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Research report

Increased resting functional connectivity of the medial prefrontal cortex in creativity by means of cognitive stimulation

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ABSTRACT

Creativity is imperative to the progression of civilization and is central to cultural life. Many neuroimaging studies have investigated the patterns of functional activity in the brain during different creative tasks, and the structural and functional characteristics of the highly creative individuals. However, few studies have investigated resting-state functional connectivity (RSFC) in the brain related to individual differences in creativity, and it is still unclear whether the RSFC underlying creativity can be changed by training. The present study therefore used resting-state functional magnetic resonance imaging (Rs-fMRI) to investigate the relationship between RSFC and creativity (divergent thinking, measured by the Torrance Tests of Creative Thinking) to explore whether RSFC can be influenced by cognitive stimulation. The results of 269 adults showed that creativity was positively correlated with the strength of RSFC between the medial prefrontal cortex (mPFC) and the middle temporal gyrus (mTG). In addition, behavioral data showed that cognitive stimulation was successful in enhancing originality in a subset of the original participants (n = 34). Most interesting, we found that there was also a significantly increased RSFC between the mPFC and the mTG by analyzing the data of Rs-fMRI after creativity training. Taken together, these results suggest that increased RSFC between mPFC and mTG, which belong to the default mode network might be crucial to creativity, and that RSFC between the mPFC and mTG can be improved by means of cognitive stimulation (reflecting creativity training-induced changes in functional connectivity, especially in the lower creativity individuals who had lower scores of Torrance Tests of Creative Thinking).

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1. Introduction

Creativity is imperative to the progression of civilization and is central to cultural life. There has been increasing interest in the gray and white matter structural magnetic resonance imaging characteristics associated with inter-individual differences in human creativity, particularly divergent thinking (creative ability to consciously generate new ideas that branch out and allow for many possible solutions to a given problem) (Kase et al., 2011; Silvia et al., 2008). However, the functions of implicated brain regions remain unclear, as does the functional connectivity associated with individual differences in creativity.

Communication between brain regions may be crucial in complex cognitive processes (e.g., creativity) (den Heuvel et al., 2010). Examination of resting-state functional connectivity (RSFC), which reflects temporal correlations between blood oxygen level-dependent signals in different brain regions during rest, can indicate direct or indirect functional relations between brain regions (Fox & Raichle, 2007; Friston, Frith, Liddle, & Frackowiak, 1993). Previous studies have demonstrated that RSFC of default mode network (DMN) is highly test–retest reliable (Shehzad et al., 2009; Zuo et al., 2010). Specifically, a recent resting-state functional magnetic resonance imaging (Rs-fMRI) study showed that higher creativity was associated with RSFC between the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC), which are key nodes of the DMN (Takeuchi et al., 2012). Thus, higher levels of creativity might be attained through increased interaction in the DMN. In other words, higher creativity may be associated with the strength of RSFC among specific brain regions, and the interactions between these brain regions might be crucial.

Few studies have investigated RSFC associated with individual differences in creativity, and although previous studies indicated that RSFC can be changed after task (Calhoun, Kiehl, & Pearlson, 2008; Fransson, 2006), the robustness of RSFC altered by creativity training is uncertain. In a series of studies, Fink et al. (2010) and Fink, Graif, and Neubauer (2009) used cognitive stimulation to enhance creative cognition, wherein participants performed the alternative uses task after exposure to other people's ideas (participants are required to come up with unusual use of those common and everyday life objects after being showed the example answers from others). In fact, cognitive stimulation is a person's creative cognition, which can be influenced by other's cognition (confronting with ideas produced by other people) (Fink et al., 2010; Osborn, 1957). The authors found that originality (the statistical rarity of the unusual uses of common, everyday objects) performance improvement was associated with activation increases in the temporal–parietal junction, mPFC and PCC (Fink et al., 2010). Therefore, the present study used Rs-fMRI to examine the relationship between RSFC and creativity measured by the Torrance Tests of Creative Thinking (TTCT) which is a questionnaire included seven tasks to measure individual's verbal creativity ability, and explore whether RSFC in a post-task (creativity training task) resting state can be influenced by cognitive stimulation.

As the anterior core of the DMN backbone, mPFC has been associated with individual differences in creativity with its structure and function (Ellamil, Dobson, Beeman, & Christoff, 2012; Moore et al., 2009; Takeuchi et al., 2012). Thus, the current study explored correlations between the TTCT scores and the strength of RSFC between the mPFC and other brain regions. Based on previous studies (Gansler et al., 2011; Jung et al., 2009; Qiu et al., 2010; Takeuchi et al., 2010), we hypothesized that higher creativity might be associated with RSFC between the mPFC, and other brain regions including the PCC (Takeuchi et al., 2012), temporal gyrus (implicated in novel association and conceptual expansion) (Ellamil et al., 2012); and inferior parietal lobe (associated with spatial representations and processing) (Gansler et al., 2011). We also predicted that RSFC between the mPFC and other brain regions would be altered after creativity training (cognitive stimulation), which can improve participants' originality of creative response (Fink et al., 2010, 2009). Specifically, we presumed that RSFC between the mPFC and other specific brain regions would be increased during the post-task resting state. The applications of creativity-related neural plasticity evoked by training are considerable, particularly regarding educational practice.

