Individual differences in verbal creative thinking are reflected in the precuneus

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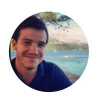

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ABSTRACT

There have been many structural and functional imaging studies of creative thinking, but combining structural and functional magnetic resonance imaging (MRI) investigations with respect to creative thinking is still lacking. Thus, the aim of the present study was to explore the associations among inter-individual verbal creative thinking and both regional homogeneity and cortical morphology of the brain surface. We related the local functional homogeneity of spontaneous brain activity to verbal creative thinking and its dimensions—fluency, originality, and flexibility—by examining these inter-individual differences in a large sample of 268 healthy college students. Results revealed that people with high verbal creative ability and high scores for the three dimensions of creativity exhibited lower regional functional homogeneity in the right precuneus. Both cortical volume and thickness of the right precuneus were positively associated with individual verbal creativity and its dimensions. Moreover, originality was negatively correlated with functional homogeneity in the left superior frontal gyrus and positively correlated with functional homogeneity in the right occipito-temporal gyrus. In contrast, flexibility was positively correlated with functional homogeneity in the left superior and middle occipital gyrus. These findings provide additional evidence of a link between verbal creative thinking and brain structure in the right precuneus—a region involved in internally-focused attention and effective semantic retrieval—and further suggest that local functional homogeneity of verbal creative thinking has neurobiological relevance that is likely based on anatomical substrates.

1. Introduction

One of the most valued human characteristics is creativity, generally defined as the ability to produce both original and valuable outcomes (Runco and Jaeger, 2012; Stein, 1953; Sternberg and Lubart, 1996). Recently, several resting-state functional magnetic resonance imaging (rfMRI) investigations have explored the relationship between spatially remote brain regions in individuals of high creative ability. Such work has consistently shown that the default mode network (DMN) is associated with individual verbal creative potential (Beaty et al., 2014; Takeuchi et al., 2012; Wei et al., 2014a, 2014b). Although resting-state networks are thought to reflect the underlying structural architecture of the human brain, the local functional underpinnings of verbal creative potential has not been explored. In addition, there is little integrated evidence from structural and functional MRI studies, which may clarify whether variability of individual creative ability in functional and structural patterns on brain surface is consistent. The present research thus sought to address these issues by examining the roles of both structural and functional brain metrics in verbal creativity.

The scientific study of creativity usually assesses the ability to generate original, novel ideas by breaking established modes of thinking. A critical component of creativity is divergent thinking, the generation of many possible ideas and the exploration of original alternatives (Guilford, 1956). Using Activation Likelihood Estimation, Wu and colleagues reported robust activation of the lateral prefrontal cortex, posterior parietal cortex (including the inferior parietal lobule and precuneus), and several regions in the

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temporal cortex in functional MRI studies of creative idea generation (Wu et al., 2015). Another recent meta-analysis, which focused on process-specific regions of creativity, showed that verbal tasks were associated with more activation within bilateral lateral PFC than those using non-verbal ones. Non-verbal tasks, in contrast, were associated with activation of the left rostral PFC and left occipital cortex. Verbal and non-verbal tasks also overlapped in several regions within the left hemisphere, including superior/inferior prefrontal gyrus, parieto-occipital cortex, posterior middle frontal gyrus, and medial prefrontal cortex (Gonen-Yaacovi et al., 2013).

Creative potential is often viewed as a normally distributed and stable trait that is reflected in brain structure (Eysenck, 1995; Fink et al., 2013). A growing body of research has focused on the brain structural characterizations or biomarkers of creative potential from an individual differences perspective. Although structural imaging research has revealed individual differences in creative potential or performance (Chen et al., 2014; Fink et al., 2013; Jung et al., 2010; Takeuchi et al., 2010; Zhu et al., 2013), such findings are not universal, possibly due to a diversity of designs and methodologies employed (Dietrich and Kanso, 2010; Fink et al., 2013). More recently, however, a more consistent picture of the creative brain has begun to emerge (Beaty et al., 2014; Fink et al., 2013; Jauk et al., 2015; Kühn et al., 2014; Takeuchi et al., 2012). For instance, a recent voxel-based morphometry study investigating verbal creative potential reported positive associations between indicators of creativity and brain structure in the precuneus (Fink et al., 2013). A subsequent study by Jauk et al. (2015) also found a relationship between ideational originality and gray matter volume in the precuneus. The precuneus, as part of the DMN, was also found to be functionally involved in verbal divergent thinking (Fink et al., 2012) and metaphor generation (Benedek et al., 2014a). This region has shown reduced deactivation during a working memory task in highly creative individuals (Takeuchi et al., 2011). Moreover, several studies from different laboratories found that verbal divergent thinking was related to regions within the DMN, using structural and functional MRI data (Beaty et al., 2014; Takeuchi et al., 2012). These observations appear to indicate that creative potential can be attributed to a combined effect of brain structure and function.

