

Common and Distinct Brain Networks Underlying Verbal and Visual Creativity

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Abstract: Creativity is imperative to the progression of human civilization, prosperity, and well-being. Past creative researches tend to emphasize the default mode network (DMN) or the frontoparietal network (FPN) somewhat exclusively. However, little is known about how these networks interact to contribute to creativity and whether common or distinct brain networks are responsible for visual and verbal creativity. Here, we use functional connectivity analysis of resting-state functional magnetic resonance imaging data to investigate visual and verbal creativity-related regions and networks in 282 healthy subjects. We found that functional connectivity within the bilateral superior parietal cortex of the FPN was negatively associated with visual and verbal creativity. The strength of connectivity between the DMN and FPN was positively related to both creative domains. Visual creativity was negatively correlated with functional connectivity within the precuneus of the pDMN and right middle frontal gyrus of the FPN, and verbal creativity was negatively correlated with functional connectivity within the medial prefrontal cortex of the aDMN. Critically, the FPN mediated the relationship between the aDMN and verbal creativity, and it also mediated the relationship between the pDMN and visual creativity. Taken together, decreased within-network connectivity of the FPN and DMN may allow for flexible between-network coupling in the highly creative brain. These findings provide indirect evidence for the cooperative role of the default and executive control networks in creativity, extending past research by revealing common and distinct brain systems underlying verbal and visual creative cognition. *Hum Brain Mapp* 00:00–00, 2017. © 2017 Wiley Periodicals, Inc.

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INTRODUCTION

Creativity is imperative to human survival, the progression of human civilization, prosperity, and well-being and is considered the ability to generate output that is both original and appropriate [Runco and Jaeger, 2012; Sternberg and Lubart, 1996]. Accordingly, the creative person is characterized by the ability to produce novel and useful ideas and to discern which ideas are appropriate, worthwhile, and meaningful [Runco, 2003]. Creative thought may pertain to goal-directed, self-generated cognition, which may involve spontaneous cognition and the top-down control of spontaneous thought [Beaty et al., 2014a, 2015, 2016]. In this context, creative thought may depend on the cooperation of control processing supported by the frontoparietal control network (FPN) and spontaneous processing supported by the default mode network (DMN). However, the neurocognitive mechanisms of creative thought remain elusive largely due to the different measurement methods and tasks used in studies [Arden et al., 2010; Chávez-Eakle et al., 2007; Dietrich and Kanso, 2010]. Past research regarding the neural mechanisms of creative cognition has focused on specific brain regions. Few studies have investigated the neural mechanisms of creativity from the perspective of functional connectivity within and across large-scale networks. Creativity is widely measured with divergent thinking (DT), which is a central aspect of creativity [Torrance, 1968]. DT requires individuals to generate several possible solutions to a given problem [Guilford, 1967], and it has strong predictive value for creative achievement [Kim, 2008]. DT is widely measured with the Torrance Tests of Creative Thinking (TTCT) in different domains. In this study, we investigate how verbal creativity, as measured by the verbal TTCT, and visual creativity, as measured by the figural TTCT, correlates with intranetwork and internetwork connectivity derived from resting-state brain imaging.

The DMN and the FPN are two of the most widely studied networks. The DMN comprises the medial frontal, precuneus, and temporoparietal junction [Raichle et al., 2001]. The DMN is involved in cognitive processes that are internally focused, including various mental states conducive to creative thought, such as mind wandering [Andrews-Hanna, 2012; Christoff et al., 2009; Mason et al., 2007], perspective-taking [Buckner and Carroll, 2007], and imagining one's personal future or recollecting one's past [Burgess, 2008; Christoff et al., 2009; Mason et al., 2007]. Recent findings suggest that the DMN plays a critical role in spontaneous cognition (e.g., imaginative thought), and spontaneous thought involving establishing new

connections among existing ideas in a quasi-random or random way is imperative to the generation of novel ideas [Jung et al., 2013; Mok, 2012]. Structural neuroimaging of DT has shown that both cortical thickness and volume of the precuneus, right posterior cingulate are significantly correlated with individual verbal creativity [Chen et al., 2015; Jauk et al., 2015; Jung et al., 2010]. Moreover, evidence from functional neuroimaging studies implicates the DMN in verbal creative cognition, including DT [Jauk et al., 2015; Niendam et al., 2012] creative story generation [Howard-Jones et al., 2005] and insight problem solving [Kounios et al., 2008; Subramaniam et al., 2009]. A recent resting-state functional magnetic resonance imaging (rs-fMRI) study showed that higher creativity was associated with increased resting-state functional connectivity (RSFC) between the posterior cingulate cortex (PCC) and medial prefrontal cortex (mPFC), which are key nodes of the DMN [Takeuchi et al., 2012]. Furthermore, Wei et al. reported that verbal creativity was positively correlated with the strength of RSFC between the mPFC and the middle temporal gyrus and that the strength of RSFC increased after creativity training [Wei et al., 2014].

Although the DMN and spontaneous cognitive processes appear to be important for creative cognition, previous research also points to an important role of the FPN in creative cognition. The FPN comprises the dorsolateral PFC, middle frontal gyrus (MFG), and posterior parietal lobule [Vincent et al., 2008]. The control network is associated with a diverse range of cognitive processes, such as selective retrieval of ideas from memory, integrating information to solve complex problems, inhibition of inappropriate information, working memory, and task-set switching [Niendam et al., 2012], all of which are essential for creative information processing [Dietrich, 2004]. Supporting evidence from structural magnetic resonance imaging studies on DT have revealed that significantly increased cortical thickness and/or volume in regions of the FPN corresponding to the right dorsolateral prefrontal cortex (DLPFC) and the bilateral inferior frontal gyrus (IFG) are associated with higher verbal creativity [Takeuchi et al., 2012; Zhu et al., 2013]. Regions of the FPN have been recruited during a variety of creative thought processes, including DT [Goel and Vartanian, 2005; Gonen-Yaacovi et al., 2013], visual art design [Aziz-Zadeh et al., 2013; Huang et al., 2013; Kowatari et al., 2009], poetry composition [Liu et al., 2015], and music improvisation [Beaty et al., 2015; Bengtsson et al., 2014; de Manzano and Ullén, 2012]. Recent research on visual creativity has also shown that the left MFG and the superior parietal lobule are recruited during visual creativity [Aziz-Zadeh et al.,

2013; Gansler et al., 2011], and other work has shown that highly creative individuals exhibit greater activation in the ventral anterior cingulate cortex during verbal DT [Maysless et al., 2015]. Furthermore, in a recent meta-analysis of DT using Activation Likelihood Estimation, Wu et al. reported robust activation of the posterior parietal cortex [including the superior parietal cortex (SPL)] and the lateral prefrontal cortex across several functional neuroimaging studies [Wu et al., 2015]. Together, these results suggest that brain regions linked to cognitive control play a central role in creative cognition by inhibiting unoriginal ideas and selecting useful and original ideas [Beaty et al., 2014a, 2015, 2016; Jung et al., 2013].

Past studies have tended to emphasize the DMN or the FPN somewhat exclusively. Emerging evidence, however, has reported coactivation of the DMN and FPN control networks within the context of cognitive tasks requiring the evaluation of internal information [Beaty et al., 2014a, 2015, 2016]. Creative cognition involves goal-directed and self-generated thought processes. Thus, creative thought needs both the DMN and the FPN [Beaty et al., 2016]. Interaction between cognitive control and the DMN was earlier proposed by Jung et al. [2013]. The brain structure can predict functional connectivity [Segall et al., 2012]. Highly creative individuals have shown greater connectivity between the DMN and the left IFG [Beaty et al., 2014a,b]—a region associated with cognitive control—and increased connectivity between the ACC within the control network and the occipital-temporal area within the DMN [Maysless et al., 2015]. Creative generation may be supported by the DMN [Andrews-Hanna, 2012; Beaty et al., 2014a, 2015, 2016; Fox et al., 2015; Stawarczyk and D'Argembeau, 2015]. Moreover, creative evaluation may depend on cooperation between control processing supported by the FPN and spontaneous processing supported by the DMN, and the FPN supports creative thought by persistently generating ideas around the current goal and inhibiting unoriginal ideas [Beaty et al., 2014a,b; De Dreu et al., 2012].