2. Materials and methods

2.1. Participants

In total, 269 healthy individuals (mean age: 20.0 ± 1.4, males: 138) from Southwest University, China participated in this study as part of our ongoing project to examine the association between brain imaging, creativity and mental health. Totally 34 individuals (mean age: 20.3 ± 2.2, males: nine) of the original 269 participants were randomly selected to take part in a subsequent cognitive stimulation task. All participants were right-handed, with no history of neurological or psychiatric problems.

The local ethics committee of Southwest China University approved this study. All participants provided written informed consent prior to the study, which was approved by the Institutional Human Participants Review Board of Southwest University Imaging Center for Brain Research.

2.2. Creativity assessment

The TTCT was designed as a measure of divergent thinking, which is a central aspect of creativity (Huang et al., 2012). The TTCT contains verbal, figural and auditory tests (Dixon & Williams, 2003; Huang et al., 2012). In this study, the verbal TTCT was used to assess individual divergent thinking abilities (Carson, Bittner, Cameron, Brown, & Meyer, 1994; Kim, Cramond, & Bandalos, 2006; Torrance, 1987, pp. 189–215). The verbal TTCT comprises seven tasks. Three of the tasks required participants to generate questions, causes and consequences in response to a scenario presented pictorially. The fourth task required participants to propose creative ideas to improve a toy elephant (for example, remake this toy elephant as a money-box or pillow). The fifth task asked participants to generate different ideas for the unusual use of cardboard boxes (e.g., the cardboard boxes can be used as feeder or

bathtub for animals). The sixth task required participants to think of unusual questions relating to a carton (e.g., why people make carton). Finally, the seventh task asked participants to imagine the consequences of an imaginary scenario (de Souza et al., 2010). For each task scoring comprised three components: fluency (the number of meaningful and relevant responses, which is associated with the ability to generate and consider other possibilities), flexibility (the number of different categories of responses, which reflects the ability to shift between conceptual fields) and originality (the degree of originality of the responses, which is associated with thinking "outside the box") (Chávez-Eakle, Graff-Guerrero, García-Reyna, Vaugier, & Cruz-Fuentes, 2007; de Souza et al., 2010). The evaluation of participates' responses including the score and the category of certain answer has been finished according to norming scoring guides (DeHaan, 2009; Runco, Millar, Acar, & Cramond, 2010; Silvia, 2011; Torrance, 1998). More specifically, the score of fluency is the number of meaningful responses, the score of flexibility is the number of different categories of response (e.g., the cardboard boxes can be used as shoes or clothes which are belong to dress category, therefore, the two responses only scoring 1 score in the fifth task), and the score of originality is the degree of originality of the response (e.g., the cardboard boxes can be In addition, analysis of used as postcard scoring 2 score, but the response the cardboard boxes can be used as vase scoring 0 score). Three raters took part in the scoring; the inter-rater correlation coefficient was .9. The current study used the total creativity scores (sum of fluency, flexibility and originality scores) (de Souza et al., 2010) for each dimension was highly correlated with the total creativity score as well as with each other (all correlations between the scores of any two dimensions had simple correlation coefficients of $>$.81) on the basis of the findings of Heausler and Thompson (1988), who suggested that the high correlations among the three subscales of the TTCT could not provide meaningfully different data (Heausler & Thompson, 1988).

2.3. Assessment of general intelligence

In order to examine intellectual ability, participants completed the Combined Raven's Test (CRT), which is a recognized intelligence test with a high degree of reliability and validity (Tang et al., 2012). The reliability coefficient was .92 (Li & Chen, 1989; Wang et al., 1989). The CRT, which included the Raven's standard progressive matrix (C, D, E sets) and Raven's colored progressive matrix (A, A_B, B sets), consisted of 72 items revised by the Psychology Department of East China Normal University in 1989. The score of this test (the number of correct answers given in 40 min) was used as a psychometric index of individual intelligence. In line with standard practice, the current study focused on the total score of the test (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; Takeuchi et al., 2011, 2010).

2.4. Experimental design and procedure

The experiment composed of three sections. The first section, defined as the pre-task resting state, was designed to acquire resting-state functional images of all the 269 participants (following the completion of the TTCT and CRT) and used to investigate the relationship between RSFC and creativity. Scanning lasted for 8 min and 8 sec and 242 volumes. During scanning, all participants were instructed to remain motionless with their eyes closed and to try not to concentrate on anything in particular, which was defined as the resting state (Yan et al., 2009).