In neuroimaging studies, functional segregation and integration are generally viewed as the two guiding principles in brain mapping as they are thought to reflect key mechanisms of neuronal processing (Friston, 2009; Tononi et al., 1994). Functional segregation is characterized by the local properties of different brain regions, whereas functional integration is defined as the global properties of the brain (Song et al., 2014). Resting-state fMRI studies on creative thinking showed that the synchronization relationship between spatially remote brain regions was associated with creative task performance (Beaty et al., 2014; Takeuchi et al., 2012; Wei et al., 2014a). Nevertheless, the local features, or functional specialization of brain regions related to creative thinking remains unclear. Regional homogeneity (ReHo) is known to reflect synchrony of time series of neighboring voxels (Zang et al., 2004; Zuo et al., 2013) and is considered to represent a short-distance connection in the human brain connectome (Sepulcre et al., 2010). On the other hand, voxel-based functional connectivity analysis neglect the intrinsic geometry of the highly folded human cortex (Zuo et al., 2013). Therefore, we conducted surface-based ReHo (2dReHo) analysis to explore regional functional variability on the cortical surface in the present research. This approach can shed further light on the relationship between verbal creative thinking and inter-individual differences in brain structure and function. Functional homogeneity can also assess correlations with regional cortical characterizations, including surface area, cortical thickness, volume, and others (Jiang et al., 2014). Considering 2dReHo's high test–retest reliability and biological meaning (Jiang et al., 2014; Zuo et al., 2013), we selected brain regions resulting from 2dReHo investigations as regions of interest (ROI) and extracted regional cortical indicators for further structural analysis.

The present study thus examines associations between inter-individual differences in verbal creative thinking, regional homogeneity, and cortical morphology of the brain surface. Previous neuroimaging studies of creative potential have shown task-related activation of regions within the DMN, executive network, as well as other regions, including the fusiform gyrus, precentral gyrus, and occipital cortex (Beaty et al., 2014; Benedek et al., 2014a, 2014b; Fink et al., 2009, 2010, 2012; Takeuchi et al., 2012; Wei et al., 2014a). In particular, structural MRI studies have shown that increased gray matter within the precuneus and prefrontal gyrus is associated with individual differences in creative potential, as measured by divergent thinking tasks (Fink et al., 2013; Jauk et al., 2015; Takeuchi et al., 2010). Besides, previous evidence has found that decreased regional functional homogeneity in high-level association areas (e.g., anterior cingulate cortex, prefrontal cortex, and precuneus) and increased functional homogeneity in the primary somatosensory cortex are associated with attention performance (Jiang et al., 2014; Wei et al., 2014b). Therefore, in the present study, we hypothesized that creative performance would be related to decreased functional homogeneity in DMN regions, including precuneus, posterior cingulate cortex, and medial prefrontal cortex, and increases in functional homogeneity in other areas involved in somatosensory and perceptual processes. Additionally, we examined whether verbal creative thinking is related to cortical morphological measures within regions identified in the 2dReHo analysis, to further illustrate the neuroanatomical basis associated with functional homogeneity.

2. Methods

2.1. Participants

All participants had been studied previously (Zhu et al., 2013). However, three participants were excluded from the present study because of missing rfMRI images, and 14 were excluded to satisfy exclusion criteria of head movement during rest-fMRI scanning (i.e., >2.5 mm translation in any axis and $>2.5°$ angular rotation in any axis; see Supplementary Table 1). The final sample therefore consisted of 268 participants (143 females; mean age$=19.89\pm1.19$; mean translation$=0.38\pm0.33$; mean angular rotation$=0.47\pm0.37$; see Supplementary Table 2). Most participants were recruited from Southwest University by means of the campus network or advertisements on bulletin boards. All participants were healthy and right-handed, and none had a history of psychiatric disorder, cognitive disability, or substance abuse (including illicit drugs and alcohol). After providing written informed consent, participants were required to undertake a series of psychological tests and MRI scans, and they subsequently received payment for their time. The Southwest University Brain Imaging Center Institutional Review Board approved this project.

2.2. Assessment of creativity

The verbal form of the Torrance Tests of Creative Thinking (TTCT; Torrance et al., 1974) was used to assess creativity (i.e., divergent thinking ability). The verbal TTCT consists of seven tasks: generating questions, causes and consequences; improving products; alternate uses; manipulating objects; and imagining the consequences of a scenario. The TTCT provides a total creativity score as well as indices and scores for evaluating different creative processes or dimensions, which generally include (a) originality (the degree of originality of the responses, which is associated with thinking "outside of the box"), (b) flexibility (the number of different categories of responses, which reflects the ability to shift between conceptual fields), and (c) fluency (the number of meaningful and relevant responses, which is associated with the ability to generate and consider several different possibilities). The total creativity score is the sum of three dimensions. The TTCT demonstrates adequate reliability ($r > 0.90$) and high predictive validity ($r > 0.57$) for future career and creative achievements (Torrance, 1993). It has been translated into more than 35 languages (Millar, 2002) and is used frequently in several fields, such as psychology, education, and even business.

Three trained postgraduates scored the creative quality of responses to all items for all participants. The three raters majored in psychology and were blind to the goal of this research. The reason raters were recruited from school of psychology was that they can easily understand the TTCT scoring guide (Wu et al., 1981). Firstly, they were trained to master the method of manual scoring and the definition of creativity. Then, they independently assessed all items of 30 participants and yielded relatively uniform scoring criterion through discussing with experts in the field. This step was used to adjust the scoring guide for flexibility in the present sample, such as how to evaluate a special answer that was nonexistent in the original guidelines. Finally, raters were asked to assess the answers of all participants based on this guidance, and their inter-rater correlation coefficient was significant (ICC > 0.90).

2.3. Assessment of general intelligence

The Combined Raven's Test (CRT), which was revised by the Psychology Department of East China Normal University in 1994, is widely used for psychometric measurement of individual intelligence. It has good reliability and validity (Wang, 2007). The CRT consists of 72 nonverbal items. Each item comprises a matrix with a missing piece that is to be completed by selecting the best answer from six or eight alternatives. The score is computed by summing the number of correct answers.

