prior to weighted graph construction, which resulted in only positive pairwise functional connections because negative correlations may be statistically "noisy" or topologically distinct from networks based on positive correlations (Wang et al., 2011). To construct functional brain networks for each participant, we assessed each ROI as a node and the value of the correlation coefficient of the brain regions as the weight of the edge. Thus, we obtained a weighted symmetric functional connectivity matrix for each participant.

2.4.4. Network analysis

2.4.4.1. Global parameters. We analyzed the topological properties of brain networks based on graph theory. The following 8 parameters were used to describe the global network attributes in detail (defined according to Rubinov & Sporns, 2010; Tian, Wang, Yan, & He, 2011): 1) Weighted clustering coefficient (C_w) which reflects the extent of connectedness of nodal neighbors; 2) weighted characteristic path length (L_w), the average shortest path length between all pairs of nodes in the network which indicates potential functional integration between brain regions; 3) global efficiency (E_{glob}) which indicates the efficiency of parallel information transfer in the whole network; and 4) local efficiency (E_{loc}), the average values of the local efficiency within all nodes in the brain, which reflects the local cliquishness of a network. Normalized global parameters used to quantify small-world topography were: 5) normalized global efficiency (α), 6) normalized local efficiency (β), 7) normalized weighted clustering coefficient, $\gamma = C_w^{real}/C_w^{rand}$, and 8) the normalized weighted characteristic path length, $\lambda = L_w^{real}/L_w^{rand}$, where C_w^{real} and L_w^{real} represent the clustering coefficient and characteristic path length of the real brain network, respectively, and C_w^{rand} and L_w^{rand} represent the mean values of the corresponding parameters derived from 100 matched random networks with the same number of nodes, edges, and distribution of degrees as the real brain network. Typically, a small-world network satisfies the following criteria: $\gamma > > 1$ and $\lambda \approx 1$ or $\sigma = \gamma/\lambda > 1$ (Watts & Strogatz, 1998). Using a similar approach, $\alpha = E_{glob}^{real}/E_{glob}^{rand}$ and $\beta = E_{loc}^{real}/E_{loc}^{rand}$.

2.4.4.2. Nodal parameters. The following 4 parameters were used to depict the local network topological organization (Rubinov & Sporns, 2010; Tian et al., 2011): 1) nodal global efficiency (E_{glob}^{w}) and 2) nodal local efficiency (E_{loc}^{w}), which together represent the efficiency of parallel information transfer of a node (i.e., nodal efficiency (E_{glob}^{w}); 3) nodal strength (S_i^w), the sum of the edge weights of all connections of a node, represents the extent to which a node is related to other nodes in the network; and 4) nodal betweenness (B_i^w), the number of shortest paths from one node to another node that pass through a third node, represents the information flow of the third node with other nodes in the whole network.

In this study, all elements of the connectivity matrix were thresholded using a previously measured sparsity, which was computed by dividing the maximum possible number of edges in a network by the total number of edges. However, different sparsity values lead to variant effects on the topological organization of networks (Rubinov & Sporns, 2010; Tian et al., 2011), and there is no definitive approach to select a single threshold. Thus, we empirically thresholded each correlation matrix repeatedly over a wide range of $0.04 \leq$ sparsity ≤ 0.5 with an interval of 0.02 to obtain sparse and weighted networks. In this study, we not only computed each parameter that corresponded to each sparsity threshold but also calculated the integrated network parameters over the whole range of sparsity values (Tian et al., 2011) to investigate group differences in network attributes. Mathematically, the integrated global parameters for a network are defined as:

$$X_{glob}^{\text{int}} = \sum_{k=2}^{25} X(k\Delta S)\Delta S \tag{1}$$

where ΔS represents the sparsity interval of 0.02, and $X(k\Delta S)$ indicates one of the global network parameters (C_w, L_w, E_{glob}, E_{glob}^{w} , E_{loc}^{w} , or λ)B_i^w at a sparsity of $k\Delta S$. Similarly, the integrated nodal parameters may be defined as:

$$Y_{nod}^{\text{int}} = \sum_{k=2}^{25} Y(i,\, k\Delta S)\Delta S \tag{2}$$

where $Y(i,\, k\Delta S)$ represents any nodal parameter (E_{glob}^{w} , E_{loc}^{w} , S_i^w, or B_i^w) at a sparsity of $k\Delta S$, and ΔS represents the sparsity interval of 0.02.

2.5. Statistical analysis

2.5.1. Between-group comparisons

Nonparametric permutation tests (Bullmore & Sporns, 1999) were used to identify between-group differences in the global parameters (weighted clustering coefficient, weighted characteristic path length, global efficiency, local efficiency, normalized weighted clustering coefficient, normalized weighted characteristic path length, normalized global efficiency, and normalized local efficiency). For each parameter, 10,000 permutations were computed, resulting in an empirical distribution of the between-group differences. The 95% distribution was used as the critical value for a two-tailed test of the null hypothesis with

5% type I error (false positive). Of note, for the permutation tests, the effects of several confounding factors, including age and gender, were regressed out as covariates (Zuo et al., 2012).

2.5.2. Correlations between nodal parameters and behavioral data

This study implemented multiple linear regression analyses to determine whether the regional properties of networks could explain individual differences in creative performance within each group. The dependent variable was TTCT performance, and the independent variables included the integrated network nodal parameters such as the integrated nodal local efficiency, as well as age and gender. To reduce the data dimensions, only nodes that were significantly correlated with creative performance were used in the regressions. Notably, to ensure the same rigidity level between the network parameters and the behavioral data, we normalized both the network parameter data and the behavioral data to investigate their relationships (Zhang, Wang, Liu, Chen, & Liu, 2015). This regression analysis was repeated for each integrated nodal parameter (e.g., integrated nodal global efficiency, integrated nodal local efficiency, integrated nodal strength, and integrated nodal betweenness) to investigate whether the parameter could explain creative performance within each group. In addition, using the same approach, we added intelligent scores as an additional covariate and further explored correlations between regional properties of networks and creative data.

3. Results

3.1. Behavioral data

Mean performance of each group on tests of creativity (TTCT) and intelligence (RSPM) are described in Table 1 and Fig. 1. We compared the groups on these measures using two-tailed independent sample *t*-tests. As expected, TTCT scores were significantly higher in the HG relative to the LG ($p < 0.01$), while there was no significant difference in intelligence scores between the two groups. Thus, HG and LG were well matched in terms of intellectual abilities as well as age and gender.