Furthermore, the theory of blind variation and selective retention (BVSR) considers blind variation—a spontaneous process that involves establishing new connections among existing ideas in a quasi-random or random way—as dependent on activation the default mode network (DMN), while selective retention—a cognitive control process that involves evaluating these novel combinations—tends to recruit the FPN [Jung et al., 2013]. Similarly, within the context of two-stage models, the generation of novel ideas may be supported by the DMN, while the evaluation of ideas may be supported by the control network. Moreover, cognitive control mechanisms may be responsible for monitoring and directing spontaneous activity stemming from the DMN [Beaty et al., 2014a], and the FPN may integrate information from the DMN. Accordingly, we speculate that the cooperation of the DMN and the FPN may play a key role in creative cognition, and the FPN may

mediate the relationship between the DMN and creative cognitive ability.

METHODS

Participants

This study is a long-term program that is a part of an ongoing project investigating the associations among brain imaging, mental health, and creativity. In total, 364 right-handed college students (145 men, mean age = 19.97) from Southwest University participated in this study. Forty-eight participants were excluded due to a potential to suffer from depression, because their Beck Depression Inventory scores were higher than 13. Three subjects were excluded because of behavioural data [intelligence (IQ) and creativity] beyond three standard deviations, and 33 participants were excluded due to issues with the imaging data: 6 subjects had missing rfMRI images, and 27 met the exclusion criteria of head movement during rest-fMRI scanning (i.e., >2 mm translation in any axis and >2° angular rotation in any axis). Consequently, a total of 282 participants (132 males; mean age = 19.98; SD = 1.25) were included in the analyses. This project was approved by the Institutional Review Board of the Southwest University Brain Imaging Center. All participants without a history of psychiatric diseases or neurological disorders provided informed consent and received payment for their participation.

Assessment of Creativity

The TTCT [Ye et al., 1988] were designed as a measure of creativity (i.e., DT ability). In this study, the verbal TTCT (TTCT-V) was used to assess individual verbal creativity abilities [Carson et al., 1994; Kim, 2006]. The TTCT-V comprises seven tasks: generating questions, causes, and consequences; improving products (a toy elephant); alternate uses (cardboard boxes); manipulating objects; and imagining the consequences of a scenario. Scoring consisted of three components: flexibility (the number of different categories of responses, which reflects the ability to shift between conceptual fields); fluency (the number of meaningful and relevant responses, which is associated with the ability to generate and consider other possibilities); and originality (the degree of originality of the responses, which is associated with thinking “outside the box”). The total TTCT-V score is the sum of these three components. Three trained postgraduates who were blind to the goal of this research took part in the scoring. The inter-rater reliability for the scoring of the TTCT-V was 0.90.

The figural TTCT (TTCT-FTTCT-F) consisted of three type of tasks used to measure individual visual creativity abilities. The first task asked participants to make an object or picture using 10 incomplete figures. The second task

asked participants to draw as many objects or pictures on three pages of parallel lines. Like the TTCT-V, the TTCT-FTTCT-F provides a total score which consists of three components: flexibility (the number of different categories of responses, which reflects the ability to shift between conceptual fields); fluency (the number of relevant and meaningful responses, which is associated with the ability to generate a number of pictures or objects); and originality (the number of infrequent ideas, which reflects the ability to produce unique or uncommon responses) [Kim et al., 2006]. The total TTCT-FTTCT-F score reflects the sum of these three components. Scoring was performed by three trained raters who were all blind to this study. The inter-rater reliability for scoring of the TTCT-FTTCT-F was 0.85.

The separate total creativity score was also used because it was correlated with each component score (each correlation coefficient > 0.88), and the scores of the dimensions were highly correlated with each other (each correlation coefficient > 0.78).

Assessment of General IQ

To examine intellectual ability, participants performed the Combined Raven's Test (CRT), which is widely used for IQ testing and has a high degree of reliability and validity [Wang, 2007]. The CRT, which includes 72 items and is based on Raven's standard progressive matrix [Raven, 1960] and Raven's coloured progressive matrix [Raven, 1958] was revised by the Psychology Department of East China Normal University in 1994. The total index score of this test, which is equal to the number of correct answers given by participants in 40 min, is used as a psychometric index of individual IQ.

Image Acquisition

All participants were scanned in a 3T Trio scanner (Siemens Medical, Erlangen, Germany) from Southwest University, China. Resting-state functional images were obtained using a gradient echo planar imaging sequence: repetition time = 2000 ms; echo time = 30 ms; slices = 32; thickness = 3.0 mm; resolution matrix = 64×64 ; flip angle = 90° ; field of view = 220×220 mm²; voxel size = $1 \times 1 \times 1$ mm; slice gap = 1 mm, voxel size = $3.4 \times 3.4 \times 4$ mm³. Each section contained 242 volumes. During the functional image acquisition, all subjects were instructed to close their eyes, not think about anything in particular, and remain awake.

Preprocessing of Imaging Data

The processing of resting-state functional MRI data was performed using the Data Processing Assistant for Resting-State fMRI (DPARSF, <http://resting-fmri.sourceforge.net/>) [Yan and Zang, 2010] based on SPM8. First, the first 10 volumes from each subject's functional imaging

data were discarded to account for steady-state magnetization. The remaining 232 volumes were included in the subsequent analysis. Second, slice timing correction was used to correct slice order effects, and head motion correction was used to correct head movement artefacts. Twenty-seven subjects who exhibited a head motion of 2 mm maximum displacement and 2° rotation throughout the course of scans were excluded. Third, each participant's functional image was spatially normalized to the standard MNI template with a resampled voxel size of $3 \times 3 \times 3$ mm. The data were then smoothed with an isotropic 8 mm full-width at half maximum Gaussian kernel. To reduce the residual effects of motion artefacts, the mean framewise displacement (FD) derived with Jenkinson's relative root mean square algorithm was regressed out in group statistical analysis as a regressor of no interest.

STATISTICAL ANALYSIS

Behavioral Data Analysis

We analysed behavioural data with SPSS 19.0 statistical software (SPSS, Chicago, IL). Pearson's correlation coefficient was used to analyse the relationship between the three sub-dimensional TTCT scores (originality, flexibility, and fluency) and the total TTCT scores (TTCT-FTTCT-F, TTCT-V). In addition, we tested sex differences on the TTCT-FTTCT-F, TTCT-V, and CRT using two-tailed t-tests. The results were considered statistically significant at $P < 0.05$ for all analyses.

Independent Component Analysis (ICA)

Emerging neuroimaging studies have focused on exploring the RSFC, which detects the synchronization of inter-regional spontaneous neuronal signals [Biswal et al., 1995] and has been shown useful for examining brain regions or networks that are related to different cognitive tasks, such as working memory [Zou et al., 2013], attention [Mennes et al., 2010, 2011]. ICA is a multivariate and data-driven method used to identify independent spatial-temporal patterns of coherent activity without prior knowledge about locations or activity waveforms [Beckmann et al., 2005; McKeown et al., 1997], and it is widely used to examine functional network connectivity (FNC), particularly with resting state fMRI data [Esposito et al., 2005]. ICA can provide greater sensitivity to detect subtle differences between individuals [Koch et al., 2010], and it takes into consideration the relationships between all voxels. Using this method, previous studies have consistently revealed several networks in the human brain, for example, the visual network, auditory network, sensorimotor network, anterior DMN (aDMN), posterior DMN (pDMN), and FP control network [Allen et al., 2011; Jafri et al., 2008; Liao et al., 2010; Smith et al., 2009]. Recent studies have shown that creative cognition does not depend on a single brain

region or cognitive process [Dietrich and Kanso, 2010; Jung et al., 2013; Wu et al., 2015]. Thus, specific neural networks and their dynamic interplay may be crucial in creative cognition.

We identified resting state networks (RSNs) using spatial ICA as performed in the GIFT toolbox (<http://mialab.mrn.org/software/gift/>) [Calhoun et al., 2001]. We chose a relatively low model order ICA (number of components, $C = 20$), as previous fMRI studies have demonstrated that 20 independent components (ICs) yield refined components corresponding to known functional and anatomical segmentations [Abou-Elseoud et al., 2010; Ray et al., 2013; Smith et al., 2009], thus providing a reliable and integrated representation of large-scale networks [Calhoun et al., 2001; Zuo et al., 2010]. Each data set was reduced by methods of principal component analysis in two steps. After we performed a single ICA analysis on each subject, decomposition was estimated on concatenated datasets using the Infomax algorithm [Bell and Sejnowski, 1995]. The Infomax algorithm was repeated 100 times in Icasto with different initial values and different bootstrapped data sets, and the components were clustered to estimate the reliability of the decomposition [Himberg and Hyvarinen, 2003]. The quality of conservative clusters was quantified using the index IQ, which reflects the difference between extra-cluster and intra-cluster similarity and ranges from 0 to 1. Then, single-subject spatial maps and time courses were back-reconstructed using the results from the data reduction step and the aggregated components [Calhoun et al., 2001; Jafri et al., 2008]. The mean spatial map of each group was transformed to Z-scores for display.

