Title: Verbal creativity correlates with the temporal variability of brain networks during the resting state

Running title: Verbal creativity and temporal variability

Jiangzhou Sun[1,2, †], Zhaowen Liu[3,4, †], Jie Zhang[4, †], Edmund T. Rolls[5,6, †], Qunlin Chen[1,2, †], Ye Yao[4, †], Wenjing Yang,[1,2] Dongtao Wei,[1,2] Jianfeng Feng,[4,5,7,8,*] Jiang Qiu[1,2,*]

[1]Key Laboratory of Cognition and Personality (SWU), Ministry of Education, Chongqing, China
[2]School of Psychology, Southwest University (SWU), Chongqing, China
[3]School of Computer Science and Technology, Xidian University, Xi'an710071, Shanxi, PR China
[4]Institute of Science and Technology for Brain Inspired Intelligence, Fudan University, Shanghai, PR China
[5]Department of Computer Science, University of Warwick, Coventry CV4 7AL, UK
[6]Oxford Centre for Computational Neuroscience, Oxford UK
[7]Collaborative Innovation Center for Brain Science, Fudan University, Shanghai, 200433, PR China
[8]Shanghai Center for Mathematical Sciences, Shanghai, 200433, P.R China
[†]These authors contributed equally.
[*]Corresponding author

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Corresponding author information:

Professor Jiang Qiu
Faculty of Psychology,
Southwest University,
No.2, TianSheng Road, Beibei district, Chongqing 400715, China,
Tel: 86-23-6836 7942 Fax: 86-23-6836 7942
E-mail: qiuj318@swu.edu.cn

Professor Jianfeng Feng
Department of Computer Science,
University of Warwick, Coventry CV4 7AL, UK
Tel: 86-21-65643621
Email: jianfeng64@gmail.com

Abstract

Creativity is the ability to see the world in new ways. Creative individuals exhibit the ability to switch between different modes of thinking and shift their mental focus. This suggests a connection between creativity and dynamic interactions of brain networks. We report here the first investigation into the relationship between the reconfiguration of dynamic brain networks during the resting state and verbal creativity using two fMRI datasets involving 574 subjects. We find that verbal creativity correlates with temporal variability of the functional connectivity (FC) patterns of the lateral prefrontal cortex, the precuneus, and the parahippocampal gyrus. High variability of these regions indicates flexible connectivity patterns which may facilitate executive functions. Furthermore, verbal creativity correlates with the temporal variability of FC patterns within the default mode network (DMN), between the DMN and attention/sensorimotor network, and between control and sensory networks. High variability of FCs between the DMN and attention networks characterizes frequent adjustments of attention. Finally, dynamic interaction between the cerebellum and task control network also contributes to verbal creativity, suggesting a relationship between the cerebellum and creativity. This study reveals a close relationship between verbal creativity and high variability of cortical networks involved in spontaneous thought, attention and cognitive control.

Keywords: Creativity, Temporal Variability, Default Mode Network, Attention/Control Networks

Introduction

Creativity is commonly defined as the ability to produce something both novel and useful (Stein MI 1953; Sternberg RJ and TI Lubart 1996; Runco MA and GJ Jaeger 2012). Creative thinking is linked not only to economic development and social progress, but also to almost all areas of daily life (Mumford MD 2002; Dietrich A and R Kanso 2010). Individuals with high creativity appear to have a richer and more flexible semantic associative network and can build relationships between apparently unrelated things or concepts (Bossomaier T et al. 2009). An important trait for creative people is that they are more capable of shifting between abstract, analytical, thinking, and dreaming, reverie thinking (Fink A et al. 2009). The ability of creative people to shift between these ways of thinking may be reflected in the variability during the resting state. Indeed, the resting state is likely to be an active state both physiologically and psychologically (Morcom AM and PC Fletcher 2007). Although the relationships between cognition and the resting state is still not fully understood (Morcom AM and PC Fletcher 2007; Morcom AM and PC Fletcher 2007), the activity of brain networks such as the default mode network (DMN) is associated with various cognitive processes such as mind-wandering, future thinking (Schacter DL et al. 2012), and perspective taking (Buckner RL and DC Carroll 2007). Previous resting-state fMRI studies showed that the coupling of large scale brain systems such as the DMN and the control network is related to creativity (Beaty RE et al. 2014; Chen Q et al. 2014; Beaty RE et al. 2015; Liu S et al. 2015). Furthermore, several studies showed that resting-state dynamical functional connectivity is related to cognitive flexibility and openness to experience which are closely related to creativity (Yang Z et al. 2014; Braun U et al. 2015; Chen T et al. 2016; Beaty RE et al. 2017; Cohen JR 2017). Based on all the above, the present study explored the relationship between dynamic functional connectivity during the resting state and creativity which was measured separately in all the participants.