In the second section, 34 (of the original 269) participants were randomly selected to perform a creativity-related training task (cognitive stimulation) similar to that used in the previous studies by Fink et al. (2010) after the pre-task resting state scanning. This task required subjects to generate as many as possible novel and unusual uses of common everyday objects (e.g., "tin", "umbrella"). There are two stages and each stage contained 10 conventional everyday objects. In the first stage, participants were presented with the pictures of one objects (e.g., "tin", "umbrella") and asked to come up with novel, unusual uses of the objects in 20 sec. And then, participants were given 8 sec to report all their ideas (Fink et al., 2010). In the second stage, participants were also presented with the pictures of objects and instructed to think of original and unusual uses of these objects following exposure to external ideas (e.g., those of other people) for 6 sec, which is an effective group-based brainstorming technique (Leggett Dugosh & Paulus, 2005). Participants were given 8 sec to report all their ideas too (Fink et al., 2010). The first stage was referred to as the no-cue condition and the second stage as the cue condition. Subjects can relax 2 min between these two stages.

The third section, defined as the post-task resting state, was acquired from the subjects ($n = 34$) who participated in the second section and designed to investigate the effect of creativity-related training task (cognitive stimulation) mentioned above on the intrinsic RSFC. In this study, we focused on the overall effect on the functional connectivity of this training task rather than the effects of no-cue condition or cue condition. This scanning acquired 242 volumes in 8 min and 8 sec.

2.5. Behavioral data analysis

Performance during the cognitive stimulation task was quantified in terms of the degree of originality of the ideas generated (Fink et al., 2010). An external rating procedure was applied, which resembled the consensual assessment technique described by Amabile (1983). For this purpose, five independent raters were instructed to score each single idea on a nine-point rating scale ranging from 1 ("not original at all") to 9 ("highly original"). The rater showed excellent inter-rater agreement, as revealed by high inter-rater correlation coefficients across all creative ideas ($r > .92$). To simplify interpretation of the results, the originality scale was inverted so that higher scores (maximum score of 9) reflected enhanced originality (Fink et al., 2010). The behavioral data were analyzed using the statistical software SPSS 16.0.

2.6. Imaging data acquisition

All functional images were obtained from a 3-T Siemens Magnetom Trio scanner (Siemens Medical, Erlangen, Germany) with a 12-channel phased-array head coil. The whole-brain resting-

state functional images were acquired using gradient-echo echo planar imaging (EPI) sequences, with the following parameters: slices = 32, repetition time (TR)/echo time (TE) = 2000/30 msec, flip angle = 90°, field of view (FOV) = 220 mm × 220 mm, slice thickness = 3 mm, slice gap = 1 mm, matrix = 64 × 64, resulting in a voxel with 3.4 × 3.4 × 4 mm^3.

2.7. Preprocessing of imaging data

The processing of the pre-task (269 participants) and post-task (34 participants) resting-state image data were performed using the data processing assistant for resting state (DPARSF) software (http://www.restfmri.net/forum/DPARSF) (Yan et al., 2009) and the REST toolkit (Song et al., 2011). Both toolboxes were based on the SPM8 software package. The first 10 volumes of the functional images were discarded to account for signal equilibrium and participants' adaptation to their immediate environment. The remaining 232 images were preprocessed, which included slice timing, head motion correction and spatial normalization to a standard template. The time courses for various covariates (global signal, white matter, cerebrospinal fluid, and six motion parameters for head movement) were extracted and regressed out in order to cancel out the potential impact of physiological artifacts. Here, we utilized the Friston 24-parameter model to regress out head motion effects from the realigned data based on recent reports that higher-order models demonstrate benefits in reducing head micro movements (Satterthwaite et al., 2013; Yan et al., 2013). We further addressed the residual effects of motion in group analyses by including mean framewise displacement (FD) derived with Jenkinson's relative root mean square (RMS) algorithm as a nuisance covariate (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; Yan et al., 2013). The images were then resampled to 3-mm cubic voxels, followed by spatial smoothing (6 mm Full Width Half Maximum – FWHM). The smoothed data were linearly detrended and filtered using a band pass filter (.01–.08 Hz) to eliminate low frequency fluctuations. The preprocessing steps of functional connectivity followed the standard protocol reported by Yan and Zang (Chao-Gan & Yu-Feng, 2010; Chen et al., 2012; Tian, Ren, & Zang, 2012).