RSN Detection

We used the DMN and FPN from previous fMRI studies [Allen et al., 2011; Biswal et al., 2010; Di and Biswal, 2015; Smith et al., 2009] as network spatial templates to classify the components. We selected RSNs corresponding to the cerebral components with the largest spatial associations with the network templates [Mantini et al., 2009; van de Ven et al., 2004, 2008]. We visually inspected all components to verify the automated component selection [Zuo et al., 2010]. This led to the identification of 4 RSNs: left and right FPN, anterior DMN (aDMN), and posterior DMN (pDMN). The ICs corresponding to four RSNs were extracted from all participants. We then entered the spatial maps of each RSN for all participants into a one-sample t-test in SPM8. The statistical threshold was set at $P < 0.05$, corrected for multiple comparisons using family wise error, forming a binary mask for further analysis (see Table III, Fig. 1).

Second-Level Analysis of the RSNs

To identify regions where functional connectivity was significantly correlated with individual verbal creativity in

DMN and FPN, we performed multiple linear regression in SPM. The verbal and visual creativity scores were considered variables of interest, while gender, age, and general IQ were used as covariates of no interest. The binary mask was used as an explicit mask in the analysis. A multiple comparison correction was performed within an ICA-derived network using the AlphaSim program in the REST software [Yan and Zang, 2010], with individual voxel $P = 0.001$ and cluster-level $P < 0.05$.

We examined the regions that were significantly related to individual visual creativity in the same way. To further investigate whether the exclusive regions of verbal or visual creativity were affected by the correction standard, we also examined regions at a less conservative level of $P < 0.05$, 200 voxels, uncorrected (see Fig. A1 in the Appendix).

IQ, as a cognitive component, may facilitate creative thought [Beatty et al., 2014b; Nusbaum and Silvia, 2011]. To determine whether the effect is specific to “creativity” or to “cognition” writ large, multiple regression was used to investigate the correlation between regions of RSN and individual IQ, controlling for possible confounding variables (creativity, gender, FD, and age).

Association between Regions–Networks Connectivity and Creativity Scores

To test whether the association between ROIs and functional networks was related to visual creativity scores, we calculated the association between ROIs that were significantly correlated with TTCT-F and the functional network. First, the representative mean time series was computed by averaging the time series of voxels in this ROI and these networks. Then, we calculated the Pearson correlation coefficient between each ROI and every other network, averaging the time course for each subject. The correlation coefficients were standardized using Fisher’s r -to- z transformation, allowing further correlation analysis. Then, to examine whether the correlation between ROIs and FNC was related to visual creativity, we correlated the TTCT-F scores with associations between ROIs and FNC, regressing out age, IQ, gender, and mean FD. We also examined whether correlation between ROI and the functional network was related to verbal creativity. Correction for multiple comparisons was performed using the false discovery rate (FDR) for the final results.

FNC in Relation to Creativity Scores and General IQ

We conducted FNC analysis using the Pearson correlation between each and every other summary time courses. This allowed us to assess whether the effects of specific network hubs and functional networks on creativity were consistent with the FNC analysis. The results consisted of an FNC matrix with dimensions of 4 times 4 times 282 (subjects). The correlation coefficients were standardized using Fisher’s r -to-

TABLE I. Descriptive statistics of behavioral measures (n = 282)

	Males		Females	
	Means	SD	means	SD
Age	20.23	1.30	19.75	1.17
CRT	66.02	3.40	66.25	3.50
TTCTF	64.87	17.06	67.18	19.18
TTCTV	126.14	39.47	135.78	38.58

Note: *n*, number; SD, standard deviation; TTCTF, figural torrance tests of creative thinking; TTCTV, verbal torrance tests of creative thinking; CRT, combined Raven’s test.

z transformation, allowing further correlation analysis. We then correlated creativity scores (TTCT-F scores and TTCT-V scores) with FNC separately. Multiple comparisons were performed using the FDR for the final results.

To determine whether the effect is specific to “creativity” or to “cognition” writ large, we further correlated the general IQ scores with FNC in the same way. Multiple comparisons were performed using the FDR for the final results.

Mediation Analysis

Mediation analysis was then employed to explore whether the FPN mediated the relationship between the DMN and both verbal and visual creativity, using an INDIRECT macro implemented in SPSS [Preacher and

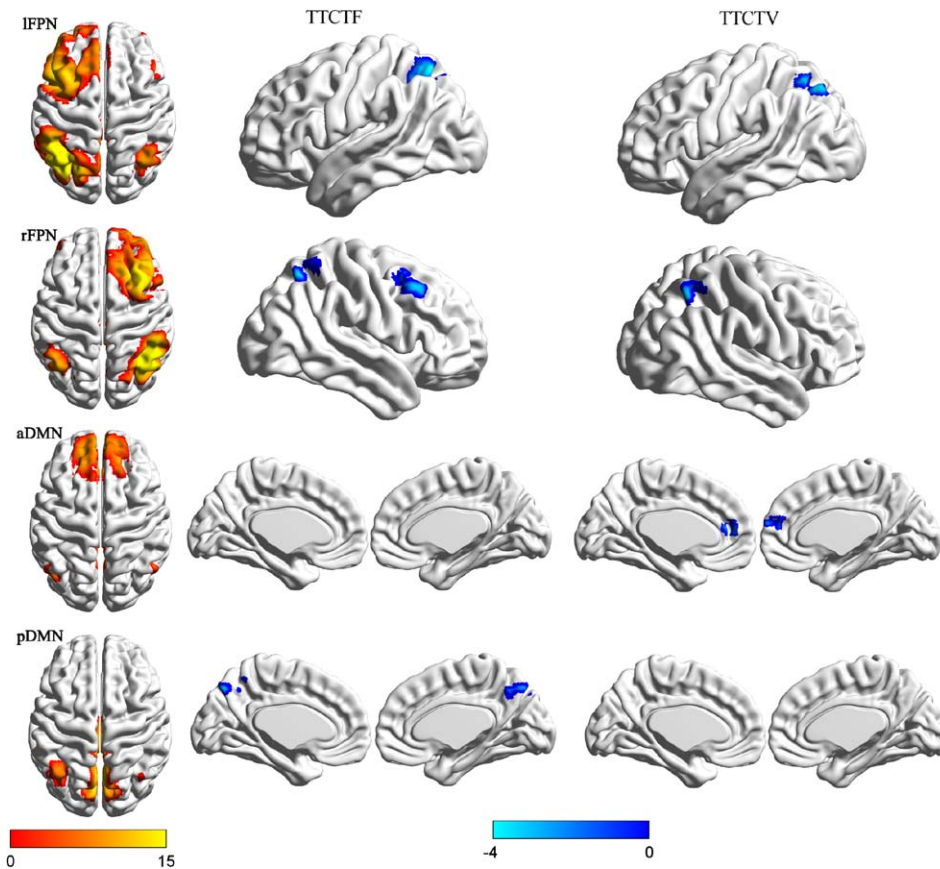


Figure 1.

Regions in which the functional connectivity strengths within each RSN (IFPN, rFPN, aDMN, pDMN) were significantly related to creativity. Higher visual creativity was negatively correlated with decreased functional connectivity in the precuneus of the pDMN, the right middle frontal and superior parietal regions of the right FPN, and the left superior parietal region of the left FPN. Higher verbal creativity was correlated with decreased

functional connectivity in the medial frontal region of the aDMN, the right superior parietal region of the right FPN, and the left superior parietal region of the left FPN. Significant clusters are shown at a statistical threshold of $P < 0.05$ (corrected by the AlphaSim program in REST with a combined threshold of $P < 0.001$ for each voxel). [Color figure can be viewed at wileyonlinelibrary.com]

Hayes, 2008] This macro utilized bootstrapped sampling (10,000 bootstrapped samples) and bias-corrected 95% bootstrap confidence intervals (CI). Note that if the CIs do not include zero, there is a significant indirect effect of the independent variable on the dependent variable through the mediators [Preacher and Hayes, 2008].

We began by examining whether the FPN mediated the relationship between the DMN and visual creativity. The proposed mediators included the mean z values within the bilateral FPN, which were correlated with the verbal creativity scores. Moreover, the mean z values of the precuneus were added as an independent variable, and the figural creativity scores were added as a dependent variable in the model; IQ, age, and gender were modelled as covariates of no interest.