3.2. Network parameters

3.2.1. Global parameters

The functional brain networks of both groups met the criteria for classification as small-world networks (i.e., $\gamma > > 1$ and $\lambda \approx 1$ or $\sigma = \gamma/\lambda > 1$) (Fig. 2a). However, there were significant differences between the network metrics of the two groups. Compared with the LG, there was a significant decrease in the integrated normalized weighted characteristic path length and a significant increase in the integrated normalized global efficiency in the HG (Fig. 2a and b, respectively). Furthermore, at specific sparsity levels, there were significantly decreased normalized weighted characteristic path length and significantly increased normalized global efficiency in the HG compared with the LG (λ: $0.14 \le \text{sparsity} \le 0.3$; α: $0.12 \le \text{sparsity} \le 0.3$) (Fig. 2a and b, respectively). Despite the existence of group differences in these global network parameters, we did not identify significant brain-behavior correlations between the global network parameters and TTCT scores.

Table 1
Demographic information of participants in this study.

	HG (M ± SD)	LG (M ± SD)	*t*-value (df)
Age	18.86 ± 1.08	19.13 ± 0.99	−0.87 (42)
RSPM scores	54.95 ± 4.85	55.68 ± 3.15	−0.59 (42)
TTCT scores	65.54 ± 4.09	38.20 ± 5.85	17.96** (42)

Note: HG, high-creativity group; LG, low-creativity group; RSPM, Raven's Standard Progressive Matrices; TTCT, Torrance Tests of Creative Thinking; M, mean; SD, standard deviation; df, degrees of freedom; Two-tailed independent sample *t*-tests were used to investigate the between-group differences.

** $p < 0.01$.

3.3. Relationships between regional network parameters and TTCT performance

Using the MLRA method, we further assessed the associations between regional network parameters and creative performance. The integrated regional (nodal) parameters (i.e., integrated nodal global efficiency, integrated nodal local efficiency, and integrated nodal betweenness) significantly explained individual differences in TTCT scores (Table 2). In particular, integrated nodal betweenness and integrated nodal global efficiency predominately and consistently explained the variation in TTCT performance in both groups. With respect to integrated nodal betweenness, regions associated with TTCT scores in the HG included right fusiform gyrus (FFG), left precuneus (PCUN), left temporal cortex (TC), left thalamus (THA), and right posterior occipital cortex (POC). In contrast, for the LG, associated regions included right ventral medial prefrontal cortex (vmPFC), right ventral inferior prefrontal cortex (vIPFC), right precuneus (PCUN), right posterior cingulate cortex (PCC), left parietal cortex (PC), left precentral gyrus (PreCG), right dorsal frontal cortex (dFC), and right inferior parietal lobule (IPL) (Table 3).

Specifically, left TC, right FFG, left PCUN, right POC, and left THA exhibited important effects in explaining creative performance in the HG, predicting 43%, 34%, 31%, 31% and 29%, respectively, of the variation in creativity (Fig. 3).

In the LG, left PreCG, right dFC[1], right vmPFC, and right vIPFC predicted 61%, 52%, 48%, and 47%, respectively, of the variation in TTCT scores (Fig. 4). Of note, these findings were not identified for other nodal parameters.

In addition, regional network global efficiency also explained inter-individual variation of TTCT performance. In the HG, the integrated nodal global efficiency of left TC, left inferior cerebellum (ICER), and right anterior insula (AINS) (Table 4) predicted 50%, 39%, and 27% of the variance in TTCT scores, respectively. Using the same metric, in the LG, left occipital cortex (OC[1]), left POC[1], and right POC[1] (Table 4) predicted 57%, 49%, and 49% of the variation in TTCT scores, respectively.

We also explored associations between nodal parameters and creative data using MLRA with intelligence (RSPM scores) included as a covariate. Adding this covariate did not change the overall pattern of results. Specifically, we still found that integrated nodal betweenness and integrated nodal global efficiency were the metrics that predominately and consistently explained individual differences in TTCT scores in both groups (Table 5).

In the HG, integrated nodal betweenness was again associated with left TC, left PCUN, right POC and left THA, predicting 43%, 31%, 31%, and 29% of the variation in creativity, respectively (Table 6; Fig. 5). In contrast, in the LG, associated regions included left PreCG, right dFC, right vmPFC, right vIPFC, right PCUN, right PCC, and right IPL. In particular, left PreCG, right dFC[1], right vmPFC, and right vIPFC predicted 61%, 52%, 48%, and 47% of the variation in the LG's TTCT scores, respectively (Table 6; Fig. 6).

Additionally, integrated nodal global efficiency also still explained inter-individual variation in TTCT performance. For the HG, left TC, left ICER, and right AINS predicted 50%, 39%, and 27%, respectively, of the variance in TTCT scores (Table 7). For the LG, left OC[1], left POC[1], and right POC[1] (Table 7) predicted 57%, 49%, and 49% of the variation in TTCT scores, respectively.

Of note, both integrated nodal betweenness and integrated nodal global efficiency patterns, which significantly explained TTCT performance, failed to explain intelligence (as measured by the RSPM scores) using the same approach (the same consequence in the multiple linear regression analysis adding intelligence as a covariate).