A wide variety of neuroimaging studies (Jung-Beeman M et al. 2004; Qiu J et al. 2010; Abraham A et al. 2012; Aziz-Zadeh L et al. 2013; Zhu F et al. 2013; Sun J et al. 2016) have been conducted to explore the neural bases of creativity, and widespread brain areas have been implicated in divergent thinking (Dietrich A and R Kanso 2010; Jung RE et al. 2013; Fink A and M Benedek 2014). Our recent meta-analysis of task-fMRI showed that the lateral prefrontal cortex, the posterior parietal cortex, the precuneus, the anterior cingulate cortex, and the temporal cortex are typically activated in creativity-related processes (Wu X et al. 2015). Resting-state fMRI analysis reveals that creativity is associated with functional connectivity (FC) between a large set of brain regions and networks (Takeuchi H et al. 2012; Beaty RE *et al.* 2014; Wei D et al. 2014; Beaty RE et al. 2016). For example, higher creative ability was related to greater resting-state functional connectivity in the inferior frontal cortex and DMN (Beaty RE *et al.* 2014). The DMN is more active at rest than it is in a range of tasks (Raichle ME et al. 2001; Raichle ME and AZ Snyder 2007). The DMN has been related to the generation of creative thinking (Jung RE *et al.* 2013), and the coupling between the DMN and other networks has also been closely related to creativity (Jung RE *et al.* 2013).

The frontal lobe, which is closely related to executive functions (such as cognitive flexibility, inhibitory control, and working memory), also contributes to creative thinking (Miller EK and JD Cohen 2001; Koechlin E et al. 2003; Aron AR et al. 2004; Petrides M 2005; Alvarez JA and E Emory 2006; Dietrich A and R Kanso 2010). Cooperation between brain regions associated with cognitive control (such as dorsolateral prefrontal areas) and other brain regions helps to generate original ideas (Beaty RE *et al.* 2014). In addition, the role of the cerebellum in creativity has received more and more attention. The cerebellum is involved in high-level functions, and cortical-cerebellar interaction is associated with creative thinking (Akshoomoff NA et al. 1997; Vandervert LR et al.

2007; Bostan AC et al. 2013; E KH et al. 2014; Leggio M and M Molinari 2015; Vandervert L 2015).

Most existing studies, however, have only paid attention to the static FC in resting-state fMRI or activations in task-related fMRI, ignoring the dynamic reorganization of brain networks. Recently the temporal variability of brain networks has attracted great attention due to its important role in learning and task performance (Bassett DS et al. 2011; Garrett DD et al. 2011; Kang J et al. 2011; Bassett DS et al. 2013; Hutchison RM et al. 2013; Calhoun VD et al. 2014; Kopell NJ et al. 2014; Bassett DS et al. 2015; Braun U *et al.* 2015; Betzel RF et al. 2016; Chen X et al. 2017), and in serving as a sensitive bio-marker for a number of brain disorders (Yu Q et al. 2015; Liu F et al. 2016). Currently, studies on the relationship between the dynamic properties of brain networks and creativity are rare. Creativity is complex and is involved in cognitive processes such as the generation and evaluation of ideas (Finke RA et al. 1992). Beaty RE et al. (2016) proposed that the default mode network contributes to the generation of ideas, and the control network contributes to the evaluation of ideas. Both task-related fMRI and resting-state fMRI studies showed that coupling of large scale brain systems such as the default mode network and control network is related to creativity (Beaty RE *et al.* 2014; Chen Q *et al.* 2014; Beaty RE *et al.* 2015; Liu S *et al.* 2015). Rich functional connectivity patterns between these networks may contribute to frequent information exchange which is related to creativity.

Given this background, we therefore hypothesized that the dynamic FC patterns of regions of the DMN, and the dynamic interactions between the DMN, and executive control related networks (control networks and attention networks), and between the cerebral cortex and cerebellum during the resting state, may be related to individual creative thinking. In the present study, we chose verbal

