



Brain hemispheric involvement in visuospatial and verbal divergent thinking

Qunlin Chen^{a,b,c}, Roger E. Beaty^d, Zaixu Cui^e, Jiangzhou Sun^{a,b}, Hong He^{a,b},
Kaixiang Zhuang^{a,b}, Zhiting Ren^{a,b}, Guangyuan Liu^{f,**}, Jiang Qiu^{a,b,*}

^a School of Psychology, Southwest University, Chongqing, 400715, China

^b Key Laboratory of Cognition and Personality, Ministry of Education, Chongqing, 400715, China

^c School of Mathematics and Statistics, Southwest University, Chongqing, 400715, China

^d Department of Psychology, Pennsylvania State University, University Park, PA, 16801, USA

^e Department of Psychiatry, Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA, 19104, USA

^f College of Electronic and Information Engineering, Southwest University, Chongqing, 400715, China

ARTICLE INFO

Keywords:

Asymmetry
Creativity
Divergent thinking
Hemispheric lateralization
Prediction modeling

ABSTRACT

Hemispheric lateralization for creative thinking remains a controversial topic. Early behavioral and neuroimaging research supported right hemisphere dominance in creative thinking, but more recent evidence suggests the left hemisphere plays an equally important role. In addition, the extent to which hemispheric lateralization in specific brain regions relates to individual creative ability, and whether hemispheric dominance relates to distinct task performance, remain poorly understood. Here, using multivariate predictive modeling of resting-state functional MRI data in a large sample of adults ($N = 502$), we estimated hemispheric segregation and integration for each brain region and investigated these lateralization indices with respect to individual differences in visuospatial and verbal divergent thinking. Our analyses revealed that individual visuospatial divergent thinking performance could be predicted by right-hemispheric segregation within the visual network, sensorimotor network, and some regions within the default mode network. High visuospatial divergent thinking was related to stronger functional connectivity between the visual network, fronto-parietal network, and default mode network within the right hemisphere. In contrast, high verbal divergent thinking performance could be predicted by inter-hemispheric balance within regions mainly involved in complex semantic processing (e.g., lateral temporal cortex and inferior frontal gyrus) and cognitive control processing (e.g., inferior frontal cortex, middle frontal cortex, and superior parietal lobule). The current study suggests that two distinct forms of functional lateralization support individual differences in visuospatial and verbal divergent thinking. These findings have important implications for our understanding of hemispheric interaction mechanisms of creative thinking.

1. Introduction

Hemispheric lateralization or asymmetry is considered to result from an evolutionary conservation mechanism allowing fast and efficient information processing in the human brain (Duboc et al., 2015; Levy, 1969; Toga and Thompson, 2003; Wang et al., 2014). Several studies have demonstrated subtle structural or functional differences between the two hemispheres corresponding to dominant processing of specific cognitive tasks (Duboc et al., 2015). One of the cognitive processes hypothesized to show hemispheric dominance is creative thought (McCallum and Glynn, 1979) which is generally defined as an ability to come up with novel and

useful ideas to open-ended problems (Runco and Jaeger, 2012; Sternberg and Lubart, 1996). A long-standing yet controversial theory suggests that creativity results solely from right hemisphere processes (Bowden and Beeman, 1998; Bowden and Jung-Beeman, 2003; Torrance, 1982; Wheatley, 1977), while a moderate view emphasizes a right-hemisphere advantage in figurative or metaphoric thinking (i.e., coarse semantic coding), presumably facilitating novel and original idea production (Beeman et al., 2000; Folley and Park, 2005; Zhao et al., 2014). An alternate view suggests that creative thinking involves the interaction and integration of information from both hemispheres (Atchley et al., 1999; Carlsson et al., 2000; Lindell, 2011). Although the relationship

* Corresponding author. School of Psychology, Southwest University, Tiansheng Street 2, Beibei, Chongqing, 400715, China.

** Corresponding author. College of Electronic and Information Engineering, Southwest University, Tiansheng Street 2, Beibei, Chongqing, 400715, China.

E-mail addresses: liugy@swu.edu.cn (G. Liu), qiu318@swu.edu.cn (J. Qiu).

<https://doi.org/10.1016/j.neuroimage.2019.116065>

Received 7 April 2019; Received in revised form 3 July 2019; Accepted 31 July 2019

Available online 7 August 2019

1053-8119/© 2019 Elsevier Inc. All rights reserved.

between creative thinking and hemispheric differences is often emphasized in the literature (Lindell, 2011; Mihov et al., 2010; Moore et al., 2009), patterns of hemispheric lateralization support creativity in different modalities (e.g., verbal and figural) remains an open question.

Visual creativity requires people to output the production (e.g., via drawing) of novel and useful visual forms, a process thought to involve divergent thinking (Aziz-Zadeh et al., 2012; Dake, 1991). Previous neuroimaging studies have found that the right hemisphere was more strongly engaged during visuospatial (i.e., figural) creative thinking (Bhattacharya and Petsche, 2002; Gansler et al., 2011; Kenett et al., 2015; Kowatari et al., 2009; Miller et al., 2000; Miller and Hou, 2004). A common view proposes that the right hemisphere may attenuate inhibitory process from the left hemisphere (Mayseless et al., 2014). Furthermore, lesion studies have linked left-lateralized brain disorders or lesions, such as frontotemporal lobe dementia (FTD), to a “release” of right frontal and posterior cognitive functions previously shown to enhance creative drawing (Miller and Hou, 2004; Seeley et al., 2007). However, recent studies have shown higher activation within left fronto-parietal brain regions, premotor cortex, inferior frontal cortex, and lateral occipital gyrus associated with visuospatial creativity (Aziz-Zadeh et al., 2012; Huang et al., 2013; Saggar et al., 2015). While a clear consensus has not emerged from such studies, the existing research more generally has shown that the right hemisphere may play a critical role in visual creativity. Thus, the asymmetries of the right hemisphere compared with left may facilitate visuospatial (i.e., figural) creative thinking.

Similarly, verbal creativity refers to the ability to generate novel and useful solutions through verbal forms such as oral response or writing down ideas. According to the coarse semantic coding hypothesis, the right hemisphere is more specialized for processing loosely-related semantic information than the left hemisphere (Beeman and Bowden, 2000; Kounios and Beeman, 2014). However, recent views hold that verbal creativity benefits from the interaction and integration of information from both hemispheres (Lindell, 2011; Takeuchi et al., 2010). Past work has shown that the two cerebral hemispheres code semantic information in different ways (Jung et al., 2013; Mirous and Beeman, 2012). Bilateral temporo-parietal regions are thought to be crucial for semantic activation, whereas the right anterior middle/superior temporal gyrus and inferior frontal gyrus may contribute to semantic integration and selection, respectively (Jung-Beeman, 2005). Accordingly, verbal creativity may be based on the interaction or integration between both hemispheres, rather than only depend on the right hemisphere. More recently, Faust and Kenett (2014) postulated that semantic processing involves the whole brain and thus creative verbal processing requires efficient semantic integration that is achieved via well-balanced hemispheric communication (Faust and Kenett, 2014).

In the present research, we employed resting-state fMRI to assess whether high-creative thinking ability results from neuropsychological markers of cerebral lateralization. Particularly, recent neuroimaging studies using resting-state fMRI data indicated that left-hemisphere regions are biased to interact more strongly within the same hemisphere—such as the fronto-parietal control network preferentially coupling to the default network and language-related regions in the left hemisphere—whereas right-hemisphere regions interact more strongly with both hemispheres (Gotts et al., 2013; Wang et al., 2014). Importantly, the magnitude of lateralization measured for individual participants in these regions predicted the level of cognitive ability, such as language and motor abilities (associated with a left-lateralization; Amunts et al., 1996; Joliot et al., 2016) and visuospatial attention (associated with right-lateralized; Cai et al., 2013; Wang et al., 2016). In the light of these findings, we hypothesized that if functional lateralization benefits creative thinking ability—as has been suggested in theories and popular culture of creative individuals as being “right-brained”—a quantitative relationship should exist between the strength of lateralization and the level of creative thinking. We tested two hypotheses regarding the relationship between hemispheric

lateralization and creative thinking. First, hemispheric segregation benefits creative thinking, which is consistent with previous research reporting reduced inter-hemispheric connectivity between brain areas and increased right-hemispheric connectivity during rest in highly-creative individuals (Lotze et al., 2014). Second, well-balanced inter-hemispheric processing benefits creative thinking, supported by evidence that creativity does not appear to depend on activation differences between hemispheres (Badzakova-Trajkov et al., 2011), but rather balanced hemispheric activation (Mayseless and Shamay-Tsoory, 2015; Shamay-Tsoory et al., 2011).