Next, we examined whether the FPN mediated the relationship between the DMN and verbal creativity. The proposed mediators again included the mean z values within the bilateral FPN, which were correlated with verbal creativity scores. Moreover, the mean z values of the mPFC were added as an independent variable, and the verbal creativity scores were added as a dependent variable in the model; IQ, age, and gender were modelled as covariates of no interest.

RESULTS

Behavioral Results

Table I shows the mean and SD for age and the CRT, TTCT-FTTCT-F, and TTCFV scores of the females and males in our sample. For the TTCT-FTTCT-F, the correlations among flexibility, originality, fluency, and the total TTCT score were high ($r > 0.93$, $P > 0.001$). For the TTCT-FTTCT-F, the correlations among flexibility, originality, fluency, and the total TTCT score were similarly high ($r > 0.88$, $P > 0.001$). No statistically significant difference was found between females and males on the TTCT-FTTCT-F ($P = 0.289$) or the CRT ($P = 0.564$). However, a significant difference between females and males was found on the TTCT-V ($P = 0.039$, see Table I).

Visual Creativity Correlations with Functional Networks

Multiple regression was used to investigate the correlation between regions of RSNs and individual visual creativity, controlling for possible confounding variables (IQ, gender, and age). The regression analysis showed that the TTCT-F score was significantly and negatively associated with functional connectivity in the precuneus of the posterior DMN, the left superior parietal region of the left FPN, and the right superior parietal and MFG of the right FPN (see Table II, Fig. 1). To eliminate the residual effects of head motion in this analysis, we added FD as a nuisance covariate. After controlling for sex, age, FD, and IQ, the

TABLE II. Regions in which functional connectivity strengths within each RSN were significantly related to creativity

	Regions	Coordinate (X Y Z) MNI	Voxels	Z Value
	<i>rFPN</i>			
TTCTF	SPL	39 -57 66	49	-4.02
	MFC	48 15 48	9	-3.52
TTCTV	SPL	33 -66 57	37	-4.21
	<i>lFPN</i>			
TTCTF	SPL	-27 -66 54	16	-3.79
	MFC	-36 18 36	29	-4.07
TTCTV	SPL	-24 -72 51	26	-3.75
	<i>pDMN</i>			
TTCTF	precuneus	9 -75 45	17	-3.62
TTCTV				
	<i>aDMN</i>			
TTCTF				
TTCTV	mPFC	-3 45 15	9	-3.66

MFC indicates middle frontal cortex; SPL, Superior parietal; mPFC, medial prefrontal cortex; rFPN, right frontoparietal network; lFPN, left frontoparietal network; aDMN, anterior default network; pDMN, posterior default network.

regression analysis showed that the statistical values and coordinates of the peak voxel did not change.

Correlation analysis revealed that the figural creativity scores were significantly and negatively correlated with mean Z values of the right MFG ($r = -0.212$, $P < 0.001$), left SPL ($r = -0.256$, $P < 0.001$), right SPL ($r = -0.245$, $P < 0.001$), and precuneus ($r = -0.194$, $P = 0.002$). Verbal creativity scores were significantly and negatively correlated with mean Z values of the left SPL ($r = -0.181$, $P = 0.002$) and the right SPL ($r = 0.202$, $P = 0.001$) but not significantly correlated with the mean Z values of the right MFC ($r = -0.055$, $P = 0.356$) or the precuneus ($r = -0.009$, $P = 0.879$). Thus, the right MFG and precuneus may be distinct neural correlates for visual creativity.

Verbal Creativity Correlations with Functional Networks

Multiple regression was used to investigate regions where functional connectivity was significantly related to individual verbal creativity, controlling for possible confounding variables (IQ, gender, and age). The regression analysis showed that verbal creativity was significantly and negatively associated with functional connectivity in the anterior DMN, left FPN, and right FPN. The hubs included the left SPL in the left FPN, the right SPL in the right FPN, and the medial frontal cortex in the anterior DMN (see Table II, Fig. 1). To assess the residual effects of head motion, we added FD as a nuisance covariate. After controlling for sex, age, FD, and IQ, the regression analysis showed that the statistical values and coordinates of the peak voxel did not change.

TABLE III. Peak foci for the group-level IPFN, rFPN, aDMN and, pDMN defined by ICA

Regions	Coordinate (X Y Z) MNI	No. Voxels
aDMN (IC 13)		
mPFC	-3 54 18	2262
PCC	-3 -51 30	125
L angular Gyrus	-45 -69 36	49
R angular Gyrus	51 -60 33	27
pDMN (IC 5)		
Precuneus	-3 -72 33	2464
Inferior Parietal Lobule	-39 -60 48	173
IPFN (IC 6)		
Inferior Frontal Gyrus	-48 -18 33	3404
Inferior Parietal Lobule	-36 -66 39	2606
Inferior Temporal Gyrus	-60 -45 -6	433
Angular Gyrus	39 -66 48	276
MFG	51 24 33	32
rFPN (IC 1)		
Inferior Temporal Gyrus	63 -24 -21	240
MFG	39 18 51	2735
Inferior Parietal Lobule	45 -54 51	1475
Middle cingulate Gyrus	6 -36 39	189
Angule	-42 -63 48	286

rFPN, right frontoperital network; IPFN, lift frontoperital network; aDMN, anterior default network; pDMN, posterior default network.

Correlation analysis revealed that verbal creativity scores were significantly and negatively correlated with mean Z values of the left superior parietal ($r = -0.225$, $P < 0.001$) and right superior parietal ($r = -0.244$, $P < 0.001$) regions of the FPN and negatively correlated with the medial frontal region ($r = -0.214$, $P = 0.001$) of the aDMN. Visual creativity scores were also negatively correlated with mean Z values within the left superior parietal ($r = -0.119$, $P = 0.047$) and right superior parietal ($r = -0.189$, $P = 0.001$) regions within the left and right FPNs, respectively, but not significantly correlated with the mean Z values within the medial frontal region of the aDMN ($r = -0.090$, $P = 0.133$). This analysis therefore identified common (left and right superior parietal regions in the FPN) and distinct (precuneus in the pDMN, medial frontal region in the aDMN) brain regions for visual and verbal creativity.

To further examine this result, a correlation coefficient difference test was conducted. We found that the mean Z values of the left and right superior parietal regions and the visual creativity scores were not significantly different from the figural creativity scores ($t < 1.645$). However, the association between the mean Z values of the precuneus, MFG, and visual creativity was significantly greater than with verbal creativity ($t = 2.49 > 1.645$; $t = 2.38 > 1.645$), and the association between the mean Z values of the medial frontal and verbal creativity was significantly greater than with visual creativity ($t = 1.73 > 1.645$).

To test the stability and reliability of the results, we repeated the analysis using half of the subjects, selected

randomly. After controlling for age, gender, IQ, and FD, the regression analysis revealed that the coordinates and statistical values of the peak voxel in the precuneus of the posterior DMN, the left inferior parietal region of left FPN, and the right inferior parietal and MFG of the right FPN correlated with visual creativity changes as $x, y, z = -3 -78 42$ (214 voxels); $-24, -60, 57$ (56 voxels); $42, -54, 63$ (27 voxels, a threshold of $P < 0.005$, uncorrected, and a minimum cluster size of 15 contiguous voxels). The coordinates and statistical values of the peak voxel in the left SPL in the left FPN, the right SPL in the right FPN, and the medial frontal cortex in the anterior DMN correlated with visual creativity changes as $x, y, z = -27 -78 48$ (40 voxels); $33 -66 57$ (25 voxels); $-3 42 15$ (16 voxels). The findings using data from only half of the subjects were similar to those using data from all participants, which may indicate the stability of the results.

General IQ Correlations with Functional Networks

We further explored the correlation between RSN regions and individual IQ, controlling for possible confounding variables (creativity, gender, FD, and age). No significant correlation between RSN regions and individual IQ scores was found.

Association between Regions-Networks Connectivity and Creativity Scores

We then assessed the effects of association between ROIs and functional networks on both visual and verbal creativity. The visual creativity results revealed significant and positive associations between figural creativity scores and the right superior parietal and left FPN, the left superior parietal region and the pDMN, the right MFG and the aDMN, and the precuneus and the left FPN [q(FDR) = 0.05]. The verbal creativity results revealed positive and marginally significant associations between verbal creativity scores and the right superior parietal and left FPN ($P = 0.061$) and the medial frontal and right FPN ($P = 0.062$; see Table IV, Fig. 2).