creativity because semantic processing is closely related to creativity, and verbal creativity is widely used in neuroimaging studies (Dietrich A and R Kanso 2010; Green AE et al. 2012; Zhu F *et al.* 2013; Benedek M, E Jauk, A Fink, et al. 2014; Fink A et al. 2014; Wei D *et al.* 2014; Abraham A 2015). Previous functional imaging studies have shown a consistent and replicable pattern of brain activity (Fink A *et al.* 2014) in the analysis of verbal creativity. To test our hypothesis, we investigated the correlations between creativity and the temporal variability of cortical areas and networks measured with resting-state fMRI. The approach used in the present study allows localization of regions showing significant variability correlated with behavior or regions showing variability changes between groups, thus helping to define the dynamics of functional brain networks for various behaviors and brain disorders (Zhang J et al. 2016). Furthermore, it allows coupling between temporal variability of the functional architecture of a region and its neural activity to be analyzed (Zhang J *et al.* 2016). That study provided evidence that the larger the temporal variability, the more functional communities/systems this region will be relate to across time windows. We extend in this paper measures of temporal variability associated with specific brain regions (Zhang J *et al.* 2016), to the temporal variability of FCs within and between specific resting-state networks. Here, we show that high temporal variability within and between whole networks is reflected also in richer functional connectivity patterns within and between networks. Given that cerebral-cerebellar connectivity has been shown to be related to creativity (Gonen-Yaacovi G et al. 2013; Saggar M et al. 2015; Vandervert L 2015), we also analyzed the relationship between verbal creativity and the temporal variability of cerebral-cerebellar functional connectivity. We used one dataset involving 304 participants, and in addition cross-validated the findings in a separate cohort with 270 subjects.

Materials and Methods

Participants

There were two cohorts of subjects recruited in this study. The first cohort involved 304 participants recruited from the Southwest University, China. In the second dataset, there were 270 participants from the same University. Participants were excluded who did not have behavioral data, or whose head motion showed >10% displaced frames in a scrubbing procedure, or maximal motion between volumes in each direction >3 mm, or rotation about each axis >3° during scanning. All participants were right-handed and none of them had a history of neurological or psychiatric illness. In accordance with the Declaration of Helsinki (1991), written informed consent was obtained from all participants. The study was approved by the Southwest University Brain Imaging Center Institutional Review Board.

Creativity assessment

The verbal form of the Torrance Tests of Creative Thinking (TTCT) (Torrance E 1974; Ye R et al. 1988) was used to assess creativity, which demonstrates adequate reliability ($r > 0.90$) and high predictive validity ($r > 0.57$) for future career and creative achievements. The verbal TTCT consists of several subtasks (Torrance E 1974; Ye R *et al.* 1988): Asking Questions and Making Guesses (subtests 1, 2 and 3), where participants write out questions and make guesses about possible causes and consequences of situations based on a drawing of a scene; Improvement of a Product (subtest 4), where the examinees list ways to change a toy elephant so that they will have more fun playing with it; Unusual Uses (subtest 5), where the examinees list interesting and unusual uses of a cardboard box; Unusual questions (subtest 6), where participants think unusual questions relating to a cardboard box; and Supposing (subtest 7), where the examinees are asked to list all the

consequences should an improbable situation come true. For each task, 3 different creative dimensions including (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) were scored.

The total verbal creativity score is the sum of three dimensions of all subtasks. Three trained postgraduates scored the verbal creativity responses to all items of the TTCT for all participants. The three raters majored in psychology and were blind to the goal of this research. Their inter-rater correlation coefficient was significant (ICC > 0.90). For the first dataset, all 7 tasks in the verbal TTCT were performed, while in the second dataset, participants completed the improving products part of the TTCT.

Assessment of general intelligence

In the first dataset, in order to examine intellectual ability, participants completed the Combined Raven's Test (CRT), which is an intelligence test with a high degree of reliability and validity (Tang C et al. 2012). The reliability coefficient was 0.92 (Li D and G Chen 1989; Wang D and M Qian 1989). The CRT, which included Raven's standard progressive matrix (C, D, E sets) and Raven's colored progressive matrix (A, AB, B sets), consisted of 72 items revised by the Psychology Department of East China Normal University in 1989. The score on this test (the number of correct answers given in 40 min) was used as a psychometric index of individual intelligence. In line with standard practice, the current study focused on the total score of the test (Jaeggi SM et al. 2008; Takeuchi H et al. 2010).

Neuroimaging Data Acquisition

For both datasets, the neuroimaging data were collected in the Southwest University China Center for Brain Imaging using a 3.0 T Siemens Trio MRI scanner (Siemens Medical, Erlangen, Germany). A magnetization-prepared rapid gradient echo (MPRAGE) sequence was used to acquire high-resolution T1-weighted anatomical images (repetition time = 1,900 ms, echo time =2.52 ms, inversion time = 900 ms, flip angle = 9 degrees, resolution matrix = 256 × 256, slices = 176, thickness =1.0 mm, voxel size = 1 × 1 × 1 mm^3).

During resting-state fMRI scanning, the subjects were instructed to lie down, close their eyes, and rest without thinking about a particular thing, but not to fall asleep. The 8-min scan of 242 contiguous whole-brain resting-state functional images was obtained using gradient-echoplanar imaging (EPI) sequences with the following parameters: slices = 32, repetition time (TR)/echo time (TE) = 2000/30 ms, flip angle = 90 degrees, field of view (FOV) = 220 mm × 220 mm, and thickness/slice gap = 3/1 mm, voxel size 3.4 × 3.4 × 4 mm^3.