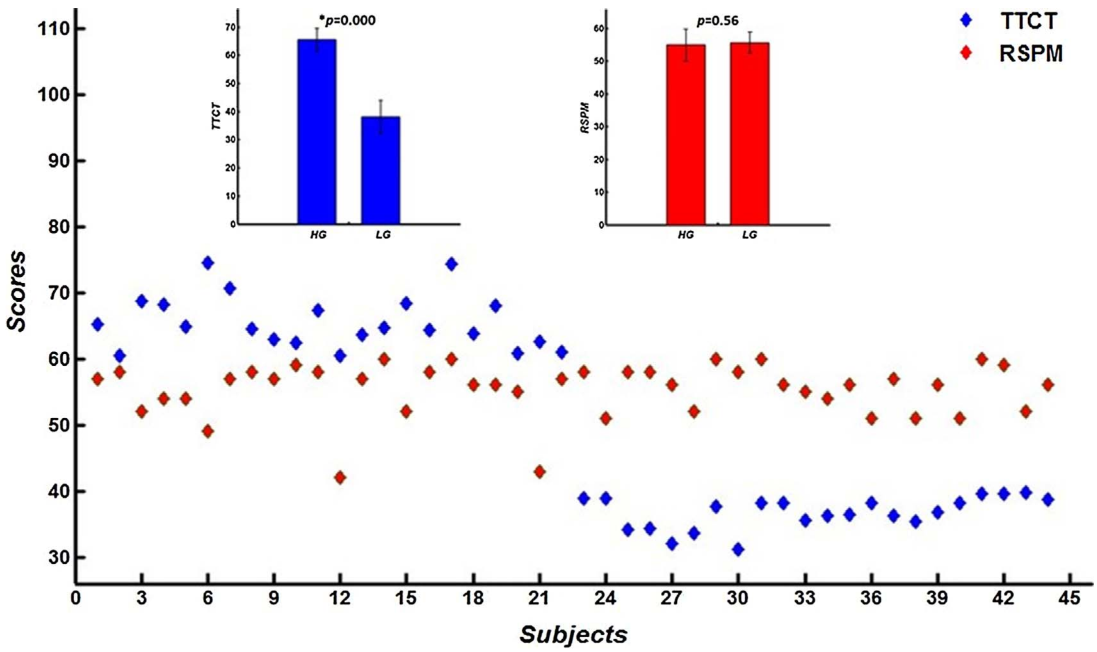

Fig. 1. Creativity and intelligence data in high-creativity and low-creativity groups. (1) Scatterplot for describing creative and intelligent data we acquired, the blue rhombus stands for creative data while the red rhombus stands for intelligent data. (2) Histograms for showing the group-difference in respect of creativity and intelligence using two-tailed independent sample *t*-tests. HG, high-creativity group; LG, low-creativity group; RSPM, Raven's Standard Progressive Matrices; TTCT, Torrance Tests of Creative Thinking; * $p < 0.0001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Resting-state fMRI has been widely used for exploring many intrinsic attributes of the human brain, usually with the aim of detecting biomarkers for neurological disorders. For instance, a previous study (Zhang et al., 2015) found that nodal efficiency of resting-state brain networks could effectively discriminate Parkinson's disease patients from healthy controls using multivariate pattern analysis, and could also explain the variability of tremor based on a multiple linear regression model. Another study has suggested that the resting-state clustering coefficient may be useful as an imaging-based biomarker to distinguish Alzheimer's disease from healthy aging (Supekar, Menon, Rubin, Musen, & Greicius, 2008). In addition, network topology may be useful in understanding cognitive function in healthy individuals. Many studies have shown that resting-state global efficiency is significantly related to cognitive abilities such as intelligence (van den Heuvel et al., 2009) and working memory (Stevens, Tappon, Garg, & Fair, 2012; Langer et al., 2013), while resting-state nodal efficiency is highly linked with attentional capability (Markett et al., 2014) and perception of biological motion (Wang et al., 2016). Therefore, the topology of resting-state brain networks is not only useful in predicting neurological disorders, but also various aspects of cognitive performance in healthy individuals.

Here, the present study further investigated the topological organization of intrinsic brain networks in participants with differing levels of creativity, as measured by the TTCT. The main findings are summarized as follows: (1) While an optimized network organization was identified for both the HG and LG, information transformation efficiency was better in the HG compared with the LG. (2) The regional functional integration properties of brain networks (i.e., integrated nodal betweenness and integrated nodal global efficiency) were able to explain inter-individual variation in creative performance in the two groups. (3) The associations of network regional properties with creative performance involved different brain regions in each of the two groups, suggesting these associations were creativity-level dependent.

4.1. Individual differences in resting network attributes

This study characterized and compared the topological properties of intrinsic brain networks between groups of individuals with high and low levels of creativity (HG and LG, respectively). We demonstrated that the two groups both have small-world attributes that reflect a relatively larger clustering coefficient and approximately equal characteristic path lengths compared with the corresponding random networks (Fig. 2a). The small-world attribute embodies an optimal balance of functional integration and segregation, and maximizes the efficiency of transferring information at a relatively low cost (Sporns & Honey, 2006). Thus, the small-world characterization of networks in the present study may reflect the ability of the human brain to support efficient information transfer and distributed information processing. In particular, we found that the topological properties of brain networks were highly associated with creative ability. Further supporting this notion was evidence that integrated normalized weighted characteristic path length was significantly decreased in the HG compared with the LG (Fig. 2a). It should be noted that the paths reflect linkages of distinct nodes and thus represent potential routes of information flow between pairs of brain regions (Rubinov & Sporns, 2010). Indeed, the average shortest path length between all pairs of nodes within the network − referred to as the characteristic path length of the network (Watts & Strogatz, 1998) − is the most commonly used measure of functional integration. Thus, the decreased integrated normalized weighted characteristic path length in the HG indicates that the high-creativity subjects likely have shorter links within local nodes for a more efficient spread from the centrality to other nodes, supporting the flexible generation of original ideas. Correspondingly, we also found that integrated normalized global efficiency was significantly increased in the HG compared with the LG (Fig. 2b). Notably, the global efficiency is computed as the inverse of the characteristic path length and describes an integrated function that indicates the efficiency of the entire network in transforming information among nodes via multiple edges (Latora & Marchiori, 2001). Thus, the finding that integration in brain networks was increased in the HG also suggests that in highly creative individuals, brain networks may propagate information flow with a