2.4. Image acquisition

All structural and functional MRI images were collected using a Siemens 3 T Trio scanner (Siemens Medical Systems, Erlangen, Germany). Resting-state fMRI images were acquired using Gradient Echo type Echo Planar Imaging (GRE-EPI) sequence (TR/TE = 2000 ms/30 ms, FA = 90°, resolution matrix = 64×64, FOV = 220×220 mm^2, and thickness = 3 mm, acquisition voxel size = $3.4 \times 3.4 \times 4$ mm^3). A total of 32 slices were used to represent the whole brain. Each section contained 242 volumes. During resting-state scanning, the scanner room was darkened, and subjects were instructed to relax and remain awake with eyes closed. Following resting-state fMRI, the experimenter asked subjects whether they had fallen asleep during the session and recorded their answers. High-resolution three-dimensional T1-weighted structure images were obtained using a Magnetization Prepared Rapid Acquisition Gradient-echo (MPRAGE) sequence (TR/TE = 1900 ms/2.52 ms, FA = 9°, FOV = 256×256 mm^2; slices = 176; thickness = 1.0 mm; voxel size = $1 \times 1 \times 1$ mm^3).

2.5. MRI data processing

Image preprocessing was carried out using the Connectome Computation System (CCS: http://lfcd.psych.ac.cn/ccs.html; (Xu et al., 2015)—an integration system that involves AFNI, FSL, Freesurfer (Cox, 2012; Fischl, 2012; Jenkinson et al., 2012), and in-house Shell/MATLAB scripts for multimodal image analysis for discovery brain science (Sporns, 2014). The structural and functional image preprocessing primarily included (1) denoising the structural image by means of a spatially adaptive nonlocal means filter (Zuo and Xing, 2011), (2) automated segmentation (cerebrospinal fluid, white matter, and gray matter) and cortical surface reconstruction to generate a smooth representation of the GM-WM interface (white surface) and of the GM-CSF interface (pial surface), (3) spatial normalization estimation of a triangular mesh tessellation and the mesh deformation over the GM-WM boundary from individual native space, (4) discarding the first 5 EPI volumes of each participant to eliminate images that were made while the magnetization was brought into equilibrium and while the subjects adapted to the scanning noise, (5) slice timing correction, (6) realigning the remaining images to the first volume for 3D motion correction and calculating motion parameters by estimating the translations in each axis and the angular rotation in each direction for the 237 consecutive volumes, (7) 4D global mean-based intensity normalization, (8) co-registering individual functional images with structural images by GM-WM boundary-based registration (BBR) algorithm (Greve and Fischl, 2009), (9) regressing out the WM/CSF mean signals and six motion parameters for head movement as nuisances, (10) band-pass temporal filtering (0.01–0.1 Hz), and (11) removal of linear and quadratic trends.

Various figures and indices were produced during the preprocessing to ensure good data quality. The structural data quality control procedure (QCP) was performed by two researchers, and included visual head motion inspection, tissue segmentation, and brain surface reconstruction. It was especially important to visually assess the quality of the brain extraction and to correct intensity bias to select the best images from the three alternative maps. The QCP of functional images included the warp distortion amount for BBR-based function-to-structure realignment as measured by the minimal cost of the co-registration (mcBBR) and the covariate of head motion as measured by the root mean square of frame-wise displacement (rmsFD; http://lfcd.psych.ac.cn/ccs/QC.html).

2.6. Surface-based ReHo analysis

Kendall's coefficient of concordance (KCC) was used to measure ReHo of the time series of a given voxel with those of its nearest neighbors in a voxel-wise fashion (Zang et al., 2004). Vertex-wise functional homogeneity analysis was performed with the CCS on the cortical surface by adopting the classic ReHo method to its 2-dimensional variant (Zuo et al., 2013). The individually preprocessed 4D RFMRI time series were initially projected onto the fsaverage5 standard cortical surface for determining the vertex of the surface space. To calculate 2dReHo, for a given vertex, length-one has six neighbor vertices in the surface space, and the KCC of rsfMRI from seven vertices (including the given vertex) was computed (Zuo et al., 2013). This computational procedure was repeated for all vertices on the surfaces of both hemispheres to produce individual 2dReHo surface maps. Finally, the individual 2dReHo maps were smoothed with a Gaussian kernel of 6 mm full-width half-maximum for subsequent statistical analysis.

2.7. Statistical analysis

A vertex-wise general linear model (GLM) was used to examine the relationship between regional functional homogeneity on the brain surface and verbal creative performance. The GLM includes one discrete factor (sex) and three continuous factors (total score, age, and general intelligence), where the total score is the variable of interest and the others are regressed out as confounding factors. We also explored the relations among regional functional homogeneity and the dimensions of verbal creative thinking—fluency, flexibility, and originality. We employed a cluster-level correction for multiple comparisons in FreeSurfer implemented in Matlab-based functions (Bernal-Rusiel et al., 2010). These maps were corrected at the cluster-level ($p < 0.05$) by using random field theory.

Linear regressions were calculated with SPSS (version 16.0) to examine the relationships between cortical characterization and verbal creative performance. We first selected a ROI on the basis of the surface-based ReHo analysis, and also created a ROI mask by using the aparc.a2009s annotation implemented in the FreeSurfer as a control region. Aparc.a2009s is a precisely defined parcellation method for automatically labeling the cortical surface (Destrieux et al., 2010). We then extracted the five cortical indicators (volume, thickness, area, curve, and folding) for each subject. These separate indices were estimated to measure different properties of the brain cortical surface morphology. *Volume* is the total amount of the structure based on the defined parcellation; *surface area* is the total area of the triangles that were connected to a given vertex; *cortical thickness* is the averaged linking distance between the pial and white surfaces along normal vector; *curve* is the maximum and minimum bending of the cortical surface at a given vertex; and *folding index* is a metric that quantifies the amount of folding overall on a surface (Jiang et al., 2014). Each cortical index was entered into regressions to predict verbal creative ability, which included the total verbal creativity score and the scores for originality, flexibility and fluency, after controlling for sex, age and, general intelligence. The level of statistical significance was set at $p = 0.05$ for each of the independent regressions.