FMRI data preprocessing

All fMRI data were preprocessed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm) and a Data Processing Assistant for Resting-State fMRI (DPARSF). We first discarded the first 10 EPI scans to suppress the equilibration effects and the remaining scans were slice timing corrected. Then, the data were realigned and normalized to a standard template (Montreal Neurological Institute) and resampled to 3 × 3 × 3 mm^3. All fMRI time-series underwent spatial smoothing (8 mm Full Width Half Maximum FWHM), band-pass temporal filtering (0.01-0.1 Hz), nuisance signal removal from white matter and cerebrospinal fluid, global mean signal regression, and 6 rigid-body motion correction parameters. We carefully performed the following procedures to ensure data quality: 1)

subjects with poor structural scans, or functional MRI data, making successful preprocessing, i.e., normalization to Montreal Neurological Institute (MNI) space, difficult or impossible, or without complete demographic information, were excluded; and 2) for head movement, subjects were excluded with >10% displaced frames in a scrubbing procedure, or maximal motion between volumes in each direction >3 mm, and rotation about each axis >3°. See supplemental information for a detailed discussion of global mean signal regression and data scrubbing.

Temporal variability of the FC profile of a brain region

The temporal variability of a brain region was obtained by correlating the FC profile of a brain region across different time windows, which reflects the dynamical reconfiguration of a brain region into distinct functional modules at different times, and is indicative of brain flexibility and adaptability (Zhang J *et al.* 2016). Here we adopted the Power-264 module parcellation, i.e., with 264 ROIs defined based on Power JD et al. (2011). These ROIs span the cerebral cortex, subcortical structures, and the cerebellum and can be divided into 13 brain network systems. To characterize the temporal variability of a given ROI (see Fig. 1), we first segmented all BOLD signals (see Fig. 1a) into *n* non-overlapping windows with length *l*. The whole-brain FC network F_i (an $m*m$ matrix, with m = 264 nodes) in the *i*th time window was then constructed, with the Pearson correlation being the measure of FC (see Fig. 1). The FC profile of region *k* at time window *i* is denoted by F_i (*k*, :) (shortened as $F_{i,k}$, denoted by the shaded column in Fig. 1b), which is an *m*-dimensional vector that represents all the functional connections of region *k*. The variability of a ROI *k* is defined as:

$$V_k = 1 - \overline{corrcoef\left(F_{i,k}, F_{j,k}\right)} \qquad i, j = 1,2,3, \dots, n, i \neq j.$$

We calculate V_k at a number of different window lengths (l = equal to 20, 22, 24,…40 seconds) and then take the average value as the final variability to avoid arbitrary choice of window

length. The variability associated with a region characterizes the flexibility of the region's functional architecture. The larger the temporal variability of a ROI, the more functional communities/systems this region will be involved in at different times. Finally, the sum of the variability of all ROI's was termed the whole brain variability, which characterizes the mean flexibility of an individual's whole-brain networks.

Temporal variability of FCs within/between cerebral networks

In addition to calculating the variability of the functional-connectivity profile of a brain region, we furthermore characterized the variability of FCs within a specific network, or between two subnetworks, i.e., within-network variability (see Fig. 2a) and between-network variability (see Fig. 2b). We followed similar procedures used in regional variability to define within/between network variability. For a given brain network *m*, we denote all FCs within this network in time window *i* as Fm_i (the columns in Fig. 2a), and all FCs between network m_1 and network m_2 in time window *i* as $Fm_{1,i}m_{2,i}$ (the columns in Fig. 2b). The within-network variability of network *m* then is:

$$Vw_m = 1 - \overline{corrcoef\left(Fm_\iota, Fm_\jmath\right)} \quad i, j = 1,2,3, \dots, n, i \neq j,$$

while the between-network variability (network *l* and network *p*) is defined as:

$$Vb_{lp} = 1 - \overline{corrcoef\left(Fm_{\iota,l}m_{\iota,p}, Fm_{\jmath,l}m_{\jmath,p}\right)} \quad i, j = 1,2,3, \dots, n, i \neq j$$

Within-network variability characterizes whether the FCs within a particular brain network are changing synchronously with time. Larger within-network variability indicates that the FC patterns are less correlated across different time windows, and that the network demonstrates more flexibility. Similarly, between-network variability depicts the extent to which the patterns of FC between two different brain networks are correlated across different time windows, and large between-network variability indicates patterns of interaction between two networks that are abundant. Larger

within/between network variability indicates that the network of interest, or the interaction between two networks, demonstrate richer FC patterns possibly underlying versatile functions, or cognitive flexibility.