Furthermore, the current study explored the relationship between hemisphere lateralization and domain performance of creative thinking. According to previous findings, we hypothesized that individuals with high segregation of right frontal-parietal and visual networks displayed enhanced visuospatial creative performance, whereas individuals with high inter-hemispheric integration of frontal-temporal and fronto-parietal networks will show higher verbal creative performance. Together, the present study provides the novel evidence of the extent to which verbal and visuospatial creative ability involve different hemispheres of the brain.

2. Materials and methods

2.1. Participants

Neuroimaging and behavioral data were acquired as part of the Gene-Brain-Behavior (GBB) Project at Southwest University, which is an ongoing and longitudinal project exploring the genetic and neural basis of complex human behavior (such as creativity) and mental health. The recruiting program and exclusion procedures of participants were described in detail elsewhere (Chen et al., 2018; Liu et al., 2017). The study protocol was approved by the Ethics Committee of the Brain Imaging Center Review Board of Southwest University. All of the participants provided written informed consent and received payment depending on time and tasks completed. In total, 684 subjects completed the creative ability tests, in which 11 subjects were excluded for being left-handed; 113 subjects were excluded due to issues from brain images, including 6 subjects didn't take part in cross-sectional neuroimaging protocol; 71 subjects with excessive head movement during resting-state fMRI, defined as more than 2.5 mm translation in any axis and more than 2.5° angular rotation, as well as mean FD (Jenkinson) greater than $\pm 2sd$ (± 0.148); and 36 subjects were excluded due to low mean signal-to-noise ratio (SNR) across all nodes (i.e., less than $\pm 2sd$ above the group mean). In addition, 58 subjects were excluded for being non-native Mandarin Chinese speakers. These exclusion criteria resulted in a final sample of 502 subjects (136 male), aged 16–26 (mean = 19.44 ± 1.44), and then the final sample was divided into sample 1 (S1, N = 242) and sample 2 (S2, N = 260) due to different scoring methods for the creativity assessment (see Fig. S1).

2.2. Assessments of psychological variables

Four tasks were administered to assess individual creative ability. In the beginning of the task, participants were told that “the tasks are not a test”; “think of them as a game and have fun with them”; and “the more ideas you list, the better”. All tasks and introductions were presented using E-prime on a computer screen. Participants were instructed to draw or write down their ideas on an answer sheet with the corresponding task number. Tasks were presented in the following order:

Product improvement task (PIT). Participants were required to generate as many ways as possible to improve a toy elephant in 10 min to make it more fun, enjoyable, and appealing (Chen et al., 2018).

Figural creativity test (FCT). FCT is a classic visual-spatial creative thinking test derived from the second activity of the TTCT-Figural (Form A, Ye et al., 1988), in which participants were required to draw pictures using ten incomplete figures as a starting point in 10 min, and then give a

title for each completed figure. Note that the title of the FCT was not used to compute fluency, originality, and total score; it was considered as a supplementary feature of the figure that helped raters understand the figure more easily and accurately.

Alternate uses task (AUT). Participants were asked to come up with as many interesting, novel, and uncommon uses as possible for a can and a brick in 6 min (Sun et al., 2016).

Divergent thinking of figure (DTF). Participants were instructed to view three complete figures (i.e., ambiguous line drawings) and to list as many ideas as they could imagine that the figures could be in 9 min (Creativity Testing Service, <https://www.creativitytestingservices.com>; 3 min each item). The received the following instructions: "Look at the figure below. What do you see? List as many things as you can that this figure might be."

Consistent with past work (Chen et al., 2018), four trained raters assessed the four tasks based on previous guidance. Responses to each item for all tasks were scored via two classic cognitive processes of creativity: (a) *fluency* was defined as the number of ideas for an item after excluding those ideas that were difficult to understand (e.g., due to illegibility), inappropriateness (e.g., brick can be eaten), and redundancy (e.g., repetitive responses in one task); (b) *originality* was defined as the degree of uncommonness and novelty of each idea using a 1 (*not at all creative*) to 5 (*very creative*) scale that based on a scoring criterion table that was described in previous research (Chen et al., 2018). For the responses beyond the criteria table, raters were asked to score it according to his or her own perception of uncommonness and novelty (Long et al., 2014; Takeuchi et al., 2010). The *total score* is the sum of ideational fluency and ideational originality. Raters were instructed to consider uncommonness, novelty, and remoteness when reviewing all responses for each task, but to only provide a single, holistic score using a 10-point (1 = uncreative, 10 = very creative) scale. Analysis of rater agreement showed good inter-rater reliability in two scoring methods, ranging from 0.87 to 0.97 using the integrated scoring, and ranging from 0.64 to 0.92 using the general creativity scoring across the four tasks (inter-rater reliability for each task shown in Fig. S2). Notably, the whole sample was partitioned into two samples in terms of how responses were coded, with sample 1 employing both scoring approaches (fluency/originality and subjective creativity) and sample 2 employing subjective creativity. Here, we used different scoring approaches across the 2 samples due to the nature of the longitudinal data collection, which would require constantly updating an ongoing project, and to decrease workload of the raters (Forthmann et al., 2017). For the two scoring approaches, total score of visuospatial divergent thinking was highly correlated with general score of visuospatial divergent thinking ($r = 0.84$, $p < 0.001$), and total score of verbal divergent thinking was highly correlated with general score of verbal divergent thinking ($r = 0.93$, $p < 0.001$) in sample 1. The high correlation between general and total score might be over-estimated, since both measures were rated by the same raters in sample 1.

In addition, Intelligence Quotient (IQ) score was computed for each participant by employing the Wechsler Adult Intelligence Scale-Revised Chinese revision (WAIS-RC; Gong, 1992) consisting of six verbal tests and five performance tests. Here, we used the sum of verbal IQ score and performance IQ score to index intelligence.

2.3. Image acquisition

Structural and functional data were acquired on a Siemens 3T Trio scanner (Siemens Medical Systems, Erlangen, Germany) at the Brain Imaging Center, Southwest University. 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 mm², thickness = 3 mm, slices = 32, interslice gap = 1 mm, acquisition voxel size = 3.4 × 3.4 × 4 mm³). During resting-state scanning, the subjects were instructed to relax, remain awake with eyes closed, and not to think of anything in particular. 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 mm²; slices = 176; thickness = 1.0 mm; voxel size = 1 × 1 × 1 mm³).

2.4. Image preprocessing

Image preprocessing was performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) and the Data Processing & Analysis for Brain Imaging (DPABI, Yan et al., 2016). Preprocessing steps included (1) discarding the first 10 functional images for magnetic field stabilization and the participants' adaptation to the scanning environment, (2) slice timing correction and head motion correction, (3) co-registrating functional data to the Montreal Neurological Institute (MNI) space via T1 image unified segmentation and spatially smoothing with a 4 mm full-width at half-maximum Gaussian kernel, (4) regressing out the confounding signals (white matter and cerebrospinal fluid) and 24 motion parameters for head movement from the time course of each voxel, (5) and applying a temporal band-pass filter (0.01–0.1 Hz) to reduce the high frequency physiological noise. Here, we did not employ global signal correction as hemispheric segregation and hemispheric integration is based on the functional connectivity between these regions and correspondingly homotopic regions (Raemaekers et al., 2018).

2.5. Hemispheric functional network construction

To construct the two hemispheric networks, we used a random partition procedure to yield 512 uniform regions of interest (ROIs) in the right hemisphere and the same number of ROIs in the left hemisphere, excluding the cerebellum (Zalesky et al., 2010; Zhong et al., 2016). The resultant template included 1024 ROIs and is absolutely symmetrical between the two hemispheres and thus enables direct comparison between hemispheric networks (see Fig. 1a). We excluded 19 paired ROIs with inadequate signal in each hemisphere (SNR > 2sd above or < 2sd below the group mean (Drysdale et al., 2017);). The SNR was calculated ROI-wise via the mean magnetic resonance signal over time divided by the s.d. of the time series. Most excluded ROIs were located in the orbitofrontal cortex, temporal pole, and posterior occipital pole. Subsequently, mean time series in each of remaining ROIs were extracted by averaging across all voxels within this ROI, and then a correlation matrix in each hemisphere as well as two correlation matrices between hemispheres were calculated for each subject. These resulting correlation matrices were converted into z values by Fisher's r-to-z transform to improve the normality.