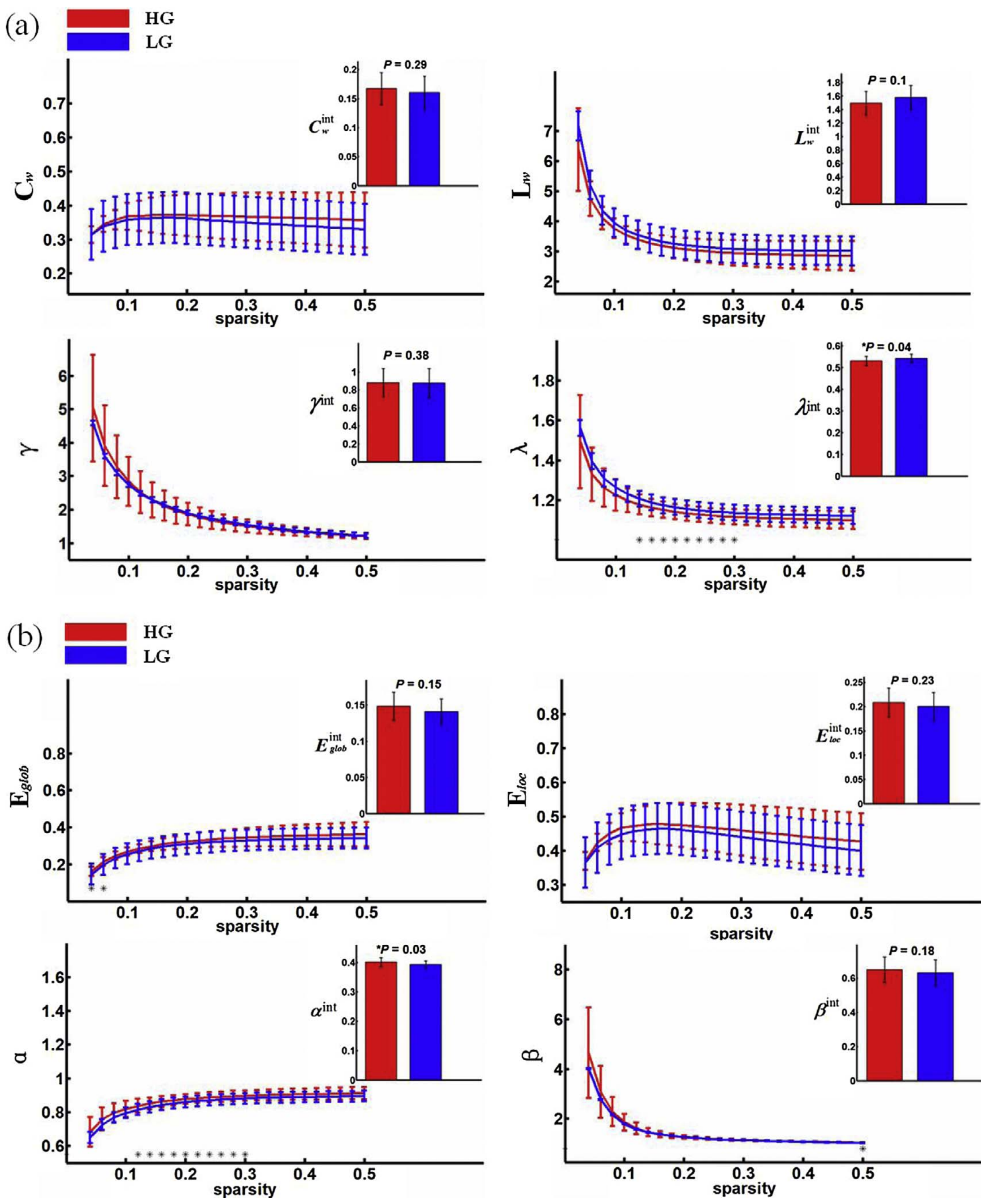

Fig. 2. Global parameters of whole brain functional networks in the HG and LG. (a) Small-world property. (b) Global parameters that changed with sparsity and group differences in integrated global topological parameters. C_w, weighted clustering coefficient; L_w, weighted characteristic path length; γ, normalized weighted clustering coefficient; λ, normalized weighted characteristic path length; E_{glob}, global efficiency; E_{loc}, local efficiency; α, normalized global efficiency; β, normalized local efficiency; '*int*' indicates the abbreviation for "integrated".

high efficiency. This finding is, to a certain extent, consistent with a previous report that more creative participants exhibited substantially increased global efficiency leading to a highly efficient information transfer across a network of brain regions linked to divergent thinking (Beaty et al., 2015).

Many previous studies have documented the relationship between network topology and aspects of cognitive ability, such as intelligence (van den Heuvel et al., 2009) and working memory (Stevens et al., 2012; Langer et al., 2013). These studies have provided evidence that the effect of network topology on increasing preparatory resources may facilitate brain responses to perceptual cues (Hashmi et al., 2014). Our findings of increased normalized global efficiency and relatively low normalized weighted characteristic path length in the HG's resting-state networks may be consistent with information theory; thus, increased efficiency is associated with a lower cost of information transfer and the capacity to transfer information locally in a network (Bullmore & Sporns, 2009). Together, the topological properties of intrinsic brain networks of creative individuals may reflect a neural substrate that promotes creative performance.

4.2. Associations between regional network attributes and creative performance

To further identify the network properties that were highly related to creative performance, we used an MLRA approach to determine the specific regional network properties that significantly explained inter-

Table 2
Performance of the MLRA in the prediction of the TTCT in two groups.

Groups	Predictors	Regress	
		Adjusted R^2	p-value
HG			
	E^{int}_{glob}	0.599	0.001
	E^{int}_{loc}	0.399	0.030
	B_i^{int}	0.683	0.001
LG			
	E^{int}_{glob}	0.769	0.006
	E^{int}_{loc}	0.518	0.040
	B_i^{int}	0.763	0.002

Note: E^{w}_{glob} , nodal global efficiency; E^{w}_{loc} , nodal local efficiency; B_i^{w}, nodal betweenness. '*int*' represents the abbreviation for "integrated".

individual variation in creative performance. First, the current findings indicated that integrated nodal betweenness had the highest predictive power of the variation in TTCT scores in both groups (Table 2). Nodal centrality is a universal concept in social network analysis, which has been widely applied to fMRI data analysis (Sporns, Honey, & Kötter, 2007; Buckner et al., 2009). The concept of integrated nodal betweenness reflects the degree to which a node resides on the shortest path between pairs of nodes within a network, and is used as a valid marker to identify key nodes and edges with respect to information flow in a network (Girvan & Newman, 2002). Based on the present findings, we speculate that how well a given node or hub is globally embedded in a network may serve as a biomarker of creative ability. Further analysis indicated that the main regions in the HG were predominately located in left PCUN, right FFG, and left TC (Table 3; Fig. 3). These findings are consistent with previous reports that the PCUN is related to self-generated thought (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009) and also potentially contributes to creative thought (Takeuchi et al., 2011; Li, Yang, Zhang, Li, & Qiu, 2016; Zhu et al., 2017). In addition, Aziz-Zadeh and her colleagues suggested that visual creativity may involve stronger motor imagery (Aziz-Zadeh, Liew, & Dandekar, 2013), and given that motor imagery is associated with increased resting-state connectivity between the FFG and PCUN (Zhang et al., 2014), our finding that nodal betweenness of both FFG and PCUN are predictive of TTCT is consistent with this notion. Therefore, our finding regarding the involvement of the right FFG and the left PCUN may suggest an important role of visual imagery in divergent thinking. This study also demonstrated that nodal betweenness of left TC was predictive of creative performance. The role of the TC is consistent with previous evidence of strong associations with dimensions of creativity, particularly originality (Chen et al., 2015).