Temporal variability of FCs within the cerebellum and FCs between the cerebellum and cerebral cortex

We also calculated the variability of the FCs within cerebellum, and the variability of FCs between the cerebellum and various networks in cerebral cortex. Following the above work, time series of cerebellar nodes and cerebral cortex nodes (Power JD *et al.* 2011) were extracted and used to calculate the temporal variability.

Correlation between variability and the TTCT score

In order to identify how the dynamic property of the resting-state functional brain networks may be related to individual verbal creativity, the Pearson correlation between the variability (including regional variability, within/between-network variability and whole-brain variability) and the TTCT verbal creativity score was calculated across all individuals, with age, sex and the Raven's score of intelligence being regressed out. Results surviving Benjamini and Hochberg FDR (BH_FDR) correction are reported (Benjamini Y and Y Hochberg 1995).

Cross-validation

We used the first dataset to identify the regions or networks whose variability correlated with creativity. To cross-validate the findings from the first dataset, we used an independent set of individuals (a second dataset) with one of the TTCT tasks ("improving products") the same as the first dataset. We pooled the two datasets (for "improving products") to validate the findings obtained using only the 1st dataset and the overall TTCT score. The TTCT score for "improving products" in

these two sets were normalized before subsequent analysis. A 10-fold cross-validation procedure was adopted: in each cross-validation run, 90% of all samples were randomly chosen to perform the correlation analysis (between the variability of ROIs and the creativity score for "improving products"), and the ROIs surviving FDR ($P < 0.05$) correction were selected. We performed such 10-fold cross-validation 1000 times, and the ROIs (whose variability had significant correlations with the score) that were present in every cross-validation were finally selected.

RESULTS

Temporal variability of brain regions

Demographic information about participants is shown in Table S1 in the Supplemental Information. The measurements used for the temporal variability at the regional level and network level are shown in Fig 1 and Fig 2.

In the first dataset with 304 subjects, the variability of 6 regions from the DMN, 1 from the salience network, and 1 from the auditory network (among all the 264 brain regions) were found to be significantly correlated (FDR corrected, $p_{BH\_FDR} < 0.05$) with the verbal TTCT score, as shown in Table 1 and Fig 3.

Within-network and between-network variability of the cerebral cortex

Among the 13 sub-networks defined in the Power 264 modules (Power JD *et al.* 2011), the within-network variability of the DMN was the only one that was significantly positively correlated with the TTCT score ($r = 0.1296$, $p = 2.6\times10^{-2}$, $p_{BH\_FDR} = 1.89\times10^{-2}$, see Fig 4). Among all 78 between-network interactions (13*12/2), we found that 7 between-network variabilities were significantly positively correlated with the TTCT score (see Table 2 and Fig 5). Specifically, the variabilities of the FCs between the DMN and the attention/sensory-motor networks were involved.

In addition, the variability of the FCs between the task control and visual/auditory network was also involved.

Within-network and between-network variability of the cerebellum

The within-cerebellum network variability was not significantly correlated with the TTCT score. The correlation between verbal creativity and variability of the connectivity between the cingulo-opercular task control network and the cerebellum was marginally significant (r = 0.1527, $p = 9.06\times10^{-3}$, $p_{BH\_FDR} = 5.44\times10^{-2}$). In addition, the variability of the functional connectivity between the cerebellum and other cortical networks, such as the dorsal attention network, salience network, and sensory and auditory network, are also found to correlated non-significantly with creativity ($p < 0.05$, uncorrected, Supplemental Information Table S2).

Whole-brain variability

The whole brain variability was also positively significantly correlated with the TTCT verbal score (r = 0.1296, $p = 2.6\times10^{-2}$).

Cross-validation

One region (ROI index: 124) that belongs to the DMN network (parahippocampal gyrus, PHG) was found whose variability positively correlated with the TTCT sub-score ("improving products") in the first dataset. Using the 2nd dataset, this region was still identified in all the 10000 runs of 10-fold cross-validation ($p_{BH\_FDR} < 0.05$). The overall correlation between the variability of this region and the TTCT sub-score was 0.1501 ($p = 3.3\times10^{-4}$).

Discussion

In the present study, we investigated the relationship between the temporal variability of brain networks during the resting state and the verbal creativity of the individual. We correlated the

temporal variability of resting-state functional brain networks at three different scales (the regional level; the network level: within networks and between networks; and the whole-brain level) to the TTCT verbal score, to identify the neural correlates of creative thinking. We found that the temporal variability of the lateral prefrontal cortex (LPFC), posterior cingulate cortex (PCC), and precuneus within the DMN correlated significantly with the verbal TTCT score. This was complemented by the findings that both the within/between network variability (associated with the DMN) and the whole-brain network variability were also correlated with verbal creativity. Dynamic interaction between the cerebellum and cerebral cortex was also related to verbal creativity. These results suggest that high temporal variability of FCs of cortical networks and cortical-cerebellar interactions involved in spontaneous thought, attention and cognitive control are important for verbal creativity.