2.8. Functional connectivity for the 269 participants

Functional connectivity was examined using a region of interest (ROI) seed method. The divergent thinking test has been shown to be closely interrelated with the strength of RSFC between the mPFC and PCC (Takeuchi et al., 2012) which are regions of the DMN (Brewer et al., 2011; Fox et al., 2005). For the current study, the seed region was defined as a sphere with a 6-mm radius centered at the mPFC (−1, 47, −4), as reported in previous studies (Fox et al., 2005; Takeuchi et al., 2012). To generate the functional connectivity map, the averaged time series was obtained from the ROI and the correlation analysis was conducted between the ROI and the voxel in the whole brain. The correlation coefficient map was converted into z-map by Fisher's *r*-to-*z* transformation to improve the normality. Then, individual *z* value maps were analyzed with a random effect one-sample *t*-test to identify voxels correlation with the ROI time series [$p < .01$, false discovery rate (FDR) correction; see Supplementary material, Fig. S1]. Besides, we also tested the relationship between individual creativity and RSFC with other ROI to determine whether creativity is also associated with RSFC in networks other than DMN. For this purpose, we investigated the networks seeded by the bilateral dorsolateral prefrontal cortices (DLPFCs), bilateral dorsal anterior cingulate cortex (dACC) (Fox et al., 2005; Takeuchi et al., 2012) and the bilateral orbital frontoinsula (FI) (Seeley et al., 2007).

Multiple linear regression analysis was employed to identify brain regions in which RSFC strength with the mPFC was significantly correlated with individual creativity measured by the TTCT (total creativity score). Previous studies have indicated that some aspects of brain asymmetries interact with gender. For example, males have a greater structural asymmetry of the plenum temporal than females (Kulynych, Vladar, Jones, & Weinberger, 1994), and male brain is more functionally lateralized or asymmetric in visual and auditory areas than the female brain (Hiscock, Inch, Jacek, Hiscock-Kalil, & Kalil, 1994; Hiscock, Israelian, Inch, Jacek, & Hiscock-Kalil, 1995). In addition, sex-related differences also exist at a microscopic level, involving differences in connectivity, neuronal density or synaptic efficiency (Frost et al., 1999). Thus, sex, age, mean FD and CRT score were included as regressors of no interest (covariates in the design matrix). Moreover, three multiple regression analyses were carried out to examine the relationship between dimensions of creativity (fluency, flexibility, originality) and the strength of RSFC between the mPFC and other brain regions. Sex, age, mean FD and CRT score were again included as regressors of no interest. Same analysis was also performed to identify brain regions in which RSFC strength with the other six seed ROIs (bilateral DLPFC, bilateral dACC and bilateral FI) was significantly correlated with individual creativity measured by the TTCT (total creativity score). Sex, age, mean FD and CRT score were included as regressors of no interest.

We subsequently examined whether there was a correlation between individual general intelligence measured by the CRT and RSFC with the mPFC. This enabled us to establish whether there was any overlap between the ROIs (i.e., between ROIs associated with creativity and RSFC and those associated with general intelligence and RSFC). Sex, age, mean FD and total TTCT creativity score were included as regressors of no interest. We also examined whether the relationship between RSFC with the mPFC and creativity differed between sexes. This was achieved using voxel wise analysis of covariance (ANCOVA; during the whole-brain analysis), whereby sex was a group factor (using the full factorial option in SPM8). Age, CRT score, mean FD and TTCT total creativity score were included as covariates. A multiple comparison correction was carried out on the whole-brain data using the voxel-level FDRs approach (Benjamini & Yekutieli, 2001). Generally, FDR is the expected proportion of false discoveries among the discoveries. Setting threshold level at .05, means that on the average we expect no more than 5% of the discoveries to be false discoveries (Assaf et al., 2010; Laird et al., 2010).

2.9. Data analysis for the 34 participants

Based upon the brain regions whose connectivity with mPFC significantly associated with creativity measured by the TTCT,

we used the task-based fMRI data from the 34 participants to examine whether these connectivities can be modulated after performance of cognitive stimulation task. To analyze the differences in RSFC between pre-task resting state and post-task resting state for the 34 participants, we extracted the time course for each ROI by averaging the time series of all voxels within each region. In order to improve the normality of the partial correlation coefficients (Fox & Raichle, 2007; Salvador, Suckling, Schwarzbauer, & Bullmore, 2005) and allow analysis of individual differences, the correlation coefficients were converted into z-values using Fisher's *r*-to-z transformation. Specifically, we analyzed the correlation between the connection strength of the two ROIs (z-transformed *r* values) and the TTCT scores in SPSS 16.0.

3. Results

3.1. Behavioral data

Table 1 shows the mean and the standard deviation of TTCT, CRT scores, and age in large sample ($n = 269$) and small sample ($n = 34$). There were no significant correlations between the psychological or epidemiological measures (CRT score, sex and age) and the total TTCT scores in the two samples.

3.2. Correlations of creativity relating to the strength of RSFC with the mPFC

We examined brain areas that showed an association between the TTCT score, which reflects creativity, and the strength of RSFC with the mPFC. After controlling for age, sex, mean FD and CRT scores, a multiple regression analysis revealed that the TTCT total score was significantly positively correlated with the strength of RSFC between the mPFC and the middle temporal gyrus [mTG (−54, −33, −15), $T = 5.55$, $p < .05$ corrected for multiple comparisons using the voxel-level FDR at the whole-brain level; see Fig. 1A]. There were no regions showing a significant negative correlation between the strength of RSFC with the mPFC and the total TTCT score.