To calculate hemispheric segregation and integration, we used modularity functions from the Brain Connectivity Toolbox (BCT, <http://www.brain-connectivity-toolbox.net/>; Rubinov and Sporns, 2010). First, hemispheric z-values were computed for each subject and then thresholded using 0.2 to remove negative and weak edges. The Louvain community detection algorithm was used to estimate the optimal partitioning of all hemispheric nodes, in which the gamma resolution parameter was set to 1.7, producing functional atlases that map onto canonical functional networks (Cisler, 2017). This step was repeated 150 times in each subject to produce a stable and consensus matrix for avoiding a stochastic partition, and then an agreement matrix across partitions was calculated using the 'agreement_weighted' function of the BCT. Second, the sum of the agreement matrices of the two hemispheres was calculated using a consensus algorithm (100 repetitions). Because this algorithm only identified a few modules, this step was repeated until obtaining more accurate partitions (Lancichinetti and Fortunato, 2012). This approach resulted in a network partition with 11 modules (see Fig. S3) that included a cingulo-opercular network (CON), a sensorimotor network (SM), a salience network (SN), a visual network (VN), a dorsal attention network (DAN), a ventral attention network (VAN), a fronto-parietal network (FPN), and four sub-networks of the larger default mode network (DMN).

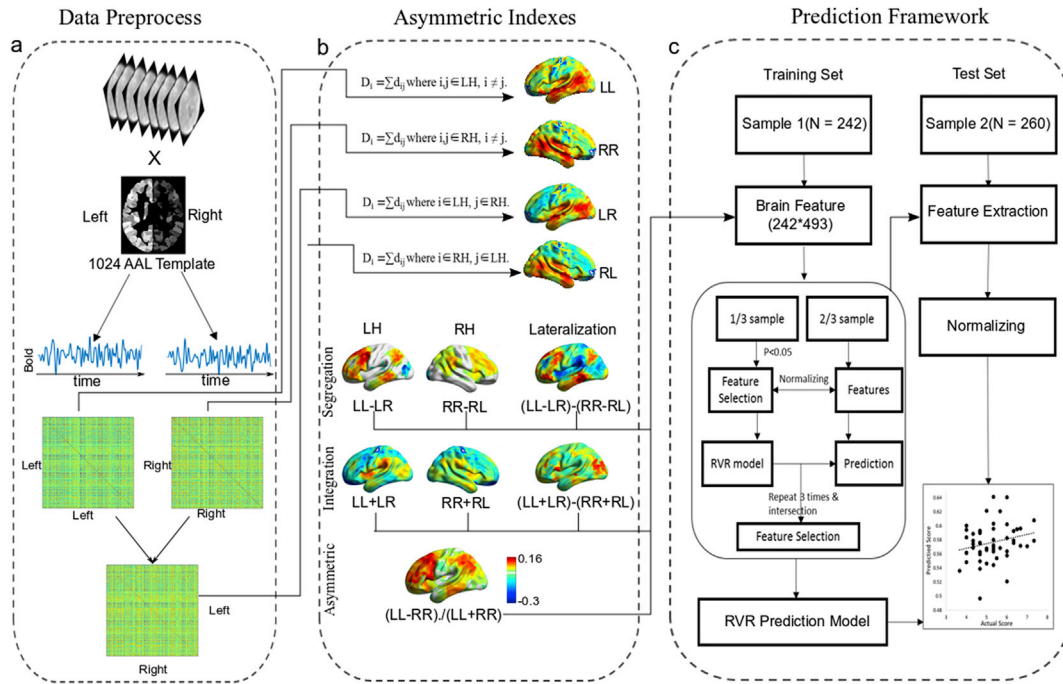


Fig. 1. A detailed step-by-step description of the asymmetric indices and prediction analysis. **Data preprocessing.** For each individual functional dataset, time-series signals were extracted in homotopic regions in the two hemispheres with a symmetrical automatic labeling (AAL) template including 1024 ROIs (each hemisphere including 512 ROIs), and then the within- and between-hemisphere correlation coefficient was calculated across nodes in each hemisphere and across all nodes, respectively. **Asymmetric indices.** Calculating node degree intra- (e.g., LL and RR) and inter-hemisphere (e.g., LR and RL), and the lateralization of segregation and integration, as well as the asymmetric index. **Prediction framework.** Sample 1 was used as the training set, in which the subjects were partitioned into 3 subsets, 2 of which were used as the training sets and the remaining one was used as the testing set. For each subject, asymmetric index was the predictor variable and the creative thinking ability (VSDT and VDT) was as the dependent variable. Inner 3-fold CVs were applied to determine the optimal features, and a prediction model was estimated by applying the relevance vector regression (RVR) to the training samples. Sample 2 was used as the test set. The model acquired by sample 1 was applied to predict the creative thinking ability for each testing subject.

2.6. Hemispheric segregation and integration

Hemispheric segregation or integration indices were based on functional connectivity within or across hemisphere, respectively. For a node (i) in the left hemisphere, degree within-hemisphere (i_{LL}) was estimated by summing the z-value of correlations between it and the rest of nodes located in left hemisphere; degree across-hemisphere (i_{LR}) was estimated by summing the z-value of correlations between it and the all nodes located in right hemisphere (see Fig. 1b). For a node (i) in the right hemisphere, i_{RR} and i_{RL} was calculated using the same approach. According to (Gotts et al., 2013), segregation was defined as the tendency for greater within-hemisphere interactions compared to between-hemisphere interactions, calculated as the difference of intra- and inter-hemispheric degree (e.g., $i_{LL} - i_{LR}$ or $i_{RR} - i_{RL}$); the patterns of hemispheric segregation within both hemispheres largely replicated in the Southwest University Adult lifespan dataset (Wei et al., 2018) and also largely replicated previous results performed by Wang and colleagues (Wang et al., 2014; see Fig. S4). Integration was defined as the combined effect of intra-hemispheric interactions and inter-hemispheric interactions, calculated as a sum of intra- and inter-hemispheric degree (e.g., $i_{LL} + i_{LR}$ or $i_{RR} + i_{RL}$). Then, we calculated the lateralization of segregation and integration. Particularly, the lateralization of segregation for a node is calculated as the difference of segregation compared to a homotopic node: $i_{asy-seg}$ (asymmetry of segregation) = $i_{LL} - i_{LR} - (i_{RR} - i_{RL})$; the lateralization of integration for a node is calculated as the difference of integration compared to a homotopic node: $i_{asy-int}$ (asymmetry of integration) = $i_{LL} + i_{LR} - (i_{RR} + i_{RL})$. In addition, we used a standard procedure to quantify the asymmetric index (AI) by the following formula: $i_{asy} = (i_{LL} - i_{RR}) / (i_{LL} + i_{RR})$. A large positive value of AI strongly implies bilateral interactions with the left hemisphere. In contrast, a large negative value of AI strongly implies bilateral interactions with the right

hemisphere. A near-zero value of AI would indicate a balance between the two hemispheres. In addition, the standard method was applied to compute the asymmetric of segregation and integration.

Nodes were labeled by functional networks (modules) obtained by the aforementioned community detection algorithm. For a given network, within-network connectivity was calculated as the sum z-values between all nodes within the network (e.g., left default mode network) to remaining nodes within the network of the same hemisphere (e.g., “ M_{LL} ” means the sum correlation of all nodes within a given network in the left hemisphere). Conversely, between-network connectivity was calculated as the sum z-value between all nodes of the ipsilateral network (e.g., left default mode network) and all nodes of the contralateral network (e.g., right default mode network; “ M_{LR} ” means the sum correlation of all nodes within a given network in the left hemisphere with all nodes in the contralateral network). The lateralization of segregation for a given network is calculated as the difference of segregation compared to a contralateral network: $M_{asy-seg} = M_{LL} - M_{LR} - (M_{RR} - M_{RL})$. The lateralization of integration for given network is calculated as the difference of integration compared to a contralateral network: $M_{asy-int} = M_{LL} + M_{LR} - (M_{RR} + M_{RL})$.

2.7. Dimension reduction

Regarding creativity assessment, a series of exploratory factor analyses (EFA) were performed to determine the number of factors and factor structure in the eight creative indexes from sample 1. Firstly, we conducted a parallel analysis using the psych package (<https://CRAN.R-project.org/package=psych>) in R to determine the optimal number of factors, and then conducted principal axis factoring with promax rotation to determine the factor structure. Next, we examined the fit of the exploratory results via confirmatory factor analysis (CFA) using the

package lavaan (<http://lavaan.ugent.be>) in the parts of sample 2 with the classical scoring. The maximum likelihood estimation method was applied to estimate the model parameters. Model fit was assessed with the chi-square test (χ^2), the Root Mean Square Error of Approximation (RMSEA), the Comparative Fit Index (CFI), Tucker-Lewis Index (TLI) and the Standardized Root Mean Square Residual (SRMR).