Temporal variability for FCs of DMN regions, LPFC and parahippocampus

We found that individuals with high verbal creativity ability displayed large temporal variability in DMN regions including the posterior cingulate cortex (PCC)/precuneus. The precuneus has wide-spread connectivity with cortical and subcortical structures in the resting state (Cavanna AE and MR Trimble 2006), and is involved in various memory tasks, such as episodic and source memories (Lundstrom BN et al. 2005; Sadigh-Eteghad S et al. 2014). In particular, the precuneus is activated in creative tasks (Fink A et al. 2010; Abraham A *et al.* 2012), and it has been shown to have stage-specific functional connectivity bilaterally with the insula, the middle temporal gyrus, and the dorsolateral prefrontal cortex (Beaty RE *et al.* 2015) in a divergent thinking task, suggesting that dynamical reorganization of precuneus connectivity is important in creativity. The high temporal variability of the precuneus indicates that it is functionally interacting with different parts of the cortex during the resting state, which may related to the retrieval of knowledge/memory

or providing the rich episodic contextual associations (Lundstrom BN *et al.* 2005) necessary for creativity (Dandan T et al. 2013).

Similarly we found that variability of the parahippocampal gyrus (PHG) was significantly correlated (positively) with the TTCT sub-score "improving products" by cross-validation. The PHG also plays an important role in memory (Bohbot VD et al. 2015), and was found to be activated in creative tasks (Fink A *et al.* 2009; Ellamil M et al. 2012). Several task-related fMRI studies showed that the medial temporal lobe system is critical for creativity (Luo J and K Niki 2003; Ellamil M *et al.* 2012; Fink A et al. 2012; Benedek M, E Jauk, A Fink, *et al.* 2014). Damage in this region has a negative effect on creative performance (Duff MC et al. 2013). Higher temporal variability of the PHG may reflect different types of information change in memory systems across different time windows during the resting state (Kesner RP and ET Rolls 2015), and a wealth of cortical connectivity patterns helps creativity.

We found a positive correlation between verbal creativity and the temporal variability of the LPFC. The LPFC is widely implicated in both domain-general and domain-specific creative thinking tasks (Abraham A *et al.* 2012; Kleibeuker SW et al. 2013; Liu S *et al.* 2015; Sun J *et al.* 2016). The FC of the LPFC has been shown to related to creativity in both task and resting-state fMRI (Beaty RE *et al.* 2014; Beaty RE *et al.* 2015; Li W et al. 2016). The fronto-parietal system is critical for creativity (Fink A *et al.* 2009; Shamay-Tsoory SG et al. 2011; Ellamil M *et al.* 2012; Shah C et al. 2013; Saggar M *et al.* 2015). Importantly, the LPFC is consistently activated in cognitive control and executive function tasks including cognitive flexibility, inhibition control and working memory that are crucial for creative thinking (Koechlin E *et al.* 2003; Petrides M 2005; Alvarez JA and E Emory 2006; Dietrich A and R Kanso 2010; Liang X et al. 2016). Increasing

behavioral evidence supports the notion that greater cognitive flexibility and inhibition control is associated with higher levels of creativity (Zabelina DL and MD Robinson 2010; Benedek M et al. 2012; Benedek M, E Jauk, M Sommer, et al. 2014; Chen Q *et al.* 2014). Here higher variability of the LPFC identified in our work indicates that the LPFC may be functionally connected with, or switch between different systems, such as the hippocampus, posterior temporal, and parietal cortex during the resting state (Cole MW et al. 2012; Cole MW et al. 2013), and this may be related to cognitive flexibility and inhibitory control to switch which is important for creativity.

Temporal variability for FCs within the DMN and between cerebral networks

At the network level, we found that high variability of the DMN was related to a high verbal creativity score. The DMN is associated with spontaneous thought such as mind wandering, autobiographical retrieval, and episodic future thinking (Raichle ME *et al.* 2001; Fox KC et al. 2015). In the process of creativity, the DMN is involved in the generation of original ideas (Jung RE *et al.* 2013). Higher variability within the DMN during the resting state reflects abundant functional-connectivity patterns which may relate to the trait of frequent transitions between different topics in spontaneous thoughts for creative people.