The results also showed a significant positive correlation the strength of RSFC between mPFC and mTG and each dimension of creativity [the statistical values and coordinates of the peak voxel were as following: mTG (−54, −33, −15), $T = 5.55$, $p < .05$ in the analysis of originality (see Fig. 1C); mTG (−54, −33, −15), $T = 5.07$, $p < .05$ in the analysis of flexibility (see Fig. 1D); and mTG (−54, −33, −15), $T = 5.16$, $p < .05$ in the analysis of fluency (see Fig. 1E)]; all the results corrected for multiple comparisons using the voxel-level FDR approach at the whole-brain level. The high correlations among the three subscales of the TTCT meant that the subscales could not provide meaningfully different information. Further investigations demonstrated that there were no significant correlations between the CRT scores and the strength of RSFC with the mPFC in any of the regions. In addition, there were no significant interaction effects between the total TTCT score and sex in terms of the strength of RSFC with the mPFC.

Moreover, in order to test whether individual creativity measured by TTCT test was associated with RSFC between mPFC and PCC in a previous study (Takeuchi et al., 2012), we relax the voxel-level $p < .05$ uncorrected, but leading to no significant correlation with the strength of RSFC between mPFC and PCC. In addition, we also examined areas showing an association between the TTCT score and the strength of RSFC with the bilateral DLPFC, bilateral dACC and bilateral FI to determine whether creativity was also associated with RSFC in networks other than DMN. After controlling for age, sex, mean FD and the CRT score, multiple regression analysis revealed no significant correlations ($p > .05$ corrected for multiple comparisons using the voxel-level FDR approach at the whole-brain level) between the TTCT test score and the strength of RSFC with the six ROIs in any of the regions.

Table 1 – The mean and the standard deviation of TTCT, CRT scores, and age in large sample ($n = 269$) and small sample ($n = 34$).

	Large sample ($n = 269$)	Small sample ($n = 34$)
Total score of TTCT-verbal	133.7 ± 42.4	146.5 ± 52.9
Score of CRT	66.0 ± 3.5	66.5 ± 3.3
Age	20.0 ± 1.4	20.3 ± 2.2

3.3. Cognitive stimulation (creativity training) task

The scores of originality for the 34 participants revealed that in the cue condition were rated as being significantly [$t(33) = 4.98$, $p < .001$] more than those in the no-cue condition (5.76 *vs* 5.48). This is in line with the findings reported in a previous study (Fink et al., 2010), and showed that this creativity training task might be an effective task which can really improve the participants' creativity.

3.4. Training-induced changes in RSFC between the mPFC and the brain region

In the pre-task resting state, the TTCT score was significantly positively correlated with the strength of the mPFC and mTG connection ($r = .41$, $p = .021$; see Fig. 2A) for the 34 participants, however, in the post-task resting state, there was no significant correlation between the TTCT score and the strength of the mPFC and mTG connection ($r = .05$, $p = .803$; see Fig. 2B), In addition, a paired *t*-test was used to explore whether creativity training was related to changes of RSFC between the mPFC and mTG during the post-task resting state compared to pre-task resting state. The result showed that the strength of the mPFC and mTG connectivity appears to be increased for the participants after creativity training task [.49 *vs* .12, $t_{(33)} = 7.20$, $p < .001$; see Fig. 2C]. In order to further test this result, we divided the 34 participants into low creativity group (participants who have lower scores of TTCT) and high creativity group (participants who have higher scores of TTCT) ($n = 17$ per group), there are no differences between the two groups in CRT score [$t_{(32)} = .71$, $p = .486$]. A paired-samples *t*-test showed that the strength of RSFC between the mPFC and mTG was indeed increased (post-task *vs* pre-task) for the two groups after training task: for the high group [.49 *vs* .22, $t_{(16)} = 3.59$, $p = .002$; see Fig. 2D], for the low group [.50 *vs* .01,