2.8. Feature selection

Considering that a majority of brain features may be redundant and invalid for prediction of creative thinking ability, we used linear and non-linear methods to select lateralization features that were significantly correlated with sub-dimension score of each task (e.g. fluency and originality) for building the predictive model in sample 1. Based on the hypotheses, two methods for feature selection were employed: (1) computing Pearson correlation coefficients to identify hemilateral features that were significantly correlated (uncorrected $p < 0.05$) with sub-scores for relevant creativity factors, and then separately merge positive and negative features for interpretation; (2) conducting quadratic regression analysis to define asymmetric features (e.g. $i_{asy-seg}$) that were significantly fitted (bootstrap method, $p < 0.05$) with sub-scores for relevant creativity factors, and then separately merge positive (significant quadratic coefficient) and negative features.

2.9. Predictive analysis

We applied a relevance vector regression model (Tipping, 2001) to predict the visuospatial and verbal creative thinking ability scores within- and across-sample (see Fig. 1c). In this linear regression model, the total score of visuospatial divergent thinking (VSDT) or verbal divergent thinking (VDT) is modeled as the predictor variable, and significant features (obtained via feature selection) are modeled as the dependent variable. Here we used sorted, 3-fold cross-validation (s3F-CV (Cui et al., 2017),) in sample 1 to evaluate the prediction accuracy. Briefly, subjects were sorted according to their VSDT/VDT scores and then assigned into 3 groups according to the rank, in which 2 groups were used as the training set and the remaining group was used as the testing set. Next, we scaled the features into range of 0–1 in the training set and then applied the acquired parameters to scale the testing set (Cui and Gong, 2018; Cui et al., 2017). We constructed a model using the training set and then used it to predict the scores of the testing set. Notably, if the number of significant features was greater than the size of the training sample, that possibly resulted in an overfitting. To address this, we selected weight vectors in the top sixty percent in the training set and then used these features to build the predicted model for predicting the actual VSDT/VDT scores of the test set. The entire procedure was repeated 3 times such that three feature sets were acquired across sample 1. Subsequently, the intersection of the three feature sets from s3F-CV were identified as optimal features for constructing subsequent the prediction model. Moreover, the Pearson correlation r and mean absolute error (MAE) between the actual creative thinking scores and predicted scores were used to quantify the accuracy of the prediction for the testing subjects in each fold (Cui and Gong, 2018; Cui et al., 2017; Franke et al., 2010). The entire procedure was repeated 3 times such that each group was used as the testing set once. Finally, two prediction accuracies (both r and MAE) were acquired.

To further validate the generalizability of the predictive models, we firstly used these optimal features to build the predicted model to predict the general VSDT/VDT scores across sample 1, after controlling for the sex, age, and FD, and then applied the model constructed using sample 1 to predict the general VSDT/VDT scores in sample 2. In addition, to assess the specificity of the predictive models, we further examined whether the model could accurately predict IQ score in sample 1 and sample 2. Moreover, we also examined the relationship between VSDT/VDT and lateralization of the relevant networks which contains valid features at the modularity level.

If the features can significantly predict the VSDT/VDT scores, the prediction model was considered as effective. The significance of prediction performance is assessed by permutation testing. Briefly, the above prediction procedure was re-applied 1000 times, each time permuted the behavioral scores across the training samples, yielding a null distribution for correlation r values. The permutation test P value (p_{pt}) of 0.05 was defined as significant which signified that only 5% of the random permutations produced a correlation value in any predicted model that exceeded the real correlation value in the test sample.

The importance of features for prediction model was determined by the absolute value of the regression coefficient (Cui et al., 2017; Erus et al., 2014; Siegel et al., 2016). In this study, the regions with the maximizing regression weight across 3 folds in the models trained using sample 1 can be considered as the contributing features for the VSDT and VDT prediction. These features were visualized using BrainNet Viewer (<http://www.nitrc.org/projects/bnv/>).

2.10. Data and code availability statement

The data supporting this study is available from the corresponding author (J. Q.) upon request, and the codes are publically available at the following link: <https://github.com/cqllogic>.

3. Results

3.1. Behavioral results

Parallel analysis of the sub-scale scores of creativity tests in the sample 1 indicated that a two-factor solution should be selected, with two eigenvalues greater than 1, and with eigenvalues from the simulated data between two and three factors (Fig. S5a). A two-factor EFA using promax rotation indicated that fit statistics is good: $\chi^2/df = 2.35$, $p < 0.001$, CFI = 0.991, RMSEA = 0.095 [0.043, 0.107], SRMR = 0.02. A two-factor solution accounted for 60% of the overall variance, as shown in Fig. S5b, the first factor had strong loadings from the items fluency of FCT and originality of FCT that accounted for 16% of variance in creative ability (termed this factor *visuospatial divergent thinking*, VSDT), and the second factor had strong loadings from fluency of PIT, AUT, and DTF, as well as originality of PIT, AUT, and DTF that accounted for 44% of in creative ability (termed this factor *verbal divergent thinking*, VDT). Each item loaded on its factor with loadings > 0.5 , meanwhile with loadings < 0.2 on other factors. VSDT and VDT were significantly correlated ($r = 0.33$, $p < 0.001$). The two-factor model was verified by CFA, and the model resulted in an excellent fit: $\chi^2/df = 2.10$, $p < 0.05$; CFI = 0.992; TLI = 0.985; RMSEA = 0.065 [0.03, 0.08], SRMR = 0.022; see Fig. S5c). These indicated that visuospatial divergent thinking and verbal divergent thinking might reflect distinct facets of creativity.

3.2. Prediction for VSDT

As shown in Fig. 2a, the predicted VSDT scores were significantly correlated with the actual scores for each CV fold ($r_{cv1} = 0.24$, $p < 0.05$, MAE = 3.41; $r_{cv2} = 0.16$, $p = 0.15$, MAE = 3.16; $r_{cv3} = 0.24$, $p < 0.05$, MAE = 3.47 for 3 CV fold) using the segregation of nodes in the right hemisphere as positive prediction features in sample 1. After controlling for sex, age, and FD, the predicted VSDT scores were significantly correlated with the actual general VSDT scores ($r = 0.20$, $p_{pt} < 0.001$; Fig. 2b). Importantly, the model constructed using sample 1 was used to predict the VSDT scores across sample 2 and the predicted VSDT scores were significantly correlated with the actual general scores of VSDT in sample 2 ($r = 0.20$, $p_{pt} < 0.001$, Fig. 2c). Additional supplementary analyses indicated that there was no significant predictive effect for VSDT using other indexes involving hemispheric segregation and integration by constructing relevant predictive models (see Table S5).

Furthermore, the predicted VDT score using the VSDT model was not significantly correlated with the general actual VDT scores both in

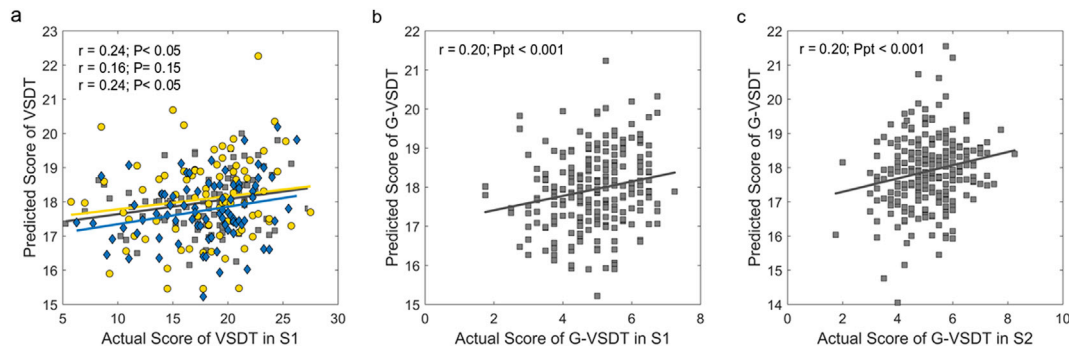


Fig. 2. Magnitude of segregation predicts VSDT using relevance vector regression model. (a) The predicted VSDT were correlated with the actual scores for each CV fold using the segregation index of the right hemisphere as positive prediction features in sample 1, and (b) were significantly correlated with the actual general VSDT in sample 1 after regressing out sex, age and FD. (c) The predicted VSDT scores were significantly correlated with the actual general scores of VSDT in sample 2 using the model constructed from sample 1. The P values in the predicted model were calculated using permutation tests (i.e., 1000 times).

sample 1 ($r = 0.05$, $p_{pt} = 0.13$) and in sample 2 ($r = 0.06$, $p_{pt} = 0.11$). Similarly, the predicted IQ score from the VSDT model was not significantly correlated with the actual IQ scores ($r = 0.02$, $p_{pt} = 0.41$). These results supported the prediction specificity of the segregation index in the right hemisphere for VSDT.