In addition to the DMN, we also found that high variability of the FCs between the DMN and the dorsal/ventral attention network (DAN/VAN) were related to high verbal creativity, indicating that the dynamic interaction between the DMN and DAN/VAN is related to creative thinking. In contrast to the DMN that generates spontaneous thought, both the DAN and VAN are primarily involved in externally oriented mental processes, and are responsible for maintaining and re-orienting attention, respectively (Christoff K et al. 2016). According to a dynamic framework of spontaneous thought, creative thinking can be defined as a special type of spontaneous thought that

is intermediate between mind-wandering and goal-directed thought (Christoff K *et al.* 2016). That is to say, deliberate constraints at various levels are needed from time to time in creative thinking processes. The DMN may provide sustained internally oriented cognition for creative thinking, while it couples with attention networks in a dynamic manner. This may lead to a frequently shifting focus of thoughts to externally oriented cognition for exploring task-related cues from environment, which favors high creativity. Here the high level of variability of FCs between the DMN and attention network appears to characterize the frequently adjusting focus of attention (Vartanian O 2009), or shifting of the focus of thoughts or concepts, which are important for creative thinking.

Finally, the variability of the FCs between the task control and visual/auditory networks also correlated positively with verbal creative performance. Creative people can utilize peripheral cues to solve the current problem (Ansburg PI and K Hill 2003). Higher variability of the FCs between the task control and visual/auditory networks may therefore facilitate dynamic selection of external information obtained by visual or auditory inputs, and thus be related to verbal creativity.

Temporal variability for FCs associated with the cerebellum

In the present study, we also found a positive correlation between verbal creativity and the variability of FCs between the cerebellum and the cingulo-opercular task control network with marginal significance. Functional imaging studies show that the cerebellum is involved in high-level functions such as control of attention, emotion, working memory, music, timing, and language (Akshoomoff NA *et al.* 1997; Bostan AC *et al.* 2013; E KH *et al.* 2014; Leggio M and M Molinari 2015). The cerebellum has also been linked with creativity. For example, the cerebellum was activated in spontaneous creativity improvisation, and was associated with higher expert-rated creative content in drawings (Saggar M *et al.* 2015). The cerebellum has functional connectivity

with the LPFC and inferior parietal lobule, which are involved in the executive control network, which is closely related to creativity (Dosenbach NU et al. 2007; Habas C et al. 2009). The role of cerebral-cerebellar connectivity during creative thinking has been previously discussed (Schmahmann JD 1991; Ito M 1993; Ito M 2006; Abraham A 2007; Chavez-Eakle RA 2007; Vandervert LR *et al.* 2007; Welling H 2007; Buckner RL 2013; Vandervert L 2015). Akshoomoff NA *et al.* (1997) and Leggio M and M Molinari (2015) proposed a role for the predictive cognitive functions of the cerebellum, and demonstrated that the cerebellum recognizes serial events, detects violations, and reconstructs correct events. Vandervert L (2015) proposed that a cerebrocerebellar blending model is the mechanism behind creativity, such as a high level of scientific discovery. These models emphasize that the interaction between the cerebellum and cerebral cortex, and especially brain regions related to executive functions, play important roles in creativity.

Some neuroimaging studies support this suggestion. For example, increased cerebral-cerebellar functional connectivity has been observed in expert musicians during improvisation (Pinho AL et al. 2014). Our data provide further evidence for the involvement of the cerebellum in creativity by demonstrating that the dynamic interaction between the cerebellum and cerebral cortex, especially the cingulo-opercular task control network, may be closely related to the production of creative ideas ($p = 0.0544$, BH_FDR corrected). In addition, the dynamic interaction between the cerebellum and other cortical networks, such as the dorsal attention network, salience network, sensory and auditory network, were also correlated with creativity ($p < 0.05$, uncorrected). The high variability of FCs between the cerebellum and cerebral cortex indicates abundant functional connectivity patterns between the cerebellum and cerebral cortex. These abundant connectivity patterns therefore serve as the functional substrate for the constantly changing “internal models” in

the cerebellum (which are affected by the external stimulus passed through the cerebral cortex) (Akshoomoff NA *et al.* 1997; Leggio M and M Molinari 2015; Vandervert L 2015), and may therefore help individuals to be more creative.

This study also has some possible limitations. This study correlates resting-state temporal variability with out-of-scanner performance. The results found in resting-state data might not be able to make direct inferences to the task-based creativity process, although in fact a correlation was found in this study between the TTCT score and the variability of the resting state fMRI. However, in future studies it might be of interest to perform fMRI during test of creativity, though these may be difficult to set up inside the scanner.