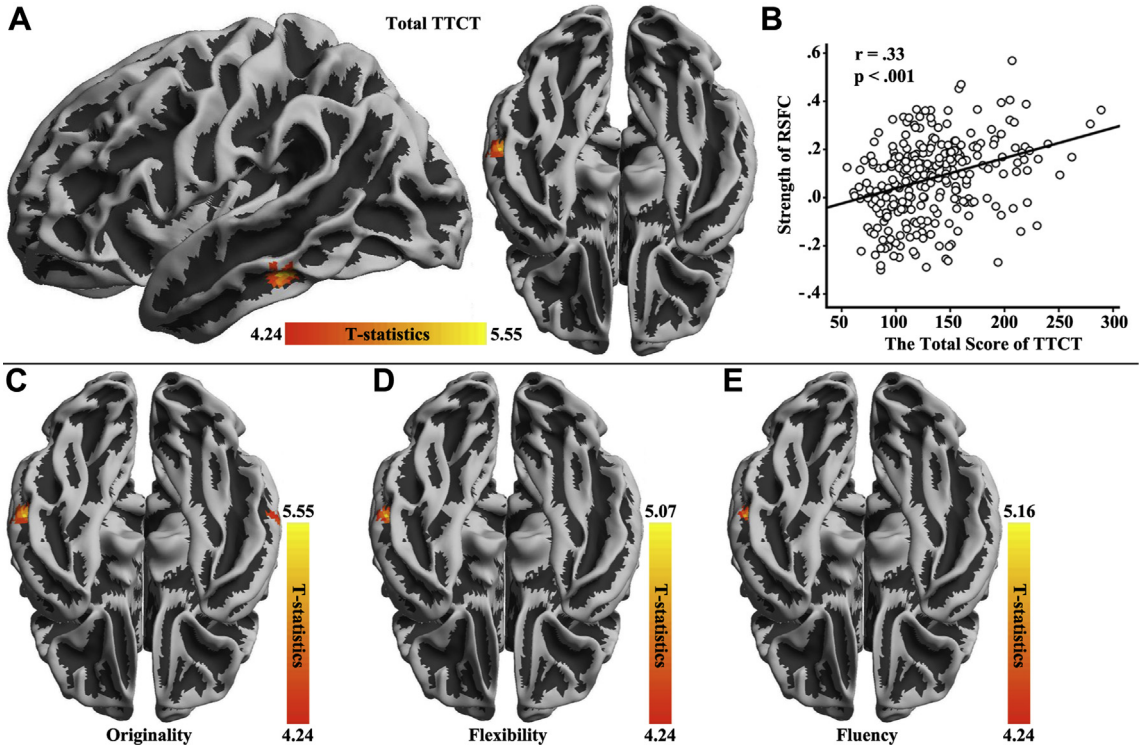

Fig. 1 – (A) Region of correlation between the strength of RSFC with the mPFC and the total score of TTCT-verbal test (the results are shown with a threshold of $p < .05$ corrected for multiple comparisons using the voxel-level FDR at the whole-brain level). (B) The scatterplot of the correlation involving RSFC between the mPFC and the mTG (−54, −33, −15) and total score of TTCT, as seen, creativity was significantly and positively correlated with the strength of RSFC between the mPFC and the mTG. (C) Regions of correlation between the strength of RSFC with the mPFC and the originality; (D) Regions of correlation between the strength of RSFC with the mPFC and the flexibility; (E) Regions of correlation between the strength of RSFC with the mPFC and the fluency (all the results are shown with a threshold of $p < .05$ corrected for multiple comparisons using the voxel-level FDR at the whole-brain level). As seen, three dimensions were significantly and positively correlated with the strength of RSFC between the mPFC and the mTG.

$t_{(16)} = 7.46$, $p < .001$; see Fig. 2D]. An independent-samples *t*-test showed that the strength of RSFC between the mPFC and mTG (post-task minus pre-task) was significantly increased in the low group compared to the high group [.49 *vs* .27, $t_{(32)} = 2.28$, $p = .029$; see Fig. 2D].

4. Discussion

The present study used Rs-fMRI to investigate the relationship between RSFC and creativity measured by the TTCT, and determine creativity training can influence RSFC in a post-task. To the best of our knowledge, this is the first study to investigate changes in RSFC induced by creativity training. Our results revealed a significant positive correlation between the strength of the mPFC–mTG RSFC and mTG and creativity, specifically divergent thinking. In addition, analysis of the post-task Rs-fMRI data revealed significantly increased RSFC between the mPFC and the mTG in individuals after creativity training. Taken together, our results suggest that increased RSFC between the mPFC and mTG (regions of the DMN) might be critically involved in creativity, and this connectivity can be improved by means of cognitive stimulation.

Previous functional imaging studies have indicated that the mPFC might be involved in conflict processing, response selection and inhibitory control (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Crottaz-Herbette & Menon, 2006; van Veen & Carter, 2005). Furthermore, some research suggests that the mPFC might be associated with individual differences in creativity measured by divergent thinking tasks, such as creative story generation (originality), the alternative uses task, the Remote Associates Test, the TTCT, the design fluency test and the S-A creativity test. In addition, many studies have indicated that the left mTG might play key roles in semantic processing, such as metaphor understanding (Cardillo, Watson, Schmidt, Kranjec, & Chatterjee, 2012; Goel & Dolan, 2001), semantic representation and control (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Whitney, Jefferies, & Kircher, 2011), and conceptual integration and comprehension (Hickok & Poeppel, 2004; Turken & Dronkers, 2011). Other studies also suggested that the left mTG might be involved in the maintenance of various processes such as verbal working memory (Collette et al., 2001; Zurowski et al., 2002), switching from one task to another (cognitive flexibility, necessary for a creativity) (Sohn, Ursu, Anderson, Stenger, & Carter, 2000). Specifically, Blackwood et al. (2001) found that the mTG might