3.3. Brain regions and networks for predicting VSDT

As shown in Fig. 3a and Table S1, the nodes with the highest contribution in predicting VSDT ability mainly involved the right VN (e.g., middle occipital gyrus, lingual gyrus and fusiform gyrus), right SM (e.g., precentral gyrus, supplementary motor area, and part of middle

frontal gyrus) and right parts of DMN (e.g., parahippocampal gyrus, middle temporal gyrus, inferior temporal gyrus and medial frontal cortex). A further analysis exploring the relationship between segregation of right-lateralized networks and VSDT across the two samples showed that VSDT performance was positively correlated with the segregation of right VN ($r = 0.14$, $p < 0.001$; Fig. 3c) and the segregation of right SM ($r = 0.1$, $p < 0.05$; Fig. 3d). The segregation in sub-networks of the DMN and the other networks were not correlated with VSDT performance (see Table S3). To further refine our account in brain network level, we assessed the differences in functional connectivity of intra- and inter-hemisphere across 11 networks between high-VSDT group (the individuals of the top 10 percent in VSDT) and low-VSDT group (the

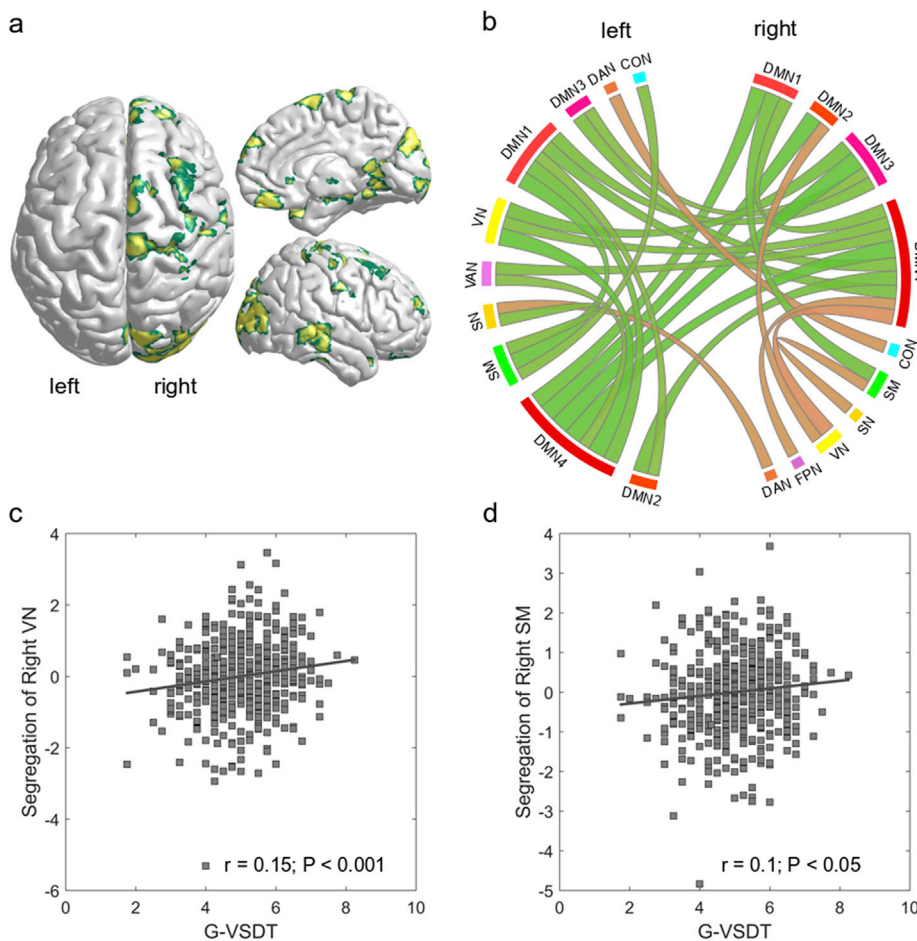


Fig. 3. The most important regions for predicting VSDT and segregation in brain networks associated with VSDT. The most important contributing regions in right hemisphere for VSDT prediction models (a). The chord diagram of network composition showing significant differences in functional connectivity of intra- and inter-hemisphere across 11 networks between high-VSDT group and low-VSDT group. Green edges refer to higher connectivity in low-VSDT than high-VSDT group, light red edges refer to higher connectivity in high-VSDT group than low-VSDT group (b). Correlation between the actual general VSDT (regressing out session, sex, age, and FD) and the segregation of right VN (c), the segregation of right SM (d).

individuals of the bottom 10 percent in VSDT) using different cutting threshold (see Fig. S6). Results revealed that increased intra-hemispheric functional connectivity between networks (e.g., VN and DMN, FPN and DMN, SN and SM) in the right side in the high-VSDT group compared with the low-VSDT group (see Fig. 3b). Thus, higher visuospatial divergent thinking was characterized by stronger segregation within right visual and sensorimotor networks.

3.4. Prediction for VDT

As shown in Fig. 4a, the predicted VDT scores were significantly correlated with the actual scores for each CV fold ($r_{cv1} = 0.27$, $MAE = 19.36$, $p < 0.05$; $r_{cv2} = 0.37$, $MAE = 18.26$, $p < 0.001$; $r_{cv3} = 0.23$, $MAE = 19.43$, $p < 0.05$) using the asymmetric index as prediction features in sample 1. After controlling for session, sex, age, and FD, the predicted VDT scores remained significantly correlated with the general VDT scores ($r = 0.40$, $p_{pt} < 0.001$; Fig. 4b). Importantly, the model constructed using sample 1 significantly predicted VDT scores across sample 2, and the predicted VDT scores were correlated with the actual general scores of VDT in sample 2 ($r = 0.19$, $p_{pt} < 0.001$; Fig. 4c). Additional supplementary analyses indicated that there was no significant predictive effect for VDT using other indexes involving hemispheric segregation and integration by constructing relevant predictive models (see Table S5).

Furthermore, the predicted VSDT score from the VDT model showed significant correlation with the actual VSDT scores in sample 1 ($r = 0.21$, $p_{pt} = 0.01$) but it was not significantly correlated with the actual VSDT scores in sample 2 ($r = 0.07$, $p_{pt} = 0.28$). The predicted IQ score from model for VDT showed no significant correlation with the actual IQ scores ($r = 0.05$, $p_{pt} = 0.38$). These results support the prediction specificity of the asymmetric index between hemispheres for VSDT.

3.5. Brain regions for predicting VDT

As shown in Fig. 4d and Table S2, the most important nodes for predicting VDT ability involved widespread regions, which mainly located within the semantic processing system (e.g., posterior superior temporal gyrus, middle temporal cortex, inferior temporal cortex, and inferior frontal gyrus), cognitive control network (e.g., DLPFC, middle frontal gyrus, and superior parietal lobule), medial parts of DMN (e.g., medial frontal cortex, anterior cingulate cortex, and precuneus) and some subcortical regions such as thalamus and putamen. Thus, verbal divergent thinking ability is characterized by hemispheric interaction mainly involved in the semantic processing network and cognitive control network. At the network level, a further analysis exploring the relationship between AI of networks and VDT across the two samples showed that VDT performance was negatively correlated with the asymmetric degree of FPN ($r = -0.1$, $p < 0.05$). The asymmetric degree in the other networks were not correlated with VDT performance (see Table S4). Furthermore, there is no significant differences in functional connectivity of intra- and inter-hemisphere across 11 networks between high-VDT group (the individuals of the top 10 percent in VDT) and low-VDT group (the individuals of the bottom 10 percent in VDT).