3. Results

3.1. Behavioral results

The behavioral data revealed an average total verbal creativity test score of 133.6 (SD=41.2, range 61–334.8) and an average general intelligence score on the Combined Raven's Test of 66.2 (SD=3.3, range 52–72). Verbal creativity performance did not show significant correlation with general intelligence ($p > 0.5$). Similarly, none of the three dimensions of verbal creativity (fluency, flexibility and originality) was correlated with general intelligence ($p > 0.5$). Table 1 shows the descriptive statistics for the demographic and psychological characteristics of all participants.

3.2. Correlation of regional functional homogeneity and verbal creativity

We examined regions that showed an association between the total score for verbal creativity and regional functional homogeneity in the whole brain. After controlling for age, sex, and general intelligence, a multiple regression analysis revealed that individuals who had a high total verbal creativity score had lower regional homogeneity in the right precuneus (*x, y, x*=7.2, −54.9, 67; Fig. 1).

Table 1
Demographic and psychological data.

Category	Data	Range
Gender (male/female)	125/143	
Age	19.9 ± 1.2	17–27
IQ	62.2 ± 3.3	52–72
TTCT-sum	133.6 ± 41.2	61–334.8
Originality	47.4 ± 17.4	17.5–131.5
Flexibility	27.5 ± 6.3	12.3–49.5
Fluency	58.7 ± 19.34	24–153.75

Age and psychological data are displayed as mean (SD).
TTCT=Torrance Tests of Creative Thinking; IQ=Combined Raven Test.

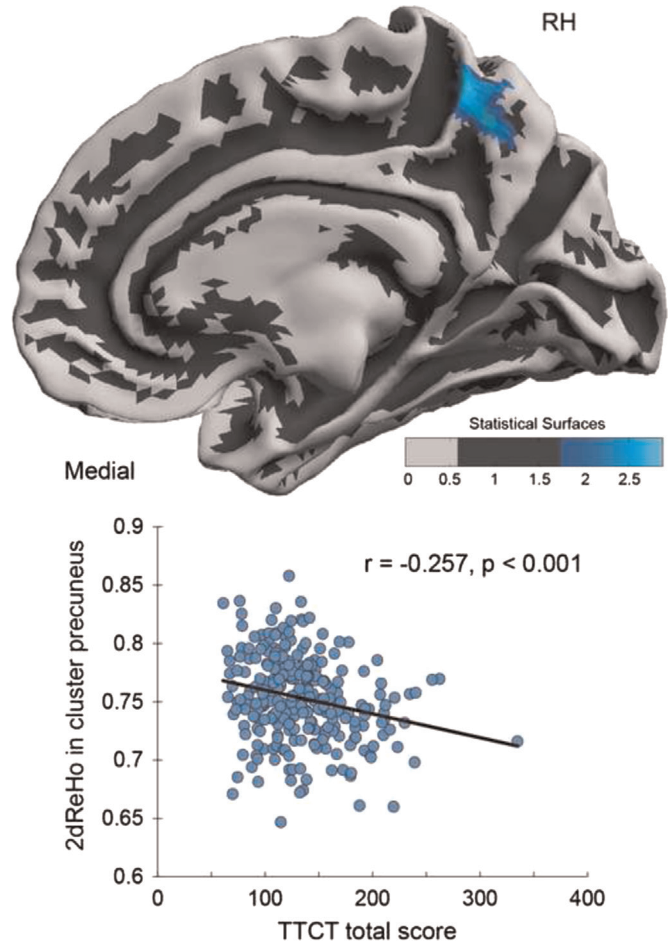

Fig. 1. Statistical maps of cortical surfaces showing a significant correlation (FTR corrected) between the total verbal creativity score and functional homogeneity as measured by 2dReHo in fsaverage5 standard apace. After controlling for age, sex, and general intelligence, a multiple regression analysis found that high total verbal creativity scores were associated with lower regional homogeneity in the right precuneus. In the lower pane, the functional homogeneity of the right precuneus cluster (top) is plotted on the *x*-axis against the total verbal creativity score on the *y*-axis. Note that this scatter plot is presented only for the purpose of visualization.

We also examined regions that showed an association between each of the creativity dimensions (fluency, flexibility, and originality) and regional functional homogeneity, using a whole-brain multiple regression analysis that included each dimension, age, sex, and general intelligence score as covariates. Subjects who had high scores for originality had lower functional homogeneity in the right precuneus (*x, y, x*=7.2, −54.5, 54.9; Fig. 2a) and left superior frontal gyrus (SFG; *x, y, x*=−22.1, 27, 46.8; Fig. 2b), and higher functional homogeneity in right occipito-temporal gyrus (*x, y, x*= 34, −72.4, −6.8; Fig. 2c). Subjects who had high scores for flexibility had higher functional homogeneity in the left superior occipital gyrus (*x, y, x*=−16.7, −82.2, 37.8; Fig. 2e) and the left middle occipital gyrus (*x, y, x*=−36, −82.8, 37.8; Fig. 2e), and lower regional homogeneity in the right precuneus (*x, y, x*=8.9, −55.1, 43.7; Fig. 2d). Subjects who had high scores for fluency had lower functional homogeneity in the right precuneus (*x, y, x*=7.2, −54.5, 65; Fig. 2f). Additional statistical information concerning brain regions is provided in Table 2.