FNC in Relation to Creativity Scores and General IQ

We examined the effects of the DMN and FPN on visual and verbal creativity. The visual creativity results showed significant and positive associations between figural creativity scores and functional connectivity between the right and left FPN ($P < 0.05$) and between the left FPN and the pDMN ($P = 0.002$, q[FDR] = 0.05). The verbal creativity results showed positive and marginally significant associations between verbal creativity scores and functional connectivity between the right FPN and the aDMN (see Table IV).

Considering that many other ICs were extracted by ICA (see Fig. 2), we explored whether and how some other

TABLE IV. Association Between ROI and networks and TTCT Scores, and Between FNC and the TTCT Scores

TTCTF Brain region ~ network pair	<i>r</i>	<i>P</i>	TTCTV Brain region ~ network pair	<i>r</i>	<i>P</i>
rMFC ~ pDMN	0.044	0.465	mPFC ~ pDMN	0.091	0.131
rMFC ~ IFPN	0.098	0.102	mPFC ~ IFPN	0.061	0.312
rMFC ~ aDMN	0.154	0.010	mPFC ~ rFPN	0.112	0.062
rIPL ~ pDMN	0.123	0.040	rIPL ~ pDMN	0.065	0.277
rIPL ~ aDMN	-0.009	0.883	rIPL ~ aDMN	0.058	0.337
precuneus ~ rFPN	-0.054	0.369	-	-	-
precuneus ~ IFPN	0.166	0.018	-	-	-
precuneus ~ aDMN	0.018	0.765	-	-	-
IIPL ~ rFPN	-0.021	0.726	IIPL ~ rFPN	-0.047	0.434
IIPL ~ pDMN	0.128	0.033	IIPL ~ pDMN	0.080	0.183
IIPL ~ aDMN	0.020	0.738	IIPL ~ aDMN	0.044	0.463
Network ~ network pair			Network ~ network pair		
rFPN ~ pDMN	-0.045	0.456	rFPN ~ pDMN	-0.015	0.806
rFPN ~ pDMN	0.137	0.022	rFPN ~ pDMN	0.111	0.063
rFPN ~ aDMN	0.021	0.726	rFPN ~ aDMN	0.129	0.032
IFPN ~ pDMN	0.194*	0.001	IFPN ~ pDMN	0.066	0.270
IFPN ~ aDMN	0.065	0.280	IFPN ~ aDMN	-0.006	0.915
aDMN ~ pDMN	0.022	0.713	aDMN ~ pDMN	0.006	0.918

* $P < 0.01$ ($q[\text{FDR}] = 0.05$); MFC indicates middle frontal cortex; r, right; l, left; IPL, inferior parietal; mPFC, medial prefrontal cortex; rFPN, right frontoparietal network; IFPN, left frontoparietal network; aDMN, anterior default network; pDMN, posterior default network.

components out of the DMN and the FPN are related to verbal and visual creativity. Multiple regression was used to investigate the correlation between the regions of all the RSNs and visual creativity, controlling for possible confounding variables (IQ, gender, and age). A multiple comparison correction was performed within an ICA-derived network using the AlphaSim program in the REST software [Yan and Zang, 2010], with individual voxel $P = 0.001$ and cluster-level $P < 0.05$.

The regression analysis showed that the TTCT-F score was significantly and negatively associated with functional connectivity in the inferior parietal region of the DAN. There were no significant associations in the other networks. We examined the regions that were significantly related to individual verbal creativity in the same way. No significant associations between verbal creativity scores and functional connectivity of these RSNs was found. To eliminate the residual effects of head motion in this analysis, we added FD as a nuisance covariate. After controlling for sex, age, FD, and IQ, the regression analysis showed that the statistical values and coordinates of the peak voxel did not change.

Next, we examined the effects of FNC on visual and verbal creativity. The visual creativity results showed no significant associations between figural creativity scores and functional connectivity among these components. The verbal creativity results showed positive and marginally significant associations between verbal creativity scores and functional connectivity between the DAN and MN (see Fig. 2).

The effects of FNC on general IQ showed no significant associations between IQ scores and FNC among the FPN and DMN.

Mediation Analysis

We examined whether the FPN mediated the relationship between the DMN and visual creativity. The results showed that the direct effect ($c' = -0.11$) was not significant ($P = 0.08$), but we found two significant indirect effects (see Fig. 3). The first indirect effect of the precuneus on the figural creativity scores through the right FPN (superior parietal) was the product of $a1 = 0.27$ and $b1 = -0.19$, $a1*b1 = -0.05$ [CI: $-0.10, -0.02$]. The next indirect effect of the precuneus on the figural creativity scores through the right superior parietal (-0.06) was also significant [CI: $-0.11, -0.01$], and the total indirect effect (-0.11) was statistically significant [CI: $-0.17, -0.06$]. The FPN mediated the relationship between pDMN and visual creativity.

Next, we examined whether the FPN mediated the relationship between the DMN and verbal creativity. The results showed that the direct effect ($c' = 0.12$) was significant ($P = 0.045$), and we again found two significant indirect effects (see Fig. 3). The first indirect effect of the mPFC on verbal creativity scores through the right superior parietal region was the product of $a1 = 0.26$ and $b1 = -0.18$, $a1*b1 = -0.046$ [CI: $-0.09, -0.02$]. The next indirect effect (-0.046) of the mPFC on verbal creativity scores through the left PFN (superior parietal and MFG) was significant [$-0.9, -0.02$], and the total indirect effect (-0.09) was statistically significant [$-0.15, -0.05$]. The FPN mediated the relationship between aDMN and verbal creativity. To further investigate whether visual and verbal creativity recruit specialized brain networks, we ran two additional mediation models (see Fig. A2 in the Appendix).

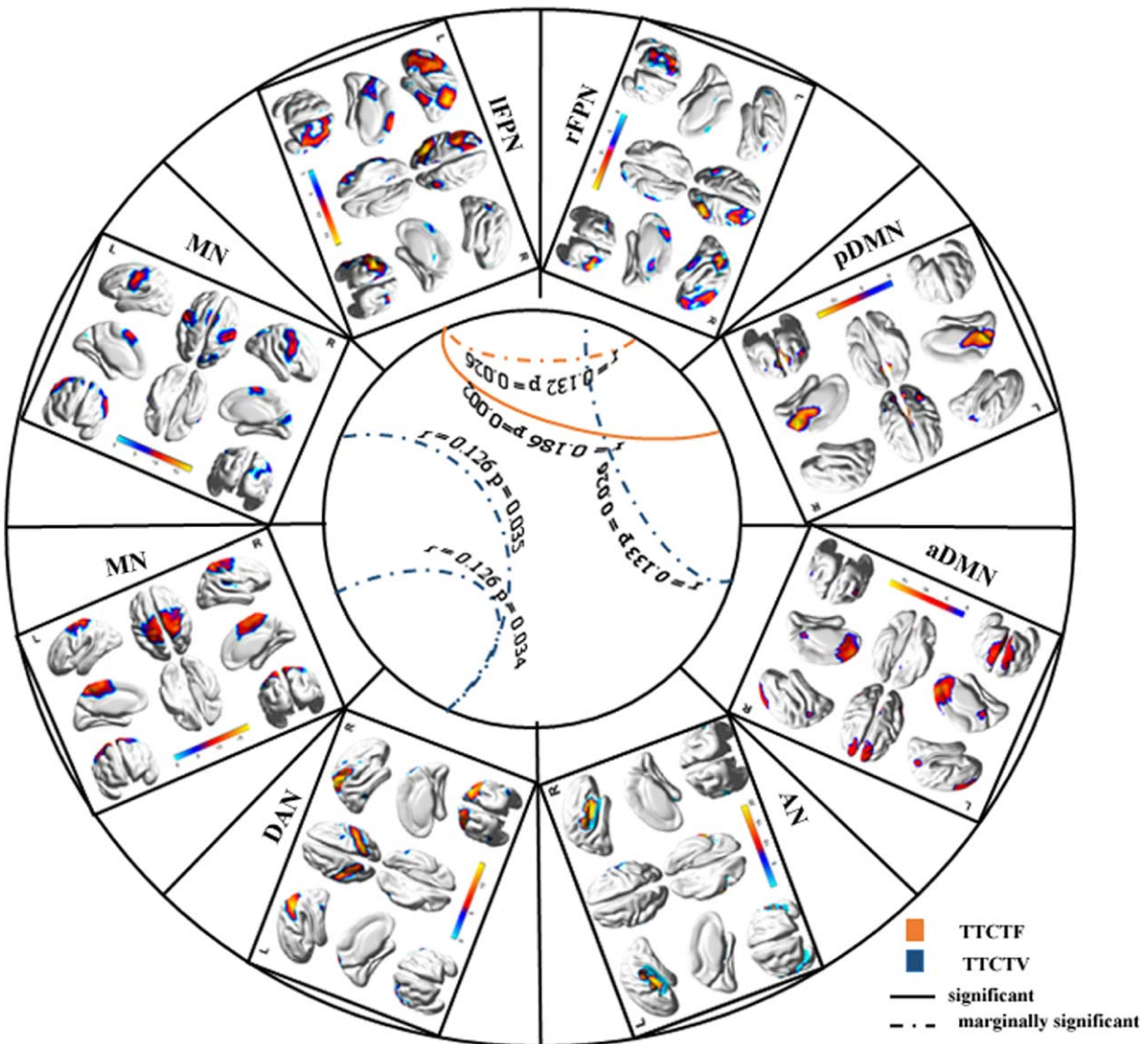


Figure 2.