4. Discussion

The aim of the current study was to uncover the relationship between functional hemispheric lateralization and creative thinking ability, as well as to characterize hemispheric interaction in relation to visuospatial and verbal creativity. Individuals with high visuospatial creativity exhibited stronger segregation within right VN, SM, and parts of DMN, suggesting that the right hemisphere has a dominant function for visuospatial creativity, while individuals with higher verbal creativity

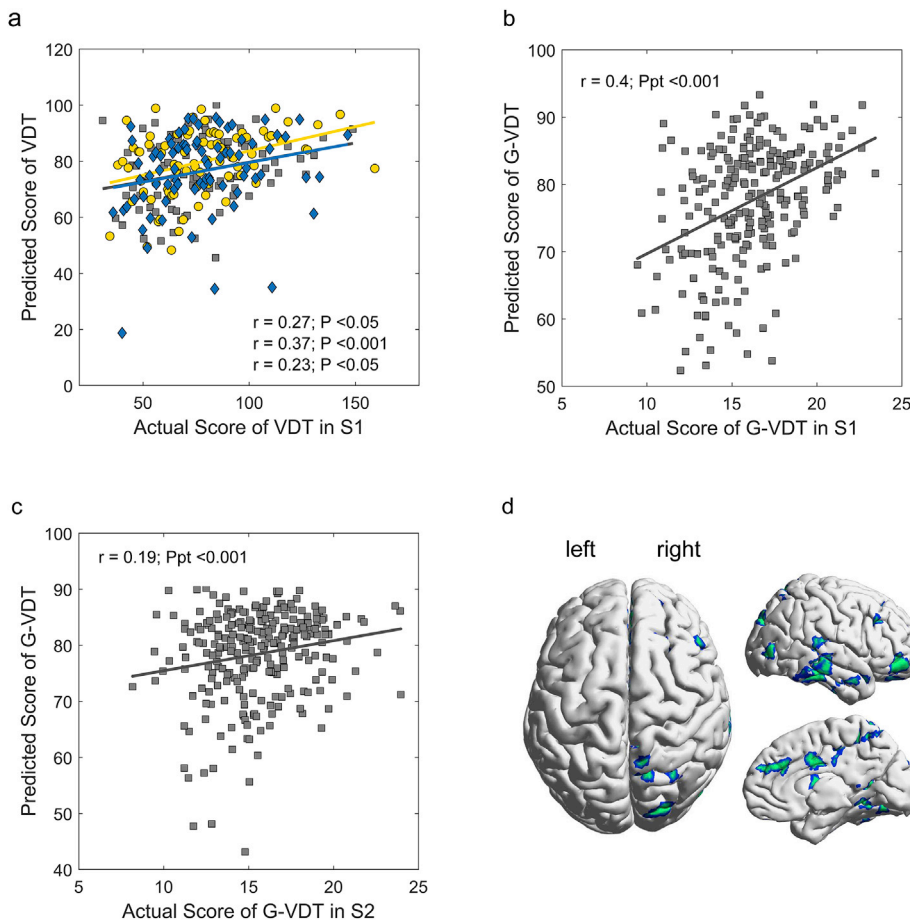


Fig. 4. Magnitude of lateralization predicts VDT using relevance vector regression model. (a) The predicted VDT were correlated with the actual scores for each CV fold using the asymmetric index as negative prediction features in sample 1, and (b) were significantly correlated with the actual general VDT regressing out sex, age and FD. (c) The predicted VDT were significantly correlated with the actual general scores of VDT in sample 2 using the model constructed using sample 1. The P values in the predicted model were calculated using permutation tests (i.e., 1000 times). (d) The most important contributing regions for VDT prediction models using the asymmetry of regions.

showed hemispheric balance within relevant semantic processing areas, indicating that verbal creativity may be more likely to rely on hemispheric interaction, rather than one dominant hemisphere. Taken together, these findings provide novel evidence for two distinct forms of functional lateralization in visuospatial and verbal divergent thinking.

As hypothesized, higher VSDT individuals showed more intra-hemispheric functional connectivity within the right VN, SM, and parts of DMN; especially, increased intra-hemispheric functional connectivity between networks (such as VN and DMN, FPN and DMN, SN and SM) in the right side in the high-VSDT group compared with the low-VSDT group. These findings are consistent with our recent results (Liu et al., 2018) as well as previous literature demonstrating that the right hemisphere is specialized for visuospatial processing (Mihov et al., 2010; Solso, 2001; Swan, 2001). A number of previous studies on artistic creativity indicated that the right hemisphere has a specific function in professional artists. For example, early EEG studies suggested that, during visual perception, artists show greater synchrony within the right hemisphere than the left hemisphere (Bhattacharya and Petsche, 2002), and long-term artistic training can lead to right hemisphere dominance during artistic action (Kowatari et al., 2009). Importantly, we found robust prediction of individual VSDT ability from the segregation of the right VN, thus VSDT is characterized by regions within VN showing greater within-hemisphere interactions compared to cross-hemisphere interactions. The visual network—including the occipital lobe, associated visual cortex, and fusiform—has shown common activation during visuospatial creativity tasks (Chrysikou and Thompson-Schill, 2011; Saggat et al., 2015). These regions are important for artistic creativity and have been linked to novelty-detection processing, construction of novel images, and mental imagery (Huang et al., 2013; Kowatari et al., 2009).

Moreover, we found some evidence that the SM in the right hemisphere, including supplementary motor area (SMA) and precentral gyrus, contributes to VSDT ability, consistent with the role of sensorimotor cortex in motor execution, planning, and goal-directed behavior underlying creative performance (de Manzano and Ullén, 2012; Pinho et al., 2015). We also found that individual VSDT can be predicted by medial temporal lobe (MTL) regions such as the hippocampus and the parahippocampus, which are particularly important for the generation of novel ideas by facilitating the recombination of stored episodic and semantic information (Beaty et al., 2018b; Ellamil et al., 2012; Madore et al., 2015; Pinho et al., 2014). Furthermore, it is important to note that high VSDT individuals exhibited weaker functional connectivity between the left VN and DMN, which is consistent with the idea that decreased inhibition from the left hemisphere can facilitate the emergence of creativity (Huang et al., 2013; Mayseless et al., 2014; Seeley et al., 2007). To some extent, these results are consistent with several recent studies on individual brain functional connectivity in creative ability. Several studies found that highly creative individuals exhibited greater cooperation between regions associated with the DMN and the executive control network (Beaty et al., 2014; Liu et al., 2015; Takeuchi et al., 2012) using resting-state fMRI data and task-fMRI data (Shi et al., 2018). Thus, the current study extends previous findings showing that VSDT may be characterized by right hemisphere dominance.

Regarding verbal creativity, several regions contributed to the prediction model, predominantly those responsible for semantic processing and internal attention, such as inferior frontal gyrus, anterior and posterior superior temporal gyrus, precuneus, and supramarginal gyrus. This finding is in agreement with a recent meta-analysis of the brain correlates of creativity (Gonen-Yaacovi et al., 2013; Wu et al., 2015) as well as with previous reviews (Dietrich and Kanso, 2010). It is worth noting that meta-analysis found regions within the left hemisphere to be preferentially activated across multiple creativity tasks (Gonen-Yaacovi et al., 2013). Nevertheless, we found that hemispheric balance among these regions was essential to verbal creative thinking, which supported the hypothesis of bilateral activation, integration and selection (BAIS) in creative processes (Jung-Beeman, 2005). In this set of brain regions, the

IFG has been shown to be critical in the interplay between evaluation and generation processes within the domain of verbal creativity (Kleinmuntz et al., 2018). Specifically, the left IFG could play a role in semantic information processing including controlled retrieval and selection of remote information from semantic memory (Hirshorn and Thompson-Schill, 2006; Jefferies, 2013; Martin and Cheng, 2006), whereas the right IFG may be important in suppression of preponent but inappropriate responses (Aron et al., 2003; Volle et al., 2011). In addition, the anterior and posterior STG, as part of the semantic system (Binder and Desai, 2011), is connected with contralateral IFG through the uncinate fasciculus (Bowden et al., 2005; Jung-Beeman et al., 2004). Previous research has demonstrated that these regions were associated with higher-order semantic processes as well as the ability to combine irrelevant information in new ways (Abraham et al., 2018; Kenett et al., 2018). In sum, this findings are consistent with the notion that inter-hemispheric balance is central to creative cognition (Faust and Kenett, 2014; Shamay-Tsoory et al., 2011), suggesting that bilateral recruitment of these regions may be a general characteristic of creative processing (Aziz-Zadeh et al., 2009; Bogen and Bogen, 1969).