Notably, the regions evident in the HG were mainly located in the DMN (the left PCUN and the right FFG) and the SMN (the left TC); these regions within DMN and SMN exhibited relatively increased levels of prediction for creative performance compared with other regions within other networks. Correspondingly, the regions with increased predictive power in the LG also belonged to DMN (the right vmPFC, right vIPFC, right PCUN, and right PCC) and SMN (the left PreCG) (Table 3; Fig. 4). Many previous studies have indicated that the DMN plays an important role in spontaneous thought, such as mind wandering, autobiographical retrieval, and episodic future thinking (Buckner, Andrews-Hanna, & Schacter, 2008; Andrews-Hanna, 2012). According to the two-stage process model of creativity, creative thought includes two important processes, namely idea generation and idea evaluation (Finke, Ward, & Smith, 1996). For the idea generation stage of creativity, the DMN may play a key role for widely distributed attention resources (Jung, Mead, Carrasco, & Flores, 2013) and retrieval of potentially useful information (Andrews-Hanna et al., 2014). Our findings are consistent with the notion that the generation of ideas is a critical aspect of the inter-individual variation in creative performance. Moreover, the involvement of the SMN overlaps to a certain extent with previous studies demonstrating that the SMN is involved in complex creative generation such as music improvisation (Bengtsson, Csíkszentmihályi, & Ullén, 2007; Limb & Braun, 2008).

In addition, we further demonstrated that the integrated nodal global efficiency had significant explanatory power in both the HG and LG. Correspondingly, a previous study demonstrated a strong association between the global efficiency of functional brain networks and intelligence (van den Heuvel et al., 2009). Moreover, the present study illustrates that integrated nodal global efficiency is also a predictor of creative ability. This result may be similar to the finding that the personality trait of openness, which is positively linked to creative performance, is related to the global efficiency of the DMN (Beaty, Kaufman et al., 2016). It should be noted that integrated nodal global efficiency instead of integrated nodal local efficiency predicted creative performance, which suggest that the functional integration of the whole brain rather than local regions likely has a more important role in

Table 3
Brain locations involved in the MLRA for nodal B_i^{int} in the two groups.

Parameters	Region	Hemisphere	Module	MNI-coordinates		
				x (*mm*)	y (*mm*)	z (*mm*)
$B_i^{int\,a}$						
	FFG	R	default	28	−37	−15
	PCUN	L	default	−6	−56	29
	TC	L	sensorimotor	−41	−37	16
	THA	L	cingulo-opercular	−12	−12	6
	POC	R	occipital	33	−81	−2
$B_i^{int\,b}$						
	vmPFC	R	default	6	64	3
	vIPFC	R	default	46	39	−15
	PCUN	R	default	9	−43	25
	PCC	R	default	10	−55	17
	PC	L	sensorimotor	−47	−18	50
	PreCG	L	sensorimotor	−54	−22	22
	dFC^1	R	fronto-parietal	40	17	40
	dFC^2	R	fronto-parietal	44	8	34
	IPL	R	fronto-parietal	54	−44	43

Note: [a] HG; [b] LG; FFG, fusiform gyrus; PCUN, precuneus; TC, temporal cortex; THA, thalamus; POC, posterior occipital cortex; vmPFC, ventral medial prefrontal cortex; vIPFC, ventral inferior prefrontal cortex; PCC, posterior cingulate cortex; PC, parietal cortex; PreCG, precentral gyrus; dFC^1 and dFC^2, dorsal frontal cortex; IPL, inferior parietal lobule; R, right hemisphere; L, left hemisphere.

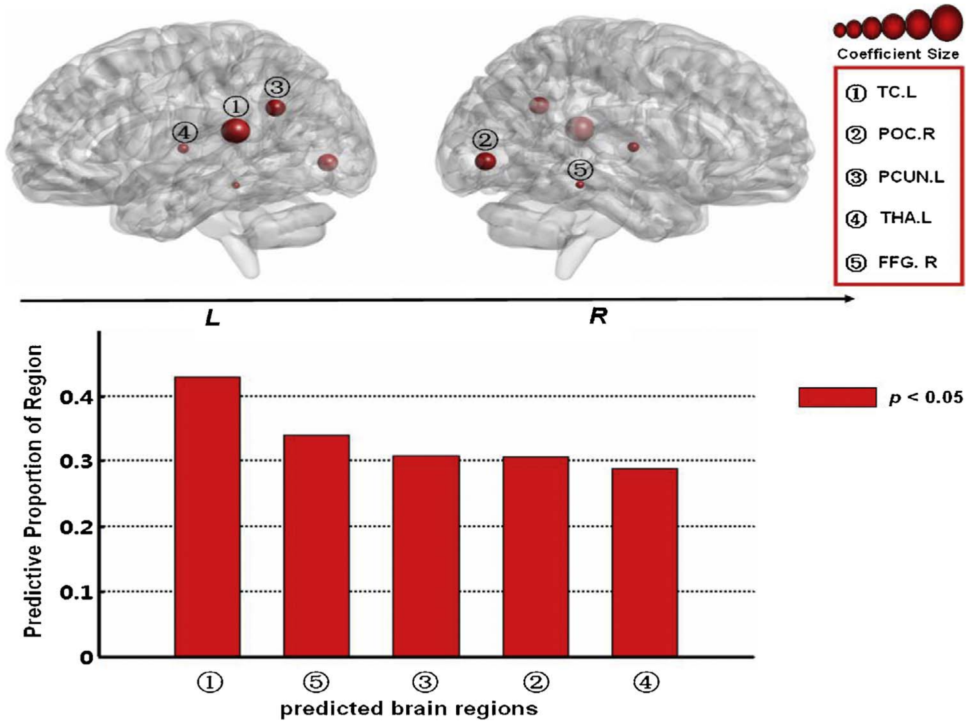

Fig. 3. Surface visualization of brain regions that exhibited significant predictions of TTCT performance in the HG. The model related to each region was significant ($p < 0.05$); the radius of the node corresponds to the coefficient size.

explaining individual differences in creativity. Crucially, we determined that the related regions were predominantly located in the DMN (i.e., left PCUN and right FFG) and SMN (i.e., left TC). The correspondence of networks identified in the prediction of creativity from the analyses of two metrics (i.e., integrated nodal betweenness and integrated nodal global efficiency) also suggests that the functional integration of intrinsic brain activity in these two networks underlies creative ability.