Association between FNC and the creativity scores. Regarding visual creativity, significant and positive associations were found between figural creativity scores and functional connectivity between the left FPN and pDMN ($P = 0.002$, $q[\text{FDR}] = 0.05$), and marginally significant associations and functional connectivity were found between the right and left FPN ($P = 0.026$).

Regarding verbal creativity, positive and marginally significant associations between verbal creativity scores and functional connectivity between the right FPN and aDMN and between the DAN and MN was found. [Color figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

The present study explored the relation between creative capacity and RSFC within the default and FP control networks using ICA. Our results showed that decreased functional connectivity within common regions of the FPN was associated with both visual creativity and verbal creativity, and the strength of connectivity between the FPN and the DMN was positively related to both creative domains.

Furthermore, the FPN mediated the relation between the DMN and creative ability. In addition, there were specialized hubs and interactive systems for verbal and visual creativity. Higher visual creativity was related to decreased functional connectivity in the precuneus and MFC of the pDMN, while higher verbal creativity was related to decreased functional connectivity in the mPFC of the aDMN. Mediation analysis revealed that the FPN mediated the relationship between the aDMN and verbal creativity.

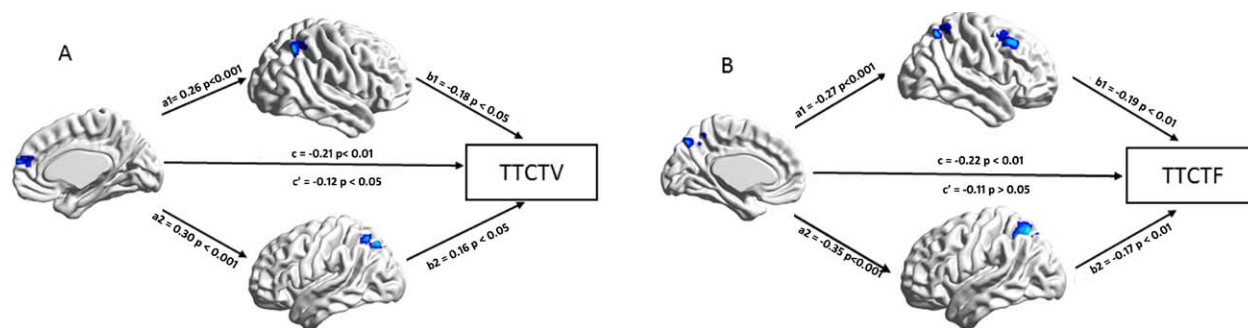


Figure 3.

Mediation analysis: (A) The FPN mediated the relationship between the aDMN and verbal creativity. (B) The FPN mediated the relationship between the pDMN and visual creativity. [Color figure can be viewed at wileyonlinelibrary.com]

It also mediated the relationship between the pDMN and visual creativity. Our results extend previous research by revealing how the DMN and FPN cooperate to contribute to creative cognitive ability during the resting state.

We found that decreased functional connectivity in common regions of the FPN (bilateral SPL) was related to both visual and verbal creativity. Previous studies have suggested that the SPL plays an important role in multimodal information processing as well as a wide range of other functions, including attention to action, monitoring in working memory, response selection, and suppression of irrelevant information [Booth et al., 2002; d'Esposito et al., 1998; Niendam et al., 2012]—cognitive processes that are central to both verbal and visual creativity [Dietrich, 2004]. Notably, the SPL has been implicated in studies of visual creativity. For example, in a study comparing brain activity during creative versus uncreative visual creativity, Aziz-Zadeh et al. [2013] reported greater activation of the SPL. The SPL has also shown increased involvement during a creative drawing task [Ellamil et al., 2012]. Studies of verbal creativity have also implicated the SPL, including DT [Gansler et al., 2011] and “brainstorming” during creative writing [Shah et al., 2013].

The findings provide direct evidence for the cooperative role of the default mode and control networks in creative cognition. The DMN is related to spontaneous and self-generated thought, such as mental simulation, mind-wandering, social cognition, and autobiographical retrieval [Andrews-Hanna, 2012; Christoff et al., 2009; Hassabis and Maguire, 2007; Schacter et al., 2012]. Such “self-generated thought” has previously been associated with creative cognition [e.g., mind-wandering, Baird et al., 2012]. Self-generated thought involves the spontaneous integration of previously unassociated information [Baird et al., 2012; Perkins et al., 2015], which could lead to more available mental elements for creative generation. Carson and coworkers [2003] required subjects to disregard inconsequential information using latent inhibition tests and found that highly creative individuals were less likely to screen

out irrelevant information and focus on the task. Further evidence suggests that creative individuals show an increased propensity to mind-wander during cognitive tasks [Perkins et al., 2015].

Notably, mind-wandering has been characterized as the antithesis of executive control processing [Kane et al., 2007]. However, recent evidence has demonstrated a critical role of cognitive control factors in creative thought, such as fluid IQ [Beaty et al., 2014b; Benedek et al., 2014], working memory capacity [De Dreu et al., 2012; Lee and Theriault, 2013], verbal fluency [Silvia et al., 2013], and attentional flexibility [Zabelina and Robinson, 2010]. Such executive functions are thought to support creative cognition by providing the cognitive control needed to inhibit salient but irrelevant information and to manage complex search processes [Beaty et al., 2015]. In the absence of such control, DT can be compromised by an inability to effectively overcome prepotent response tendencies [Gilhooly et al., 2007]. Accordingly, highly creative individuals may be characterized by both enhanced idea generation and evaluation abilities.

Cooperation of the default and control networks has been shown to be important for goal-directed, self-generated thought, including autobiographical future planning and even mind-wandering [Fox et al., 2015; Spreng et al., 2015]. Such processes appear to involve the top-down modulation of self-generated information. Considered within the context of this study, the DMN may be associated with the process of idea generation, in light of its role in self-generated cognition, while the control network may be associated with evaluating the efficacy of ideas and modifying them to meet the constraints of task-specific goals. Thus, DMN and FPN coupling may reflect the ability to exert top-down control over the process of idea generation. Increased connectivity between FPN and DMN may correspond to a greater ability of creative individuals to evaluate and revise self-generated ideas by inhibiting salient task-irrelevant information and selecting goal-congruent ideas among a wide range of competing alternatives [Beaty et al., 2015].

Our results are consistent with several recent studies on the role of brain networks in creative cognition. One such study found that highly creative individuals exhibited greater cooperation between regions associated with the control network and the DMN [Beaty et al., 2014a,b]. Other work examining functional connectivity during DT reported enhanced connectivity between the ACC within the control network and the occipital-temporal area within the DMN [Maysseless et al., 2015]. In a similar vein, Pinho et al. [2016] asked professional pianists to improvise following one of two different experiment conditions during fMRI: expressing certain emotional content or using specific piano keys (i.e., “pitch-sets”). In the pitch-set condition, the DLPFC showed increased coupling with the bilateral dorsal promotor and the supplementary motor area. In the emotional condition, in contrast, the DLPFC showed increased coupling with several regions associated with the DMN, including the mPFC [Pinho et al., 2016]. Such work provides further support for the cooperative role of the default and control networks across a range of creative tasks and domains.

Our findings are also consistent with the “two stage” model as well as the BVSR theory of creativity. Regarding the “two stage” theory, a recent study on creative drawing showed differential contributions of default and executive control networks during different stages of the drawing process [Ellamil et al., 2012]. Creative generation was related to greater recruitment of regions within the DMN, and creative evaluation was related to greater recruitment of regions within the executive control network. Regarding the BVSR theory, blind variation appears to involve spontaneous idea generation processes that may occur in the DMN, whereas selective retention may recruit cognitive control processes in the control network [Jung et al., 2013]. In a similar vein, Beaty et al. suggested that the DMN contributes to the spontaneous generation of candidate ideas, while the cognitive control network monitors, directs, and evaluates ideas stemming from the DMN [Beaty et al., 2015]. Our results extend such work by revealing how the default and control networks cooperate to support creative thought.