3.3. ROI-based correlation analysis

The total verbal creativity score was predicted by higher volume (Adjusted R^2=0.04, Beta=0.11) and larger area (Adjusted

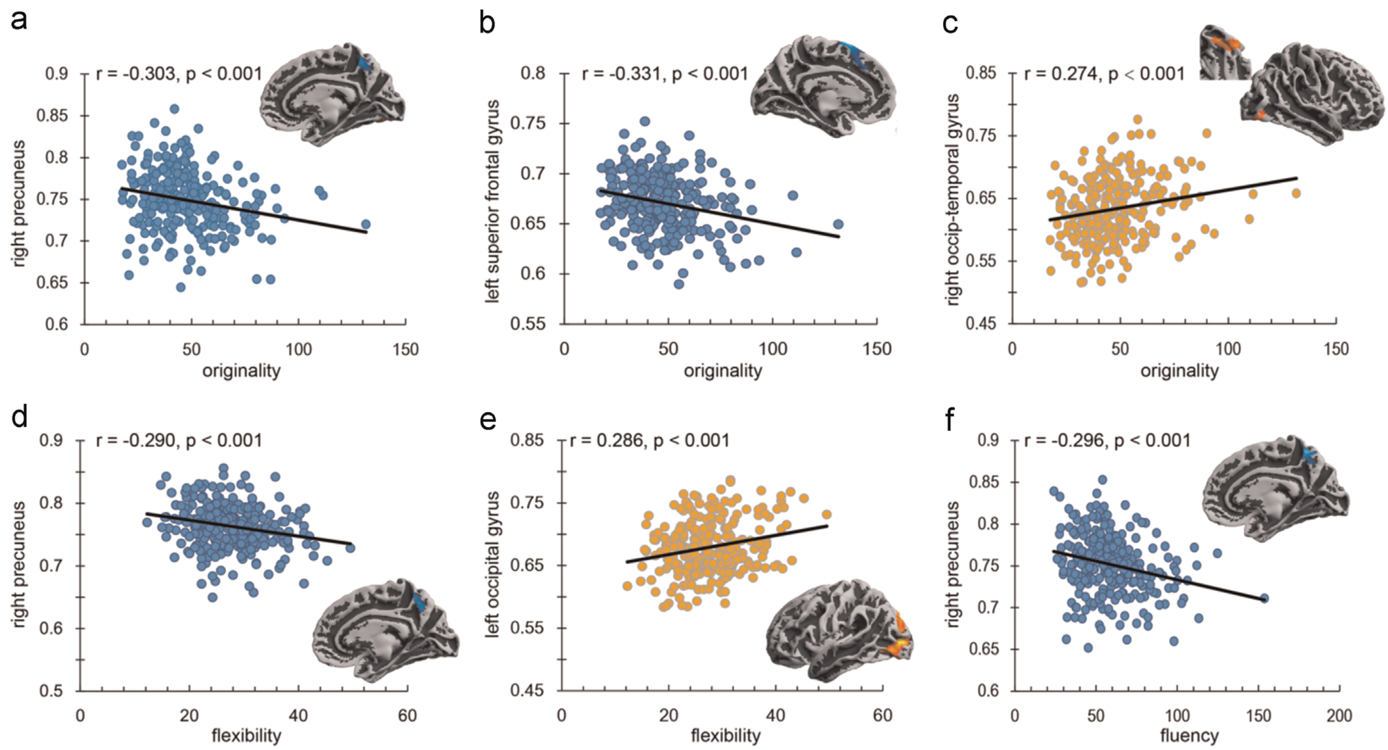

Fig. 2. Scatterplot of the correlation between regional functional homogeneity and the three dimensions of verbal creative thinking. Scatterplots a, b, and c show significant correlations between originality and 2dReHo in the right precuneus, left SFG, and right occipito-temporal gyrus, respectively. Scatter plots d and e show significant correlations between flexibility and 2dReHo in the right precuneus, and the left superior and middle occipital gyri. Scatter plot f shows the significant correlation between fluency and 2dReHo in the right precuneus.

R^2=0.04, Beta=0.12) of the right precuneus, as expressed by aparc.a2009s. Similarly, the scores for originality and flexibility were predicted by higher volume and larger area in the right precuneus (Adjusted R^2=0.04–0.05, Beta=0.11–0.13). No significant prediction values were found between the score for fluency and the structural indices, and other structural indicators (e.g., thickness, curve and folding) did not significantly predict the total score or sub-dimensions (see Table 3).

We also performed this analysis by extracting each subject's cortical indices by the chosen ROI (the right precuneus), which was identified in 2dReHo correlation, and then tested the linear relationship between all cortical indices and verbal creative thinking, controlling for sex, age, and general intelligence. The total verbal creativity score and scores on the three dimensions were significantly predicted by higher volume (Adjusted R^2=0.06, Beta=0.17–0.20) and thickness (Adjusted R^2=0.04–0.05, Beta=0.12–0.13). The flexibility score was predicted by area in right precuneus (Adjusted R^2=0.04, Beta=0.11); other structural indicators (e.g., curve and folding) did not significantly predict the total score or sub-dimensions (see Table 4).

Table 3
Correlation coefficients between verbal creative thinking scores and five measures of cortical morphology in the right precuneus (annot aparc.a2009s).