4.3. *Creativity-level dependent brain-behavior correlations*

The present study investigated the associations between network regional properties and creative performance in the HG and LG. We found that these network attributes significantly explained individual differences in creativity in both high and low creativity groups; however, the regions involved were different across the two creativity-level groupings. Specifically, we noted that the integrated nodal betweenness of right POC accounted for creative performance in the HG. Previous studies have revealed that occipital regions are involved in the

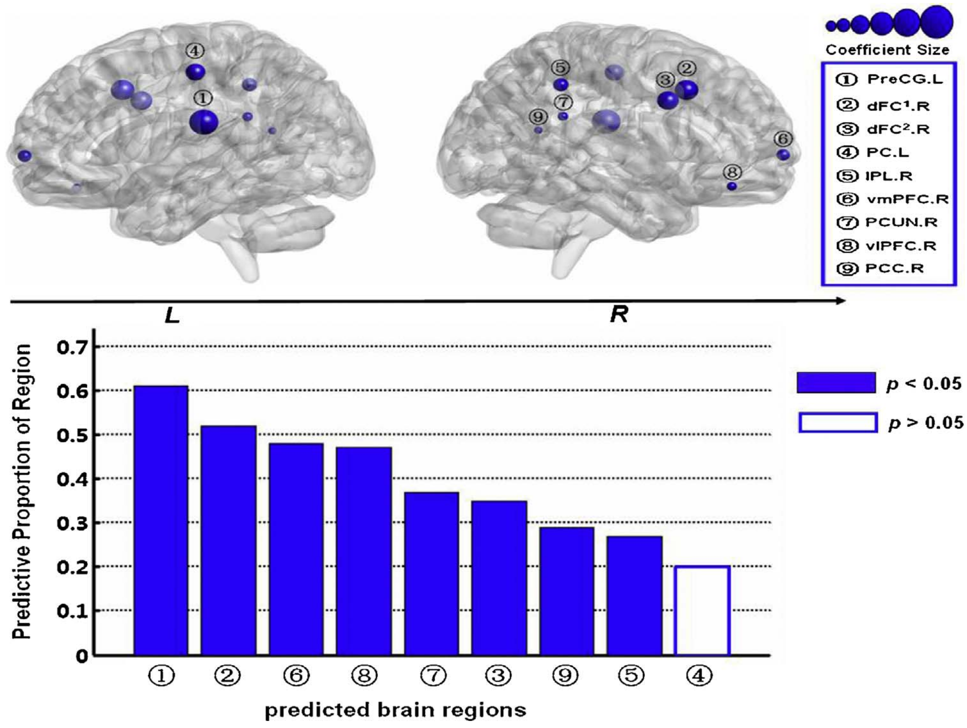

Fig. 4. Surface visualization of brain regions that exhibited significant predictions of TTCT performance in the LG. The model related to each region was significant ($p < 0.05$) with the exception of the left PC; the radius of the node corresponds to the coefficient size.

Table 4
Brain locations involved in MLRA for regional E_{glob}^{int} in the two groups.

Parameters	Region	Hemisphere	Module	MNI-coordinates		
				x (*mm*)	*y* (*mm*)	*z* (*mm*)
$E_{glob}^{int\ a}$						
	TC	L	sensorimotor	−53	−37	13
	AINS	R	cingulo-opercular	38	21	−1
	ICER	L	cerebellum	−34	−67	−29
$E_{glob}^{int\ b}$						
	OC[1]	L	default	−2	−75	32
	FFG	R	default	28	−37	−15
	PCC	L	cingulo-opercular	−4	−31	−4
	TC	R	cingulo-opercular	43	−43	8
	POC[1]	L	occipital	−29	−88	8
	POC[1]	R	occipital	29	−81	14
	POC[2]	L	occipital	−37	−83	−2
	POC[2]	R	occipital	27	−91	2
	OC	R	occipital	9	−76	14
	OC[2]	L	occipital	−34	−60	−5
	MCER	R	cerebellum	14	−75	−21

Note: [a] HG; [b] LG; TC, temporal cortex; AINS, anterior insula; ICER, inferior cerebellum; OC, OC[1] and OC[2], occipital cortex; FFG, fusiform; PCC, posterior cingulate cortex; POC[1] and POC[2], posterior occipital cortex; MCER, median cerebellum; R, right hemisphere; L, left hemisphere.

Table 5
Performance of the MLRA in predicting TTCT including IQ as a covariate in two groups.

Groups	Predictors	Regress	
		Adjusted R^2	*p*-value
HG			
	E_{glob}^{int}	0.599	0.001
	E_{loc}^{int}	0.399	0.030
	B_i^{int}	0.683	0.001
LG			
	E_{glob}^{int}	0.769	0.006
	E_{loc}^{int}	0.518	0.040
	B_i^{int}	0.763	0.002

Note: E_{glob}^{w} , nodal global efficiency; E_{loc}^{w} , nodal local efficiency; B_i^{w}, nodal betweenness. '*int*' represents the abbreviation for "integrated".

generation of creative ideas correlated with use of visual imagery (Howard-Jones, Blakemore, Samuel, Summers, & Claxton, 2005; Chrysikou & Thompson-Schill, 2011), in line with our findings. Moreover, the occipital regions have been found to activated in concert with sensorimotor regions during mental imagery processes (Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998; Mazard, Laou, Joliot, & Mellet, 2005). The present findings regarding the SMN (left TC) and the occipital network (right POC) suggests that the production of imaginary information may facilitate original ideas and products. Furthermore, we also found that the betweenness of the left THA explained TTCT performance. Given that the thalamus is a key region in the attentional network (Callejas, Lupiáñez, & Tudela, 2004; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005), this finding is consistent with previous proposals of the importance of control of attention on creativity during both resting state and tasks (Beaty et al., 2014, 2015). We speculate that the left thalamus may act as a regulator between the DMN and SMN, with highly creative individuals having a more effective resting-attentional system, enabling them to focus on more original and innovative information from both internal and external sources. Importantly, we did not find significant differences in network parameters between the two groups in our secondary analysis that is only restricted to DMN from the Dosenbach et al. anatomical atlas. Thus, the results also support in part the notion that creative ability may be impacted by coupling patterns of regions in multiple networks other than the DMN.

Table 6
Brain locations involved into MLRA for nodal B_i^{int} in the two groups adding IQ as a covariate.