In addition, our results showed specialized hubs and interactive mechanisms for verbal and visual creativity. In terms of cognitive processes, the generation of novel mental images may involve the retrieval of existing representations from memory and the establishment of new connections by transforming and synthesizing these existing memory units. The precuneus, as a core hub of the pDMN, may support highly integrated and complex behavioral functions, including the processing of visual-spatial information [Selemon and Goldman-Rakic, 1988], retrieval from episodic memory [Shallice et al., 1994], and mental imagery [Burgess, 2008; Hassabis and Maguire, 2007]—processes that are essential to visual creativity. Moreover, the right MFC is important for visual thinking [Prabhakaran et al., 1997], object representation [Takahama et al., 2010], and mental rotation [Gauthier et al., 2002],

which may account for its involvement in visual creativity. This notion is supported by Huang et al. [2013], who examined brain mechanisms underlying visual creativity using fMRI and reported decreased activity in the right middle MFC [cf., Hassabis and Maguire, 2007].

Past research suggests that verbal creativity involves the retrieval of existing concepts from semantic memory and the establishment of new connections among these existing concepts. The mPFC, a core region of the aDMN, supports the integration of linguistic information [Liu et al., 2015] and is involved in a wide range of functions, including inhibitory control, response selection, spontaneous counterfactual thinking, and conflict processing [Botvinick et al., 1999; Crottaz-Herbette and Menon, 2006; Kray et al., 2006; van Veen and Carter, 2005]—processes that are central to verbal creativity. Furthermore, previous research suggests that verbal creativity tasks frequently induce activation of the mPFC, such as verbal insight problems solving [Jung-Beeman et al., 2004] and creative story generation [Howard-Jones et al., 2005]. Recent work has also reported differential coupling of the mPFC with other brain regions associated with individual differences in creativity measured by the verbal TTCT [Wei et al., 2014] and the S-A creativity test [Takeuchi et al., 2012]. Taken together, such findings are consistent with these results and point to a central role of the default and control networks in creative cognition.

Finally, our results point to interesting patterns of within- and between-network connectivity in the creative brain. Specifically, we found that verbal and visual creativity were negatively correlated with functional connectivity within the DMN and FPN. On the other hand, creative ability was associated with increased between-network connectivity of the DMN and FPN. We suspect that decreased within-network connectivity of the FPN and DMN may allow for flexible between-network connectivity, allowing the FPN and DMN to more easily couple with each other (see more empirical evidence in the Supporting Information material). This finding may provide key insights into how brain networks that typically work in opposition come to cooperate to support complex cognitive processes. Future research should further explore the extent to which other creative thought processes involve similar patterns of within- and between-network connectivity.

However, because our conclusions stem from resting-state data, the causal relation among the DMN, FPN, and creative thinking ability should be further explored in future research. Subsequent studies should employ event-related designs to elucidate the complex network dynamics underlying creative cognition.

CONCLUSION

The present study demonstrated common and distinct brain network contributions to visual and verbal creativity.

Higher visual and verbal creativity was related to decreased functional connectivity in the bilateral SPL of the FPN. We also provided direct evidence for the notion that creative cognition benefits from the interaction of the default mode and control networks. Our analysis revealed that the FPN mediated the relationship between the DMN and both verbal and visual creative ability, but specialized hubs and interactive systems were also observed for each domain. Higher visual creativity was related to decreased functional connectivity within the precuneus cortex and the MFC of the pDMN, whereas higher verbal creativity was related to decreased connectivity within the mPFC of the aDMN. Furthermore, the control network mediated the relationship between the aDMN and verbal creativity, and it also mediated the relationship between the pDMN and visual creativity. Together, these results extend prior research by revealing how the default and control networks cooperate to support creative thought.

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APPENDIX A COMMON AND DISTINCT BRAIN NETWORKS UNDERLYING VERBAL AND VISUAL CREATIVITY

Mediation Analysis

To further investigate whether visual and verbal creativity recruit specialized brain networks, we reran another two mediation models with age, gender, and IQ as covariates. Proposed mediators again included the mean z values within bilateral FPN, which were correlated with verbal creativity scores. The figural creativity scores were added as dependent variable. However, the mean z values of the mPFC was added as an independent variable in the model. Next, Proposed mediators again included the mean

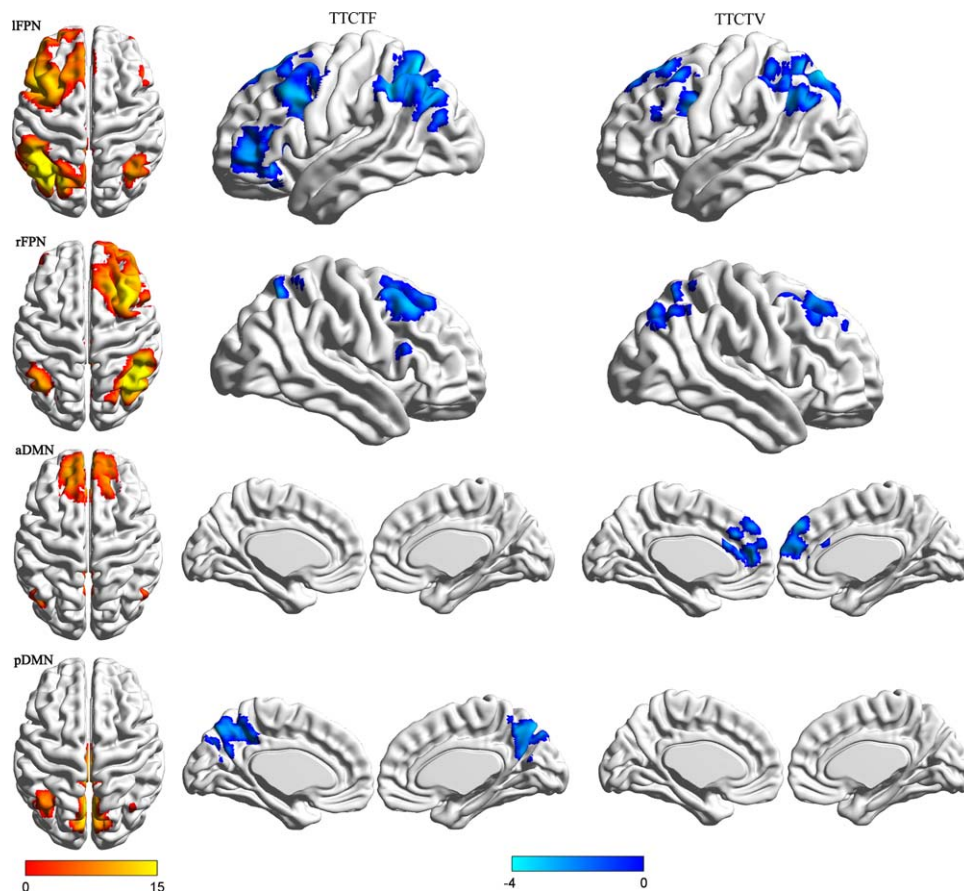


Figure A1.

Regions in which functional connectivity strengths within each RSN (IFPN, rFPN, aDMN, pDMN) were significantly related to creativity. Higher visual creativity was negatively correlated with decreased functional connectivity in the precuneus of the pDMN, right middle frontal and inferior parietal of the right FPN, and left inferior parietal, superior frontal gyrus (SFG), IFG, and DLPFC of the left FPN. Higher verbal creativity was

correlated with decreased functional connectivity in the medial frontal of the aDMN, right inferior parietal, and DLPFC of the right FPN, and left inferior parietal and superior frontal gyrus of the left FPN. We examined regions at a less conservative level of $P < 0.05$, 200 voxels, uncorrected. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE A1. Regions in which functional connectivity strengths within each RSN were significantly related to creativity

	Regions	Coordinate (X Y Z) MNI	Voxels	Z Value
<i>rFPN</i>				
Figure	MFC	48 15 48	422	-3.68
	IPL	39 -57 66	211	-3.72
Verbal	DLPFC	45 48 27	307	-3.09
	IPL	33 -66 57	313	-4.21
<i>lFPN</i>				
Figure	DLPFC	-39 18 36	354	-3.95
	IPL	-27 -66 54	823	-4.10
	IFG	-36 27 29	326	-3.83
	SFG	-6 27 48	254	-3.24
Verbal	IPL	-24 -72 51	558	-3.75
	SFG	-3 24 48	491	-3.36
<i>pDMN</i>				
Figure	precuneus	-3 -72 45	551	-3.31
<i>aDMN</i>				
Figure	—	—	—	—
Verbal	mPFC	-3 45 15	338	-3.66

MFC indicates middle frontal cortex; IPL, inferior parietal; DLPFC, dorsolateral prefrontal cortex; IFG, inferior frontal gyrus; SFG, superior frontal gyrus; mPFC, medial prefrontal cortex; rFPN, right frontoparietal network; lFPN, left frontoparietal network; aDMN, anterior default network; pDMN, posterior default network; $P < 0.05$, 200 voxels, uncorrected.

z values within the bilateral FPN, which were correlated with verbal creativity scores. The verbal creativity scores were added as dependent variable in the model. However, the mean z values of the precuneus was added as an independent variable, and IQ, age, and gender were modeled as covariates of no interest.