Intriguingly, the estimated VDT model could be used to predict individual VSDT scores, and the predicted scores were marginally correlated with the actual VSDT scores in sample 1. One reason for this may be due to similar assessments for two creative modalities in this study. Another reason for the results might be a domain-general mechanism of creative information processing. A growing body of evidence from functional connectivity analyses of creative performance across a range of domains indicates that creative thought may benefit from the cooperation of default and control network regions (Beaty et al., 2016, 2018a; Zhu et al., 2017). Consistent with this literature, we found that medial and lateral temporal regions of the DMN, implicated in the generation of novel ideas (Beaty et al., 2018b; Madore et al., 2016), were relevant for the prediction of both VSDT and VDT, thus pointing to a common neuroanatomical substrate underlying different creative modalities. Interestingly, we found that widespread regions predicted VDT, whereas concentrated regions within VN and SM predicted VSDT. One plausible explanation might be the fact that VDT was comprised of 3 tasks while VSDT was only comprised of one task, potentially yielding more homogeneity in neural correlates.

To our knowledge, the current study provides the novel fMRI evidence for hemispheric lateralization of different modalities of creativity. Nevertheless, some limitations should be noted, and some questions remain to be answered by future studies. First, although the prediction model was validated using an independent testing dataset (sample 2), interpretations should be conservative because the two samples came from the same research center, thus true external validation was not possible. It is therefore important to further validate the findings with cross-center datasets (Xia and He, 2017). Second, the prediction models identified a wide range of important regions that significantly contributed to VSDT or VDT, so results should be interpreted jointly and not in isolation (i.e., a single region, network, or system (Haufe et al., 2014)). Third, we could not fully account for the potential effect of different creativity scoring procedures used across the two samples. To address the substantial burden on human raters (Forthmann et al., 2017), an efficient, low-cost, and objective scoring approach would be highly beneficial, such as an automatic computer scoring system. Finally, the highly homogeneous sample in the present study might indicate similar intellectual ability (partly due to the old version of WAIS-RC) and/or a similar level of creative potential. It is therefore unknown whether our findings would also hold true for a general population that includes a larger age range.

The present research focused on differential patterns of hemispheric interaction between visuospatial creativity and verbal creativity. Future studies could also investigate the pattern of hemispheric interaction in artists engaging in different creative modalities such as creative drawing, creative writing, and musical composition, as well as whether patterns of hemispheric lateralization support different domains across artistic and

scientific fields. On the other hand, it remains unclear whether the current findings can be generalized to predict individual creative thinking ability using structural neuroimaging features such as gray matter volume, cortical thickness, and structural connectivity using diffusion MRI data. Considering that brain structural biomarkers were viewed as robust features for predicting individual difference in cognition and personality (DeYoung et al., 2010; Kanai and Rees, 2011), a promising direction to explore is the hemispheric interaction of creative thinking ability using structural MRI data. In addition to neuroimaging approaches, we think case studies with clinical samples, such as epileptic patients with split-brains or hemispherectomies, should be encouraged to further explore hemispheric specialization and creative thinking development.

In summary, our findings suggest that hemispheric dominance in creative thinking relies on different creative modalities. Specifically, visuospatial creativity is characterized as a right hemisphere dominant function involving VN, SM and parts of DMN, whereas verbal creativity is characterized by hemispheric interaction within the semantic processing network. Moreover, the visuospatial and verbal creativity models were found to be valid in predicting one another, supporting a domain-general mechanism of creative thinking. The current results thus provide novel insights into a longstanding and controversial question in creativity research by demonstrating that two distinct forms of functional lateralization support individual differences in visuospatial and verbal divergent thinking.

Declarations of interest

None.

Acknowledgments

This research was supported by the National Natural Science Foundation of China (NSFC 31571137; NSFC 31500885; NSFC 31600878; NSFC 31771231), Chang Jiang Scholars Program, National Outstanding Young People Plan, the Program for the Top Young Talents by Chongqing, the Fundamental Research Funds for the Central Universities (SWU1609177), Natural Science Foundation of Chongqing (cstc2015jcyjA10106), Fok Ying Tung Education Foundation (No.151023), the Research Program Funds of the Collaborative Innovation Center of Assessment toward Basic Education Quality at Beijing Normal University. Q. Chen was supported by National Science Foundation of China (NSFC 31800919), China Postdoctoral Science Foundation (2017M622935) and the Fundamental Research Funds for the Central Universities (SWU1809211). G. Liu was supported by National Science Foundation of China (NSFC 61472330 and 61872301).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.116065>.

References

- Abraham, A., Rutter, B., Bantini, T., Hermann, C., 2018. Creative conceptual expansion: a combined fMRI replication and extension study to examine individual differences in creativity. *Neuropsychologia* 118, 29–39.
- Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Andreas, A., Roland, P., Zilles, K., 1996. Asymmetry in the Human Motor Cortex and Handedness. *NeuroImage* 4, 216–222.
- Aron, A.R., Fletcher, P.C., Bullmore, E.T., Sahakian, B.J., Robbins, T.W., 2003. Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nat. Neurosci.* 6, 115–116.
- Atchley, R.A., Keeney, M., Burgess, C., 1999. Cerebral hemispheric mechanisms linking ambiguous word meaning retrieval and creativity. *Brain Cogn.* 40, 479–499.
- Aziz-Zadeh, L., Liew, S.-L., Dandekar, F., 2012. Exploring the neural correlates of visual creativity. *Soc. Cogn. Affect. Neurosci.* 8, 475–480.
- Aziz-Zadeh, L., Kaplan, J.T., Iacoboni, M., 2009. “Aha!”: the neural correlates of verbal insight solutions. *Hum. Brain Mapp.* 30, 908–916.
- Badzakova-Trajkova, G., Häberling, I.S., Corballis, M.C., 2011. Magical ideation, creativity, handedness, and cerebral asymmetries: a combined behavioural and fMRI study. *Neuropsychologia* 49, 2896–2903.
- Beaty, R.E., Benedek, M., Wilkins, R.W., Jauk, E., Fink, A., Silvia, P.J., Neubauer, A.C., 2014. Creativity and the default network: a functional connectivity analysis of the creative brain at rest. *Neuropsychologia* 64, 92–98.
- Beaty, R.E., Benedek, M., Silvia, P.J., Schacter, D.L., 2016. Creative cognition and brain network dynamics. *Trends Cogn. Sci.* 20, 87–95.
- Beaty, R.E., Kenett, Y.N., Christensen, A.P., Rosenberg, M.D., Benedek, M., Chen, Q., Fink, A., Qiu, J., Kwapił, T.R., Kane, M.J., 2018a. Robust prediction of individual creative ability from brain functional connectivity. *Proc. Natl. Acad. Sci. U.S.A.* 115, 1087–1092.
- Beaty, R.E., Thakral, P.P., Madore, K.P., Benedek, M., Schacter, D.L., 2018b. Core network contributions to remembering the past, imagining the future, and thinking creatively. *J. Cogn. Neurosci.* 30, 1939–1951.
- Beeman, M.J., Bowden, E.M., 2000. The right hemisphere maintains solution-related activation for yet-to-be-solved problems. *Mem. Cogn.* 28, 1231–1241.
- Beeman, M.J., Bowden, E.M., Gernsbacher, M.A., 2000. Right and left hemisphere cooperation for drawing predictive and coherence inferences during normal story comprehension. *Brain Lang.* 71, 310–336.
- Bhattacharya, J., Petsche, H., 2002. Shadows of artistry: cortical synchrony during perception and imagery of visual art. *Cogn. Brain Res.* 13, 179–186.
- Binder, J.R., Desai, R.H., 2011. The neurobiology of semantic memory. *Trends Cogn. Sci.* 15, 527–536.
- Bogen, J.E., Bogen, G.M., 1969. The other side of the brain III: the corpus callosum and creativity. *Bull. Los Ang. Neurol. Soc.* 34, 191–202.
- Bowden, E.M., Beeman, M.J., 1998. Getting the right idea: semantic activation in the right hemisphere may help solve insight problems. *Psychol. Sci.* 9, 435–440.
- Bowden, E.M., Jung-Beeman, M., 2003. Aha! Insight experience correlates with solution activation in the right hemisphere. *Psychon. Bull. Rev.* 10, 730–737.
- Bowden, E.M., Jung-Beeman, M., Fleck, J., Kounios, J., 2005. New approaches to demystifying insight. *Trends Cogn. Sci.* 9, 322–328.
- Cai, Q., Van der Haegen, L., Brysbaert, M., 2013. Complementary hemispheric specialization for language production and visuospatial attention. *Proc. Natl. Acad. Sci.* 110, 322–330.
- Carlsson, I., Wendt, P.E., Risberg, J., 2000. On the neurobiology of creativity. Differences in frontal activity between high and low creative subjects. *Neuropsychologia* 38, 873–885.
- Chen, Q., Beaty, R.E., Wei, D., Yang, J., Sun, J., Liu, W., Yang, W., Zhang, Q., Qiu, J., 2018. Longitudinal alterations of frontoparietal and frontotemporal networks predict future creative cognitive ability. *Cerebr. Cortex* 28, 103–115.
- Chrysikou, E.G., Thompson-Schill, S.L., 2011. Dissociable brain states linked to common and creative object use. *Hum. Brain Mapp.* 32, 665–675.
- Cisler, J.M., 2017. Childhood trauma and functional connectivity between amygdala and medial prefrontal cortex: a dynamic functional connectivity and large-scale network perspective. *Front. Syst. Neurosci.* 11, 29.
- Cui, Z., Gong, G., 2018. The effect of machine learning regression algorithms and sample size on individualized behavioral prediction with functional connectivity features. *Neuroimage* 178, 622–637.
- Cui, Z., Su, M., Li, L., Shu, H., Gong, G., 2017. Individualized prediction of reading comprehension ability using gray matter volume. *Cerebr. Cortex* 28, 1656–1672.
- Dake, D.M., 1991. The visual definition of visual creativity. *J. Vis. Lit.* 11, 100–104.
- de Manzano, Ö., Ullén, F., 2012. Goal-independent mechanisms for free response generation: creative and pseudo-random performance share neural substrates. *Neuroimage* 59, 772–780.
- DeYoung, C.G., Hirsh, J.B., Shane, M.S., Papademetris, X., Rajeevan, N., Gray, J.R., 2010. Testing predictions from personality neuroscience: brain structure and the big five. *Psychol. Sci.* 21, 820–828.
- Dietrich, A., Kanso, R., 2010. A review of EEG, ERP, and neuroimaging studies of creativity and insight. *Psychol. Bull.* 136, 822–848.
- Drysdale, A.T., Grosenick, L., Downar, J., Dunlop, K., Mansouri, F., Meng, Y., Fetcho, R.N., Zebley, B., Oathes, D.J., Etkin, A., 2017. Erratum: resting-state connectivity biomarkers define neurophysiological subtypes of depression. *Nat. Med.* 23–37, 28.
- Duboc, V., Dufourcq, P., Blader, P., Roussigné, M., 2015. Asymmetry of the brain: development and implications. *Annu. Rev. Genet.* 49, 647–672.
- Ellamil, M., Dobson, C., Beeman, M., Christoff, K., 2012. Evaluative and generative modes of thought during the creative process. *Neuroimage* 59, 1783–1794.
- Erus, G., Battapady, H., Satterthwaite, T.D., Hakonarson, H., Gur, R.E., Davatzikos, C., Gur, R.C., 2014. Imaging patterns of brain development and their relationship to cognition. *Cerebr. Cortex* 25, 1676–1684.
- Faust, M., Kenett, Y.N., 2014. Rigidity, chaos and integration: hemispheric interaction and individual differences in metaphor comprehension. *Front. Hum. Neurosci.* 8, 511.
- Folley, B.S., Park, S., 2005. Verbal creativity and schizotypal personality in relation to prefrontal hemispheric laterality: a behavioral and near-infrared optical imaging study. *Schizophr. Res.* 80, 271–282.
- Forthmann, B., Holling, H., Zandi, N., Gerwig, A., Çelik, P., Storme, M., Lubart, T., 2017. Missing creativity: the effect of cognitive workload on rater (dis-) agreement in subjective divergent-thinking scores. *Think. Skills Creat.* 23, 129–139.
- Franke, K., Ziegler, G., Klöppel, S., Gaser, C., Initiative, A.S.D.N., 2010. Estimating the age of healthy subjects from T1-weighted MRI scans using kernel methods: exploring the influence of various parameters. *Neuroimage* 50, 883–892.
- Gansler, D.A., Moore, D.W., Susmaras, T.M., Jerram, M.W., Sousa, J., Heilman, K.M., 2011. Cortical morphology of visual creativity. *Neuropsychologia* 49, 2527–2532.