In summary, the findings of the present study demonstrate that creative cognitive ability is correlated with the dynamic reorganization of resting-state functional brain networks. For the first time, we have provided support for the hypothesis that creative thought is related to dynamical reconfiguration of cortical and cerebellar networks, and in particular, of the DMN during the resting state. This study provides insight into the neural mechanisms underlying creative thinking, and simultaneously offers us a new index to predict individual verbal creativity. Considering the variety of creativity measurement methods and neuroimaging approaches, further studies combining verbal and non-verbal creativity in both resting state and task-related fMRI may further help to explore the role of brain dynamics and variability in creativity. This is the first investigation we know to draw out in a robust 'big data' analysis the relation between creativity and the temporal variability of cortical and cerebellar FCs during the resting state. The concept of variability being related to creativity is consistent with the hypothesis that randomness in the transitions from one network state to another that are influenced by the random spiking times of neurons for a given mean firing rate

is related to creativity (Rolls ET 2013, 2016).

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Table 1 ROIs whose temporal variability significantly correlated with the TTCT verbal score. The names used are those in the automated anatomical labelling atlas (REF).

ROI index	Brain Region	r	p	p_{BH_FDR}
103	Frontal_Sup_L	0.2389	3.38×10^{-5}	8.91×10^{-3}
91	Cingulate_Post_L	0.2145	2.05×10^{-4}	1.36×10^{-2}
88	Precuneus_L	0.2098	2.86×10^{-4}	1.51×10^{-2}
95	Precuneus_R	0.1990	5.87×10^{-4}	2.58×10^{-2}
90	Precuneus_L	0.1950	7.60×10^{-4}	2.87×10^{-2}
220	Frontal_Mid_L (LPFC)	0.2285	7.49×10^{-5}	9.88×10^{-3}
68	SupraMarginal_L	0.2156	1.90×10^{-4}	1.36×10^{-4}
124	ParaHippocampal_L[a]	0.1501	3.3×10^{-4}	< 0.05

[a] represents cross-validation results.

Table 2 The correlation of between network variability and the TTCT verbal score.

Network1	Network2	*r*	*p*	p_{BH_FDR}
Default mode	Ventral attention	0.2388	3.74×10^{-4}	2.92×10^{-4}
Default mode	Dorsal attention	0.1723	3.08×10^{-3}	3.43×10^{-2}
Default mode	Sensory/somatomotor hand	0.1728	3.04×10^{-3}	3.43×10^{-2}
Dorsal attention	Auditory	0.1951	7.87×10^{-4}	3.02×10^{-2}
Dorsal attention	Salience	0.1895	1.16×10^{-3}	3.02×10^{-2}
Cingulo-opercular task control	Visual	0.1771	2.43×10^{-3}	3.43×10^{-2}
Fronto-parietal task control	Auditory	0.1738	2.95×10^{-3}	3.43×10^{-2}

Captions to figures

Figure 1 Temporal variability of an FC profile associated with a brain region (the big red node in the left panel). The left part shows the brain region of interest (with its FC profile). (a) The BOLD time courses of all brain regions were first segmented into non-overlapping windows. (b) In each window the whole brain functional network was constructed (using Pearson correlations), and the FC profiles associated with brain region *k* in each time window (denoted by the shaded column) were correlated and averaged, and subtracted from 1.0, which led to a temporal variability for FC profile associated with brain region *k*.

Figure 2 Temporal variability of FCs within a network and between two networks. (a) The left part shows the network of interest (consisting of red nodes). The right part shows the BOLD time courses of all regions in the network, which were segmented into non-overlapping windows. Then the FC matrix of this network was constructed in each window, and the FCs of the network in each time window were correlated and averaged, subtracted from 1.0, which led to a temporal variability for FCs within a network. (b) The left part shows the two networks of interest (denoted by red and blue nodes, respectively). The right part shows the BOLD time courses of regions in these two networks, which were segmented into non-overlapped windows. Then the FCs between these two networks were obtained in each window. These FCs in different time windows were correlated and averaged, subtracted from 1.0, which led to the temporal variability for the FCs between two networks.

Figure 3 Regions whose temporal variability is correlated to the TTCT total score. The radar map in the middle shows the correlation coefficient between the temporal variability of each brain region and the TTCT total score. The small squares in the radar map show the specific correlation coefficient of the temporal variability and the TTCT total score. The brain maps show the location of the corresponding brain regions.

Figure 4 The within-network variability of the DMN is correlated with the creativity TTCT total score. The brain map shows the within-network connectivity of the DMN. The correlation map shows that the within-network variability of the DMN is positively related to TTCT total score.

Figure 5 Between-network variability is correlated with the TTCT total score. The radar map in the middle shows the correlation coefficients of the between-network variability with the TTCT total score. The brain maps show the corresponding two brain networks of interest (using different colors). Abbreviations: DMN: default mode network, VAN: ventral attention network, DAN: dorsal attention network, SHN: sensory/somatomotor hand network, AN: auditory network, SN: salience network, VN: visual network, FTCN: fronto-parietal task control, CTCN: cingulo-opercular task control network.