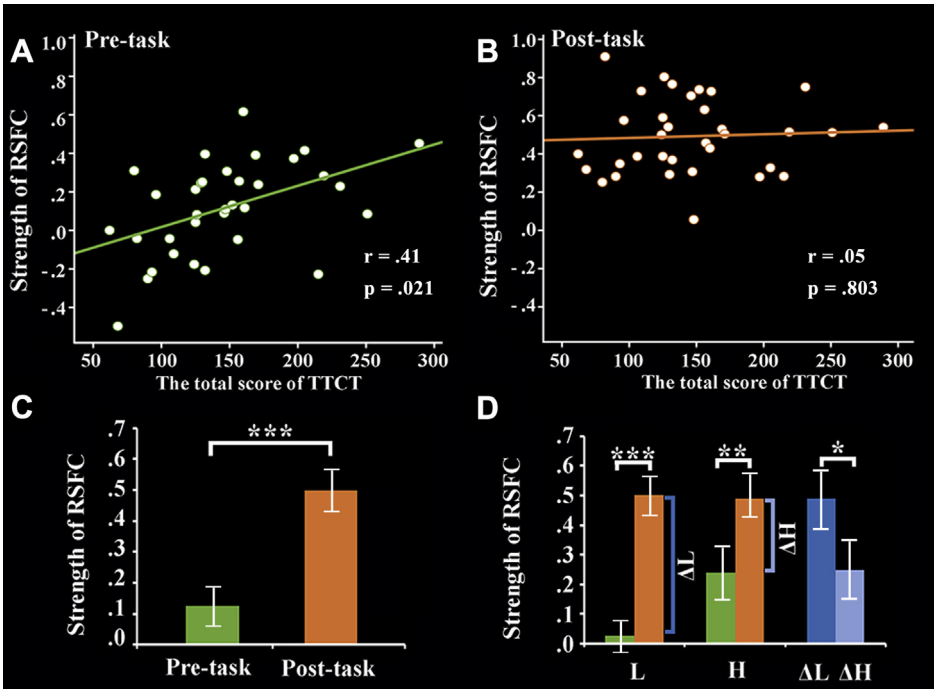

Fig. 2 – Strength of RSFC: strength of RSFC between mPFC and mTG; (A) the correlation scatterplot between the total score of TTCT and strength of RSFC in the pre-task resting state. (B) The correlation scatterplot between the total score of TTCT and strength of RSFC in the post-task resting state. (C) $^{***}p < .001$, the bar showed that the strength of RSFC significantly increased after training task (post-task *vs* pre-task). Error bars show 95% confidence interval of mean. (D) $^{**}p < .01$, $^{*}p < .05$. L: the subjects with lower score ($n = 17$) of TTCT, H: the subjects with higher score ($n = 17$) of TTCT, ΔL: post-task minus pre-task (strength of RSFC) for low group, ΔH: post-task minus pre-task (strength of RSFC) for high group. The bar showed that the strength of RSFC significantly increased after training task for two groups (post-task *vs* pre-task) and the two groups have significant difference in the Δ (post-task minus pre-task). Error bars show 95% confidence interval of mean.

be related to form paranoid delusions, which were associated with creative imagination and fantasy (Bechtereva et al., 2004). Moreover, the mTG was also found to play an important role in insight problem solving (Luo & Knoblich, 2007). What's more, previous studies had also reported enhanced visual artistic ability (visual creativity) in patients with left temporal lobes degeneration, which adversely affected their speech-language (Drago et al., 2009; Miller & Hou, 2004). Together, these studies indicate that divergent thinking (e.g., the verbal TTCT) might implicate areas of the brain that are crucial for executive control, semantic cognition and novel association, such as the mPFC and the left mTG.