Because results showed the independent variable was not significantly correlated with the dependent variable in the two models above, there was reason to suspect suppression effects in the models. According to model suppression

theories [MacKinnon et al., 2000; McFatter 1979], one reason for the nonsignificant effects of the aDMN on figural creativity and the pDMN on verbal creativity may be the suppressing effect of the FPN (see Fig. A2).

APPENDIX B

CONNECTIVITY ANALYSIS

Preprocessing of Connectivity Analysis

The processing of resting-state functional MRI data was performed using the DPARSF (<http://resting-fmri.sourceforge.net/>) [Yan and Zang, 2010] based on SPM8. First, the first 10 volumes from each subject's functional imaging data were discarded to account for steady-state magnetization. The remaining 232 volumes were included in the subsequent analysis. Second, slice timing correction was used to correct slice order effects, and head motion correction was used to correct head movement artifacts, respectively. Twenty-seven subjects, who exhibited head motion of 2 mm maximum displacement and 2° rotation throughout the course of scans, were discarded. Third, each participant's functional image was spatially normalized to the standard MNI template with a resampled voxel size of $3 \times 3 \times 3 \text{ mm}^3$. The data was then smoothed with an isotropic 8 mm full-width at half maximum Gaussian kernel. Then, the linear trend and a band-pass filter (0.01–0.08 HZ) was performed to reduce low-frequency drift and high-frequency noise [Biswal et al., 1995]. Finally, the nuisance signals (cerebrospinal fluid, white matter, head-motion profiles, and global signal) were regressed out to remove the impact of those physiological artifacts.

CONNECTIVITY ANALYSIS

To further explore the relationship between intra- and inter-network connectivity, we conducted connectivity analysis using the seed regions selected based on a study by [Dosenbach et al., 2010]. Fifty-five spherical (3 mm radius) regions of interest (ROI) represented the DMN and the

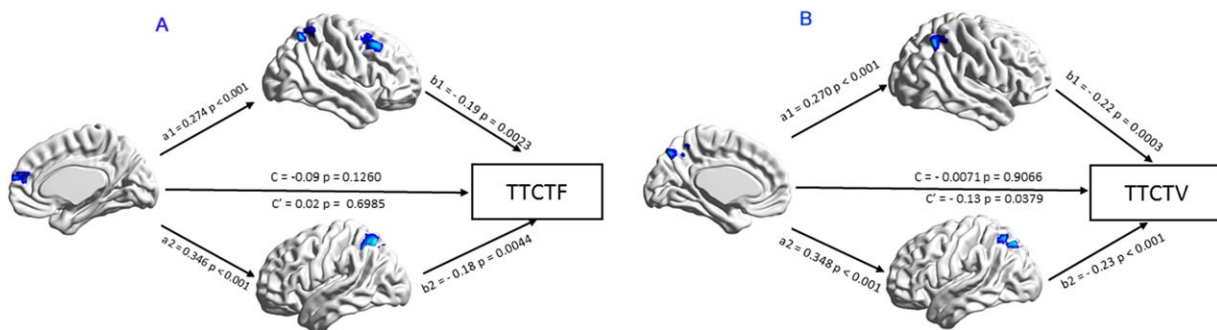


Figure A2.

Mediation analysis: (A) and (B) show the suppressing effects of the FPN in the model, which may account for the nonsignificant correlation of the aDMN with visual and the nonsignificant correlation of the pDMN with verbal creativity scores TTCTF. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE AII. This set of ROIs are from Dosenbach et al. [2010], Science

Regions	MNI coordinates (x y z)	Subnetwork	Regions	MNI coordinates (x y z)	Subnetwork
vmPFC	6 64 3	Default	precuneus	11 -68 42	Default
mPFC	0 54 32	Default	IPS	-36 -69 40	Default
aPFC	-25 51 27	Default	Occipital	-9 -72 41	Default
vmPFC	9 51 16	Default	Occipital	45 -72 29	Default
vmPFC	-6 50 -1	Default	Occipital	-2 -75 32	Default
vmPFC	-11 45 17	Default	Occipital	-42 -76 26	Default
vmPFC	8 42 -5	Default	aPFC	29 57 18	FPN
ACC	9 39 20	Default	aPFC	-29 57 10	FPN
vIPFC	46 39 -15	Default	vent aPFC	42 48 -3	FPN
SFG	23 33 47	Default	Vent aPFC	-43 47 2	FPN
SFG	-16 29 54	Default	vIPFC	39 42 16	FPN
ITG	52 -15 -13	Default	dIPFC	40 36 29	FPN
ITG	-59 -25 -15	Default	ACC	-1 28 40	FPN
Post cingulate	1 -26 31	Default	dIPFC	46 28 31	FPN
Fusiform	28 -37 -15	Default	vPFC	-52 28 17	FPN
Precuneus	-3 -38 45	Default	dIPFC	-44 27 33	FPN
post cingulate	-8 -41 3	Default	dFC	40 17 40	FPN
ITG	-61 -41 -2	Default	dFC	44 8 34	FPN
Occipital	-28 -42 -11	Default	dFC	-42 7 36	FPN
Post cingulate	-5 -43 25	Default	IPL	-41 -40 42	FPN
Precuneus	9 -43 25	Default	IPL	54 -44 43	FPN
Precuneus	5 -50 33	Default	post parietal	-35 -46 48	FPN
Post cingulate	-5 -52 17	Default	IPL	-48 -47 49	FPN
Post cingulate	10 -55 17	Default	IPL	-53 -50 39	FPN
precuneus	-6 -56 29	Default	IPL	44 -52 47	FPN
Post cingulate	-11 -58 17	Default	IPS	-32 -58 46	FPN
AG	51 -59 34	Default	IPS	32 -59 41	FPN
AG	-48 -63 35	Default			

vmPFC, ventromedial prefrontal cortex; mPFC, medial prefrontal cortex; aPFC, anterior prefrontal cortex; ACC, Anterior cingulate cortex; vIPFC, ventromedial prefrontal cortex; SFG, superior frontal gyrus; ITG, inferior temporal gyrus; AG, Angular gyrus; IPS, Intraparietal sulcus; dIPFC, dorsolateral prefrontal cortex; dFC, dorsal frontal cortex; IPL, inferior parietal lobule.

FPN (see Table AII). The representing mean time series was computed by averaging the time series of voxels in this ROI. We conducted intranetwork and internetwork connectivity using the Pearson correlation between each pair of ROIs for each subject. The correlation coefficients were standardized using Fisher's r -to- z transformation, increasing the normality of the distribution and allowing further correlation analysis. For each of the two RSNs, the intranetwork strength was calculated as the mean connection strength of all ROIs in the same network. The internetwork connectivity was calculated as the mean connection strength between each ROI of a network and all of ROIs of the other network. And we explored the relationship between the intranetwork and internetwork connectivity using the Pearson correlation. The result showed that reduced intranetwork connectivity in the DMN and FPN was significantly correlated with increased interconnectivity of the DMN and

FPN ($r = -0.449$, $P = 0.000$; $r = -0.284$, $P = 0.000$), which provide more evidence to support the idea that the reduced intranetwork connectivity within the DMN and FPN may allow for more flexible internetwork connectivity in the highly creative brain.

Previous studies showed the effect of local overconnectivity would positively stabilize and reinforce local physical connections while is coupled with long-range underconnectivity [Belmonte et al., 2004; Cerliani et al., 2015; Courchesne and Pierce, 2005]. Accordingly, at the network level, the effect of connectivity within networks negatively affect the development of efficient connections between networks [Cerliani et al., 2015; Rudie et al., 2012; Shih et al., 2011]. In this study, the increased connectivity between DMN and FPN may mean increasing synchrony in the activity of the two networks and more effective information transfer between the two networks.