Parameters	Region	Hemisphere	Module	MNI-coordinates		
				x (*mm*)	*y* (*mm*)	*z* (*mm*)
$B_i^{int a}$						
	PCUN	L	default	−6	−56	29
	TC	L	sensorimotor	−41	−37	16
	THA	L	cingulo-opercular	−12	−12	6
	POC	R	occipital	33	−81	−2
$B_i^{int b}$						
	vmPFC	R	default	6	64	3
	vIPFC	R	default	46	39	−15
	PCUN	R	default	9	−43	25
	PCC	R	default	10	−55	17
	PreCG	L	sensorimotor	−54	−22	22
	dFC[1]	R	fronto-parietal	40	17	40
	dFC[2]	R	fronto-parietal	44	8	34
	IPL	R	fronto-parietal	54	−44	43

Note: [a] HG; [b] LG; PCUN, precuneus; TC, temporal cortex; THA, thalamus; POC, posterior occipital cortex; vmPFC, ventral medial prefrontal cortex; vIPFC, ventral inferior prefrontal cortex; PCC, posterior cingulate cortex; PreCG, precentral gyrus; dFC[1] and dFC[2], dorsal frontal cortex; IPL, inferior parietal lobule; R, right hemisphere; L, left hemisphere.

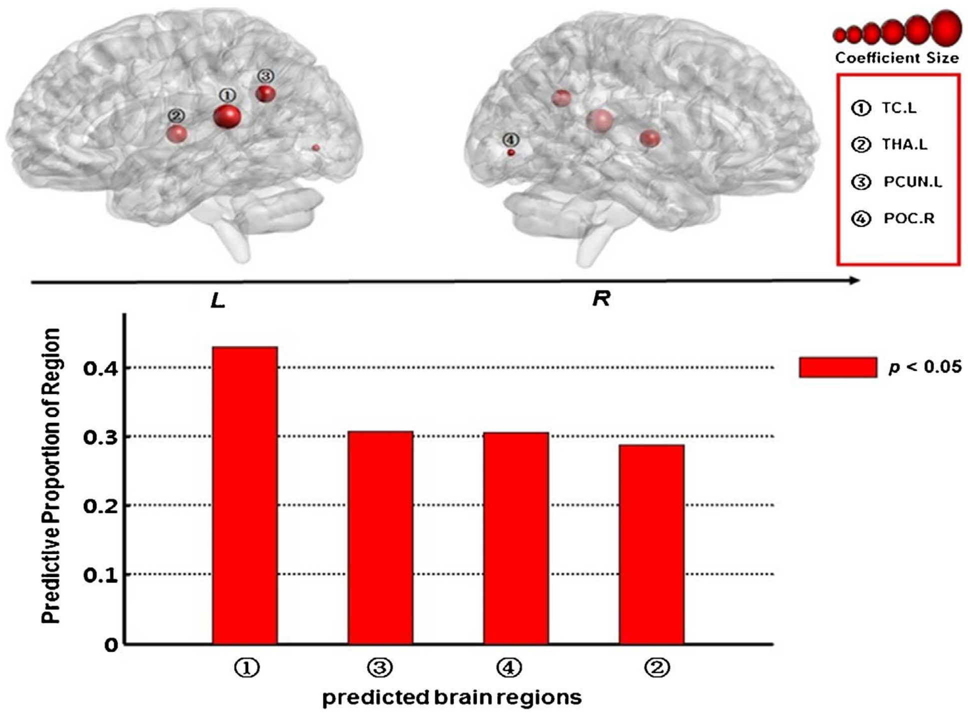

Fig. 5. Surface visualization of brain regions that significantly predicted TTCT performance in the HG after adding IQ as a covariate. The model related to each region was significant ($p < 0.05$); the radius of the node corresponds to the coefficient size.

In contrast, in the LG, regions in the SMN and fronto-parietal network (FPN) tend to jointly account for TTCT performance, which may lead to lower creativity as a result of more stringent top-down control. A recent study (Liu et al., 2015) supports this hypothesis. Specifically, compared with experts, the poems of novices which exhibited less creativity were associated with substantially stronger connectivity between prefrontal regions and motor regions. Another speculation is that the brain exists as an internal hierarchical model (Friston, 2009) in which each system attempts to suppress the free-energy of its subordinates through a process of optimizing predictions to reduce prediction-errors. Thus, we propose that when in the resting state, the DMN of highly creative individuals may play a greater role in preparing resources, and may reduce top-down control to save energy for the search for more original ideas. This free-energy principle may explain why the local network attributes of the HG were unexpectedly less correlated with creative performance compared with the LG.

Regarding the integrated nodal global efficiency, we determined that the right AINS is associated with higher levels of creativity. Many studies have indicated that the AINS is a hub within the salience network (SN), which prepares attention for an external stimulus (Bressler & Menon, 2010) and integrates multiple sensory states, including gustatory, olfactory, auditory, and somatosensory (Ibañez, Gleichgerrcht, & Manes, 2010). Importantly, the AINS may exert an important role as a dynamic switch between the DMN and the ECN

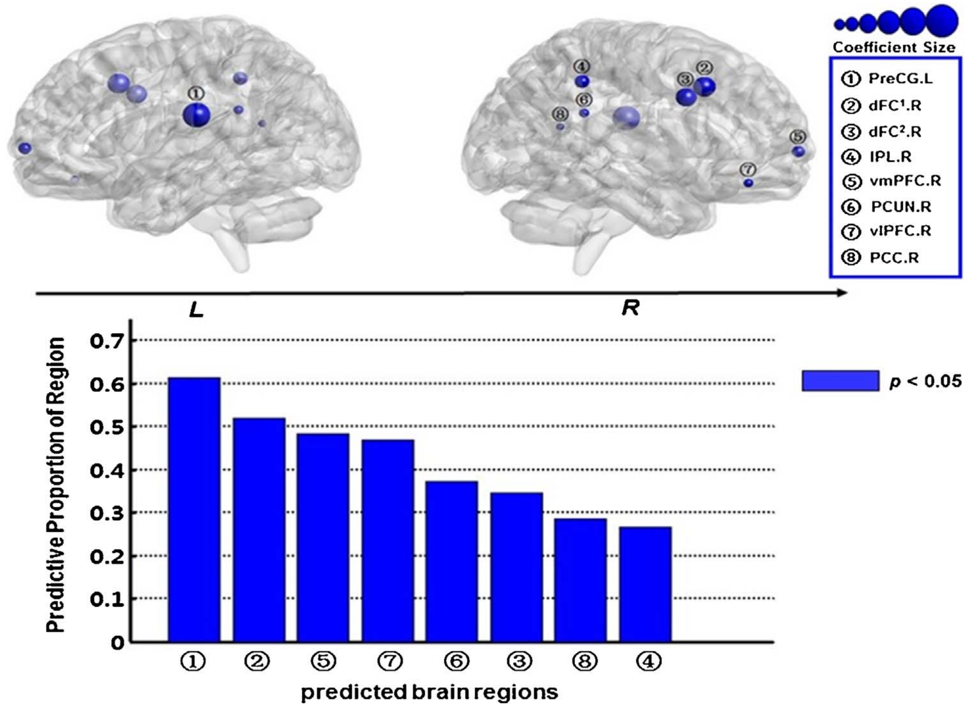

Fig. 6. Surface visualization of brain regions that significantly predicted TTCT performance in the LG after adding IQ as a covariate. The model related to each region was significant ($p < 0.05$); the radius of the node corresponds to the coefficient size.