Increased RSFC between the mPFC and the mTG was linked to the higher level of creativity (divergent thinking). As described above, the mTG might be related to semantic processing, such as novel association, conceptual expansion and unique response (Abraham, Schubotz, & Von Cramon, 2008; Binder, Desai, Graves, & Conant, 2009; Cappa, 2008; Fiebach, Friederici, Smith, & Swinney, 2007). Chávez-Eakle et al. (2007) also found that fronto-temporal functioning might be crucial for creative achievement during performance of the TTCT (e.g., originality). It is well known that the verbal TTCT is primarily a measure of the cognitive abilities associated with the generation of ideas that are innovative or uncommon (e.g., the alternative uses test). That is to say, participants need to represent and integrate multiple conceptual relations (different ideas) in working memory during the performance of creative tasks. It has also been suggested that the mPFC is implicated during the manipulation of information that is being actively maintained in working memory (Cairo, Liddle, Woodward, & Ngan, 2004; DeYoung et al., 2010). Thus, we propose that individual differences in creativity measured by the TTCT (e.g., originality, flexibility and fluency) might be related to these basic cognitive abilities (e.g., executive control, semantic processing and novel association) associated with increased RSFC between the mPFC and the mTG within the DMN during rest. In addition, Andrews-Hanna, Reidler, Sepulcre, Poulin, and Buckner (2010) pointed out that the DMN might consist of two separate subsystems, for example, the dorsal mPFC-lateral temporal cortex (including the mTG), temporal–parietal junction and temporal pole subsystem, which has been shown to be preferentially active when participants reflect on their current mental states (Andrews-Hanna et al., 2010) in terms of metacognition (Ochsner et al., 2004) for example. That is, individuals with higher creativity might have an enhanced metacognitive ability to evaluate and regulate their thoughts (as revealed by divergent thinking) based on their awareness of effectiveness (or originality). Therefore, increased RSFC between the mPFC and the mTG in the DMN might help to facilitate the generation of novel ideas that requires self-regulated information transfer between the mPFC and the mTG (Dorfman, Martindale, Gassimova, &

Vartanian, 2008; Howard-Jones & Murray, 2003; Vartanian, Schwartz, & Brownell, 2007). Overall, the results of the present study indicate that higher creativity may be associated with resting-state brain connectivity and the functions of the mPFC and the mTG.

Most importantly, after creativity training, we found that there was a significant increase in RSFC between the mPFC and the mTG during the post-task resting state. The current study used cognitive stimulation to enhance participants' divergent thinking based on the findings of Fink et al. (2009, 2010). Our behavioral data showed that there was a significant training effect (improved originality) associated with exposure to other people's ideas regarding unusual uses of an everyday object. Fink et al. (2009, 2010) found that the intervention (training effect) was associated with an increase in prefrontal alpha in the upper alpha bandwidth (10–12 Hz) that was specifically related to the temporal–parietal junction, mPFC, and PCC regions. The authors postulated that improvements in performance might be due to heightened internal awareness (an efficient bottom–up regulation of attention). That is, during the performance of creative tasks (creativity training), participants tried to represent and integrate multiple conceptual relations in order to form novel associations, which implicates the mPFC and the mTG. After creativity training, increased RSFC between the mPFC and the mTG might be related to improved semantic processing abilities in conceptual expansion, novel association and unique response (Abraham et al., 2008; Binder et al., 2009; Cappa, 2008; Fiebach et al., 2007). Thus, we suggest that the performance improvement in the present study might be associated with the facilitation of novel ideas and the enhanced metacognitive ability (especially in the lower creativity), which require self-regulated information transfer between the mPFC and the mTG (Dorfman et al., 2008; Howard-Jones & Murray, 2003; Vartanian et al., 2007). Previous investigations of training-related changes in RSFC (e.g., the DMN) have shown that the RSFC changes are often robust (Buckner, Andrews-Hanna, & Schacter, 2008; Tambini, Ketz, & Davachi, 2010; Voss et al., 2012). Together, the findings indicate that from a practical point of view, it is suggested that creativity (e.g., divergent thinking) can be trained or stimulated during educational practice. The instigation of longitudinal studies will be particularly valuable in elucidating the nature of the relationships between divergent thinking, creativity training, and relevant changes in brain structure and functional connectivity.

The present study found increased RSFC between the mPFC and the mTG in the region of the DMN, which might be critically involved in creativity. In addition, the strength of RSFC (between the mPFC and mTG) in the post-task resting state could be improved by means of cognitive stimulation. However, further research is necessary to elucidate our understanding of the RSFC networks implicated in creativity. Future investigations should focus on neural plasticity in response to creativity training tasks that are effective, complex and more analogous to real-life. There are also some issues needed to be explored in further studies. For example, in this study, we did not find increased RSFC between the mPFC and the PCC associated with creativity (Takeuchi et al., 2012). The possible reasons for those different results might be that we used different creativity tests (e.g., the verbal TTCT in our study, the S-A creativity test in Takeuchi et al.'s study) and different parameters for image acquisition and analysis software. In addition, there was no significant effect between the total verbal TTCT score and the inferior parietal lobe in terms of the strength of RSFC with the mPFC, which might be due to the role of inferior parietal lobe associated with spatial representations and processing (Gansler et al., 2011).

5. Conclusion

In a word, the present study found increased RSFC between the mPFC and the mTG in the regions of the DMN might be critically involved in creativity, and the RSFC (mPFC–mTG) can be improved by means of cognitive stimulation (creativity training-induced change of functional connectivity). In this study, we firstly proved that the RSFC can be improved by means of cognitive stimulation in the post-task resting state.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2013.09.004.

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