Index	Volume	Area	Thickness	Curve	Folding
Total score	0.192*	0.194**	0.162	0.164	0.163
Originality	0.205*	0.212*	0.179	0.179	0.179
Flexibility	0.193*	0.191*	0.161	0.161	0.163
Fluency	0.169	0.167	0.141	0.146	0.144

* Indicates $p < 0.05$.
** Indicates $p < 0.005$.

After controlling for age, sex, and general intelligence, an additional linear regression analysis revealed that total verbal creativity score was strongly predicted by the combined variation of 2dReHo and volume in the right precuneus (Adjusted R^2=0.10, Beta for 2dReHo=−0.24, Beta for volume=0.19). Similarly, we performed 4 linear regressions analyzes to explore the relationship between regional cortical characterizations of the other regions identified in the 2dReHo and both the total verbal creativity

Table 2
Cortical areas that are significantly correlated with total scores and scores on the dimensions of verbal creative thinking.

Index	Brain region	Cortical hemisphere	Brodmann area (BA)	Cluster size (mm^2)	Talairach coordinates (peak)		
					X	*Y*	*Z*
Total score	Precuneus	Right	BA7	397.66	7.2	−54.9	67
Originality	Superior frontal gyrus	Left	BA6	807.27	−22.1	27	46.8
	Precuneus	Right	BA7	374.96	7.2	−54.5	54.9
	Occipito-temporal gyrus	Right	BA17	820.7	34	−72.4	−6.8
Flexibility	Middle occipital gyrus	Left	BA17	1307.69	−36	−82.8	2.3
	Superior occipital gyrus	Left	BA19	973.87	−16.7	−82.2	37.8
	Precuneus	Right	BA7	339.92	8.9	−55.1	43.7
Fluency	Precuneus	Right	BA7	382.04	7.2	−54.5	65

Cluster size (mm^2) is the surface area of the cluster in square millimeters; *X* is the Talairach region *X* plane; *Y* is the Talairach region *Y* plane; *Z* is the Talairach region *Z* plane.

Table 4
Correlation coefficients between verbal creative thinking scores and five measures of cortical morphology in the right precuneus as identified in the 2dReHo correlation.

Index	Volume	Area	Thickness	Curve	Folding
Total score	0.251**	0.177	0.208*	0.163	0.167
Originality	0.246**	0.180	0.214*	0.180	0181
Flexibility	0.253**	0.197*	0.203*	0.162	0.163
Fluency	0.238**	0.169	0.193*	0.141	0.149

* Indicates $p < 0.05$.
** Indicates $p < 0.005$.

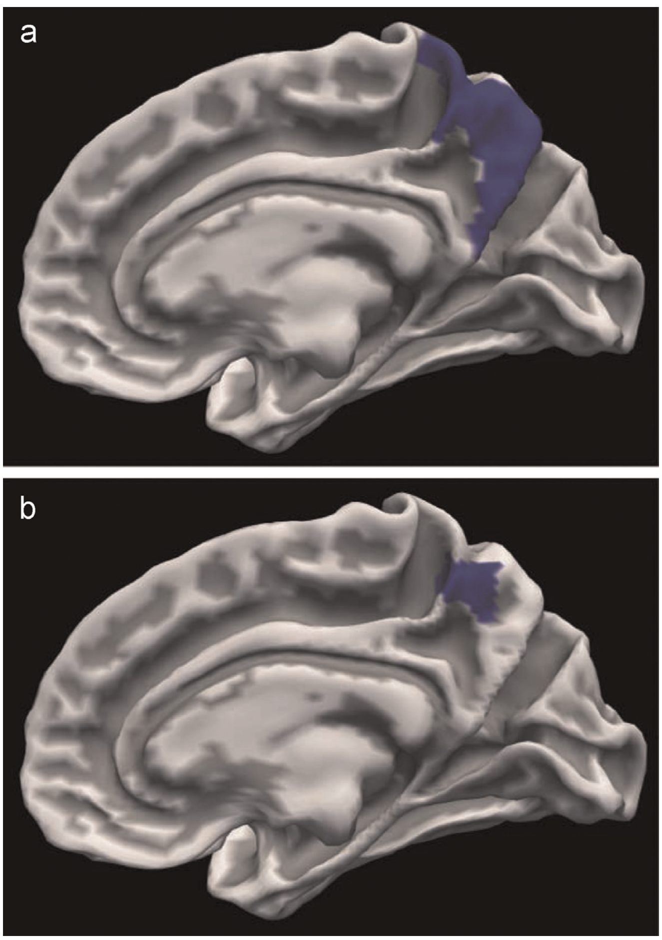

Fig. 3. Topography of the right precuneus based on aparc.a2009s (a); the local precuneus as an ROI that was identified in the 2dReHo correlation (b), displayed on fsaverage5 standard space.

score and the score for each dimension, with age, sex, and general intelligence as covariates. However, similar tendencies for the relationship between regional cortical characterizations and both total score and its dimensions were not observed in these analyzes Fig. 3 (see Supplementary Tables 3–6).

4. Discussion

The goal of this study was to examine regional functional homogeneity and structural correlates of individual verbal creativity. We first related regional functional homogeneity of spontaneous surface brain activity to verbal creative thinking and its sub-dimensions (i.e., fluency, originality, and flexibility). Decreased functional homogeneity in the right precuneus was associated with higher total verbal creative scores and higher scores on its three dimensions. Moreover, the creativity dimension scores were associated with regional functional homogeneity in left superior frontal gyrus and right occipito-temporal gyrus. By employing the ROI analysis of brain morphometry, individual verbal creativity and its sub-dimensions were positivity associated with cortical volume and thickness in the right local precuneus, rather than the right total precuneus. The roles of the precuneus and other areas for verbal creativity thinking, as well as the functional implications for regional functional homogeneity and corresponding cortical characterization, will be discussed in the following section.