Table 7
Brain locations involved into MLRA for regional E_{glob}^{int} in the two groups adding IQ as a covariate.

Parameters	Region	Hemisphere	Module	MNI-coordinates		
				x (*mm*)	y (*mm*)	z (*mm*)
E_{glob}^{int} [a]						
	TC	L	sensorimotor	−53	−37	13
	AINS	R	cingulo-opercular	38	21	−1
	ICER	L	cerebellum	−34	−67	−29
E_{glob}^{int} [b]						
	OC^1	L	default	−2	−75	32
	PCC	L	cingulo-opercular	−4	−31	−4
	TC	R	cingulo-opercular	43	−43	8
	POC^1	L	occipital	−29	−88	8
	POC^1	R	occipital	29	−81	14
	POC^2	L	occipital	−37	−83	−2
	POC^2	R	occipital	27	−91	2
	OC	R	occipital	9	−76	14
	OC^2	L	occipital	−34	−60	−5
	MCER	R	cerebellum	14	−75	−21

Note: [a] HG; [b] LG; TC, temporal cortex; AINS, anterior insula; ICER, inferior cerebellum; OC, OC^1 and OC^2, occipital cortex; PCC, posterior cingulate cortex; POC^1 and POC^2, posterior occipital cortex; MCER, median cerebellum. R, the right hemisphere; L, the left hemisphere.

(Andrews-Hanna et al., 2014; Beaty et al., 2015). Similarly, in the present study, the right AINS may reflect the flexible switching between the resting state and divergent tasks.

The current findings also revealed that the network properties of specific regions play unique role in explaining individual differences in creativity. Notably, we found that the integrated nodal global efficiency of occipital network nodes (the bilateral POC^1) exhibited a strong relationship with creative performance in the LG, and a similar trend was also identified in the integrated nodal betweenness of the HG. These findings may indicate that the intrinsic activity of the occipital network influences creative ability, which is consistent with a previous study (Howard-Jones et al., 2005). Nevertheless, these occipital regions tend to play distinct roles in different levels of creativity. Specifically, in the HG, the integrated nodal betweenness was important, emphasizing the information flow of a given node and global connections in a network. In contrast, the integrated nodal global efficiency, which represents the nodal transfer efficiency within the global network, plays a part in the LG. Thus, the HG appear to rely more on occipital intercommunication with other nodes across the whole brain. Given the importance of occipital regions in visual creativity (Chrysikou & Thompson-Schill, 2011), we speculate that increased information flow through this region may be beneficial for fluently generating more creative ideas overall on the TTCT.

Of note, many studies have shown that intelligence and creativity are correlated constructs (Kim, 2005; Batey & Furnham, 2006; Benedek et al., 2014). In the current study, intelligence scores were matched across both groups, thus our findings changed little after adding intelligence as a covariate. Most importantly, we also found that the related nodes that strongly predicted the TTCT scores did not correlate significantly with intelligence scores in either group. This pattern of findings leads us to infer that the role of these regions in explaining TTCT is specific to creative thinking. According to previous evidence, intelligence primarily focuses on the identification of the correct solution, which may be correlated with working memory (Conway, Kane, & Engle, 2003; Ackerman, Beier, & Boyle, 2005; Shelton, Elliott, Hill, Calamia, & Gouvier, 2009), whereas creative thought primarily focuses on the generation of novel approaches. Thus, in the absence of external tasks, the node centrality of the DMN may play a substantially more important role in creativity compared with intelligence, which facilitates an increased generation of spontaneous thought (Buckner et al., 2008; Andrews-Hanna, 2012).

4.4. Limitations

There are several issues that should be addressed in future research. First, creativity is a high-level, complex, cognitive ability that includes multiple processes such as self-generated thought (Beaty, Benedek et al., 2016), executive control (Silvia & Beaty, 2012), top-down control of attention (Nusbaum & Silvia, 2011), and working memory capacity (Lee & Therriault, 2013). Moreover, it is influenced by many psychological factors, such as mood, personality (Ding et al., 2015), and intelligence (Benedek et al., 2014). The present study mainly focused on divergent thinking and investigated the neural factors that may explain individual difference of divergent thinking performance. Divergent thinking is a key element of creative thought (Kim, 2008); however, it remains necessary to further investigate the neural basis of other aspects of the creativity in future studies. Of note, other factors, such as age, genetics, and learning, all of which impact, to some extent, on brain topological attributes (Uhlhaas, Roux, Rodriguez, Rotarska-Jagiela, & Singer, 2010; Fornito et al., 2011; Cao et al., 2014), will also be interesting issues to explore in future research. Second, the present study combined a graph-based network analysis with MLRA approach to demonstrate the importance of regional functional integration properties of resting-state networks in explaining creativity; however, the structural substrates of creativity, such as the white matter connections and morphological structure, remain unclear and should be considered in future studies. Moreover, we concentrated on using the multiple linear regression approach to detect differential contributions of specific regional attributes of particular network nodes to creativity within each group. Future work could expand on this by exploring between-group differences of regional attributes using other approaches, such as multiple variation analysis. Third, the current findings were obtained during resting state, and creative performance was measured using the TTCT. Additional creativity-related cognitive tasks could be employed in which real-time response metrics, such as response time and the accuracy ratio, are recorded; moreover, predictive power of neural response to creative tasks should also be explored. Combining these approaches with the current study will enable a fuller analysis of the inter-individual variation of creativity and neural responses, and the origin of these individual differences in creativity should ultimately be determined.

5. Conclusions

The present study investigated associations between the topological organization of resting-state brain networks and creative performance. We demonstrated that an optimized organization of intrinsic brain network sustains creative thought. Of the brain network properties related to creativity, the functional integration properties performed best in explaining inter-individual differences in creative performance. Regions of the DMN and SMN were consistently and tightly related to creative performance and the difference in resource control and allocation may be an important aspect of individual differences in creativity. This study has important implications for understanding the neural substrates that underlie creative performance.

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