4.1. The right precuneus as a neural substrate of verbal creative thinking

As expected, we found decreased functional homogeneity in the precuneus, a part of the DMN, in individuals with higher verbal creative ability. A large body of evidence suggests that the precuneus is involved in complex and highly integrated behavioral functions, including processing of visual-spatial information (Selemon and Goldman-Rakic, 1988), retrieval of episodic memory (Shallice et al., 1994), mental imagery (Burgess, 2008; Hassabis et al., 2007), and metaphor comprehension (Mashal et al., 2014). As a multifunction brain area, the precuneus is required to segregate the actualization of different cognitive processing, and it reflects high functional segregation at the local micro-scale level. Decreased functional homogeneity in the right precuneus thus reflects complexity of information processing or a degree of functional segregation. This may provide an alternative explanation for why less functional homogeneity was associated with higher verbal creativity performance.

Most studies on creativity have indicated that creative thought is closely linked to spontaneously occurring thought processes, which is associated with lower working memory demands (Limb and Braun, 2008), defocused attention (Vartanian, 2009; Wegbreit et al., 2012), and mind wandering (Baird et al., 2012). For instance, Takeuchi et al. (2012) found that high divergent thinking performance was predicted by strong resting-state functional connectivity within the DMN, including the posterior cingulate cortex adjacent to the precuneus. Similarly, a recent study found that compared to a group of low-creative participants, a group of highly-creative participants—assessed with a battery of divergent thinking tests—showed greater connectivity between prefrontal-executive regions and the DMN (Beaty et al., 2014). These results provide support for the notion of spontaneous creativity emphasized in the literature on creative insight, and suggest that original ideas might rely on automatic processing and a flexible modulation of bottom-up attention (Dietrich and Kanso, 2010; Jung-Beeman et al., 2004).

On the other hand, an integrated view posits that deliberate processing is necessary to complete creative thinking tasks (Flaherty, 2005). In line with this notion, EEG research has reported alpha synchronization in parietal brain regions during creative thinking, which might reflect efficient memory processing (i.e., cognitive resources devoted to effective memory search and retrieval; (Fink and Benedek, 2012). Fink and others have speculated that the parietal cortex may be associated with the bottom-up activation of attentional and semantic/visuospatial memory necessary for creative problem solving (Fink and Neubauer, 2006; Fink et al., 2009; Grabner et al., 2007). Similarly, fMRI studies also indicated that activation in the precuneus might support the episodic memory retrieval or self-processing operations when individuals performed an internal attention task (Cavanna and Trimble, 2006). In sum, activation of the precuneus is thought to play a key role in ideational generation and evaluation by internally-focused attention and effective memory retrieval.

4.2. Local functional homogeneity and fluency, originality and flexibility

Previous neuroscience studies of creative thinking have been limited to analyzing total creativity scores and not the score for each dimension, primarily due to high correlations between dimensions and with total creativity score (Torrance et al., 1974). On the one hand, scores for each dimension has not provided additional meaningful information in some previous studies (Heausler and Thompson, 1988). On the other hand, the results of behavioral studies show that each dimension is differentially related to psychological variables that are important for creativity (Shaw and DeMers, 1986). In the present study, we explored the extent to which three dimensions of verbal creative thinking—fluency, flexibility, and originality—relate to functional organization and structural characteristics.

Specifically, we found that fluency was related to regional functional homogeneity in the right precuneus. This finding is consistent with previous results reporting an association between ideational fluency/flexibility and gray matter density in the right precuneus and cuneus (Fink et al., 2013). Related research on verbal fluency has shown significant activation in the right precuneus during the resting state compared with the letter condition (Halari et al., 2006). Additionally, the inhibitory path coefficient from the middle frontal gyrus to the precuneus and the facilitative path coefficient from the precuneus to the anterior cingulate, activated during verbal fluency tasks, are further indications of the role of the precuneus in retrieving and visually "reading" information (Fu et al., 2006). Moreover, the "phonological store" was related to the posterior parietal cortices including the precuneus (Baddeley, 2003). We thus suspect that the precuneus is an important node that collects and stores relevant semantic information during verbal creative task performance.

Originality—thought to be a vital aspect of every form of creativity and a criterion for novelty (Runco and Jaeger, 2012)—was associated with reduced regional homogeneity in the left SFG (BA6). This result is consistent with research on creative analogical reasoning showing increased recruitment of frontopolar cortex, including left SFG (x, y, $x = -2$, 20, 59; BA6)—a region crucial role for integrating semantically distant information to generate solutions. Several lesion studies also showed that localized lesions within the medial PFC region were associated with impaired performance on divergent thinking tasks (Abraham et al., 2012; Shamay-Tsoory et al., 2011). Specifically, the extent of lesion in the left hemisphere may produce more original responses, while lesions in the right medial PFC may result in decreased originality (Shamay-Tsoory et al., 2011). Likewise, a meta-analysis on creativity revealed that medial frontopolar cortex may contribute to combining dissimilar semantic information and freely generating unusual responses (Gonen-Yaacovi et al., 2013). Previous research also indicated that the bilateral superior/middle frontal gyrus are involved in novelty detection and are an important hub connected to posterior cortical association areas, such as temporal cortical regions and the precuneus (Yamaguchi et al., 2004). Thus, the relative role of SFG is in agreement with the involvement of verbal creative tasks reported by previous studies, and may be involved in integration of semantic information and novelty generation (Benedek et al., 2014b; Flaherty, 2005; Ganesan et al., 2005; Green et al., 2012).

An unexpected finding of the present study is that functional homogeneity in posterior parietal and occipital brain areas were positively associated with ideational flexibility, which is a characteristic of flexibly generating ideas or choosing ideas from many different alternatives. There is consensus that the precuneus and visual cortices are activated in visual mental imagery, which a key component of creativity and is involved in the processing of verbal creativity demands (Cavanna and Trimble, 2006; Kosslyn and Ochsner, 1994). An fMRI study exploring perception of novel objects reported increased neural activity in the lingual gyrus and the middle occipital cortex, regions involved in the detection of unusual features (Zhang et al., 2013). Structural research has also suggested that an overlapping cluster in the right cuneus, as a portion of the occipital lobe, is related to different facets of verbal creativity, such as fluency and flexibility (Fink et al., 2013). An alternative explanation for the enhancement of functional homogeneity is that the posterior parietal and occipital cortices, as the part of the primary cortex, play a key role in the early stages of creative actions, such as integration of visual mental imagery. Taken together, a more refined analysis that differentiates the dimensions may be better able to elucidate the diverse dimensions of creativity, and improve our understanding of the underlying mechanisms of creative thinking.

4.3. Variations in structure and function contribute to verbal creative thinking

Results showed that individual creative thinking could be predicted on the basis of cortical characterization in the right local precuneus (i.e., greater volume and thicker cortical thickness). Thus, total individual verbal creativity and its dimensions were associated with less functional homogeneity. We indeed found that joint variations in synchronized spontaneous fluctuations and anatomical features on the brain surface strongly predicted individual verbal creative ability. In a similar vein, Wei et al. (2013) reported that Tai Chi Chuan practitioners had greater cortical thickness in the right DLPFC, compared to the controls. A subsequent study observed that Tai Chi Chuan practitioners had less functional homogeneity decreases in the right DLPFC using the same samples (Wei et al., 2014b). These findings provide evidence for a relationship between structural plasticity and intrinsic architecture of the brain. Changes in cortical volume or thickness may be driven in part by alterations at the synaptic level, such as synaptic and neuronal pruning or regeneration processes, which may be reflected in patterns of functional connectivity. Additionally, the biological implications of 2dReHo indicate that functional segregation and integration within brain regions may be linked to corresponding anatomical variation (Jiang et al., 2014). In light of these findings, we concluded that local functional homogeneity of verbal creative thinking has neurobiological relevance and an anatomical basis. In sum, our findings may provide important insights into how the brain affects verbal creative thinking, although the nature of this structure–function relationship is complex and should be further investigated.

The present study also showed that volume and thickness in the local right precuneus were both good predictors of individual verbal creativity and its dimensions. Change in cortical volume in the human brain has been attributed mainly to change in surface area rather than to change in thickness (Im et al., 2008; Pakkenberg and Gundersen, 1997). However, the findings of a recent study suggest that change in thickness is the best predictor of cortical volume change across the adult life span (Storsve et al., 2014). Notably, this degree of brain maturation plays a critical role in cognitive development and has different age-related activation (Bunge and Wright, 2007). A recent study also reported that the left lateral PFC was more activated in adults than in adolescents during performing divergent thinking task (Kleibeuker et al., 2013). Although age range of this sample appears to be larger across the adolescence and adult—age of most subjects is between 18 and 21 years—it may bring about unbiased results to discuss particular regions that mature late after adolescence. Of course, brain maturation or degeneration might be one cause in terms of creative thinking, so longitudinal or development investigation will be needed to clarify this question in the future.

4.4. Limitations and future work

The present study found that functional and structural regions were consistently associated with verbal creativity. Nevertheless, some limitations should be noted. First, previous findings suggested that individual creativity is related to subcortical regions, such as the dopaminergic system (Takeuchi et al., 2010), but the surface-based ReHo approach used in this study only focuses on the cortical cortex, and not on ReHo in the subcortical cortex. Second, the similar backgrounds of the subjects in the present study might lead them to have high intellectual ability and a corresponding high level of creative potential. It is therefore unknown whether our findings would also hold true for a general population that includes a full range of ages and levels of intellectual ability. Third, the present study only concerned verbal creativity ability, although creative potential can be measured by visual, spatial, and musical abilities. Therefore, the results from this study may be difficult to interpret in the context of non-verbal cognitive processes. The distinct cognitive processes induced by different creative tasks will be an interesting question to clarify in further studies. Finally, although local functional homogeneity of verbal creative thinking might have an anatomical basis, the mechanism of the relationship or the existence of interaction effects between structure and function remain unknown. Future research should explore the joint contribution of structural and functional brain networks in creative thinking using diffusion weighted imaging and rfMRI data.

5. Conclusion

The findings of the present study demonstrate that individuals with high verbal creative ability had less regional homogeneity in the right precuneus. Reduced regional homogeneity in the right precuneus was not only related to the overall score for verbal creative ability, but also to the different dimensions of verbal creative ability. Additionally, structural measures (volume and thickness) of the local right precuneus were positivity associated with individual verbal creative ability. These observations suggest that optimized functional heterogeneity affected by brain structure might facilitate individual creative potential. The findings of this study provide additional evidence of the association between verbal creative thinking and brain structure in the right precuneus, a region involved in internally-focused attention and effective semantic retrieval.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2015.07.001

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