- Gonen-Yaacovi, G., De Souza, L.C., Levy, R., Urbanski, M., Josse, G., Volle, E., 2013. Rostral and caudal prefrontal contribution to creativity: a meta-analysis of functional imaging data. *Front. Hum. Neurosci.* 7, 465.
- Gong, Y.X., 1992. Wechsler Adult Intelligence Scale-Revised in China. WAIS-RC) Hunan Map Publishing Company, Changsha, 1992.
- Gotts, S.J., Jo, H.J., Wallace, G.L., Saad, Z.S., Cox, R.W., Martin, A., 2013. Two distinct forms of functional lateralization in the human brain. *Proc. Natl. Acad. Sci.* 110, E3435–E3444.
- Haufe, S., Meinecke, F., Görgen, K., Dähne, S., Haynes, J.-D., Blankertz, B., Bießmann, F., 2014. On the interpretation of weight vectors of linear models in multivariate neuroimaging. *Neuroimage* 87, 96–110.
- Hirshorn, E.A., Thompson-Schill, S.L., 2006. Role of the left inferior frontal gyrus in covert word retrieval: neural correlates of switching during verbal fluency. *Neuropsychologia* 44, 2547–2557.
- Huang, P., Qiu, L., Shen, L., Zhang, Y., Song, Z., Qi, Z., Gong, Q., Xie, P., 2013. Evidence for a left-over-right inhibitory mechanism during figural creative thinking in healthy nonartists. *Hum. Brain Mapp.* 34, 2724–2732.
- Jefferies, E., 2013. The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex* 49, 611–625.
- Jung-Beeman, M., 2005. Bilateral brain processes for comprehending natural language. *Trends Cogn. Sci.* 9, 512–518.
- Jung-Beeman, M., Bowden, E.M., Haberman, J., Frymiare, J.L., Arambel-Liu, S., Greenblatt, R., Reber, P.J., Kounios, J., 2004. Neural activity when people solve verbal problems with insight. *PLoS Biol.* 2, e97.
- Joliot, M., Tzourio-Mazoyer, N., Mazoyer, B., 2016. Intra-hemispheric intrinsic connectivity asymmetry and its relationships with handedness and language lateralization. *Neuropsychologia* 93, 437–447.
- Jung, R.E., Mead, B.S., Carrasco, J., Flores, R.A., 2013. The structure of creative cognition in the human brain. *Front. Neurosci.* 7, 330.
- Kanai, R., Rees, G., 2011. The structural basis of inter-individual differences in human behaviour and cognition. *Nat. Rev. Neurosci.* 12, 231–242.
- Kenett, Y.N., Anaki, D., Faust, M., 2015. Processing of unconventional stimuli requires the recruitment of the non-specialized hemisphere. *Front. Neurosci.* 9.
- Kenett, Y.N., Medaglia, J.D., Beaty, R.E., Chen, Q., Betzel, R.F., Thompson-Schill, S.L., Qiu, J., 2018. Driving the brain towards creativity and intelligence: a network control theory analysis. *Neuropsychologia* 118, 79–90.
- Kleinmuntz, O.M., Abecasis, D., Tauber, A., Geva, A., Chistyakov, A.V., Kreinin, I., Klein, E., Shamay-Tsoory, S.G., 2018. Participation of the left inferior frontal gyrus in human originality. *Brain Struct. Funct.* 223, 329–341.
- Kounios, J., Beeman, M., 2014. The cognitive neuroscience of insight. *Annu. Rev. Psychol.* 65, 71–94.
- Kowatari, Y., Lee, S.H., Yamamura, H., Nagamori, Y., Levy, P., Yamane, S., Yamamoto, M., 2009. Neural networks involved in artistic creativity. *Hum. Brain Mapp.* 30, 1678–1690.
- Lancichinetti, A., Fortunato, S., 2012. Consensus clustering in complex networks. *Sci. Rep.* 2, 336.
- Levy, J., 1969. Possible basis for the evolution of lateral specialization of the human brain. *Nature* 224, 614–615.
- Lindell, A.K., 2011. Lateral thinkers are not so laterally minded: hemispheric asymmetry, interaction, and creativity. *Laterality: Asymmetries Body Brain Cognit.* 16, 479–498.
- Liu, S., Erkkinen, M.G., Healey, M.L., Xu, S., Swett, K.E., Chow, H.M., Braun, A.R., 2015. Brain activity and connectivity during poetry composition: Toward a multidimensional model of the creative process. *Hum. Brain Mapp.* 36, 3351–3372.
- Liu, W., Wei, D., Chen, Q., Yang, W., Meng, J., Wu, G., Bi, T., Zhang, Q., Zuo, X.-N., Qiu, J., 2017. Longitudinal test-retest neuroimaging data from healthy young adults in southwest China. *Sci. data* 4, 170017.
- Liu, Z., Zhang, J., Xie, X., Rolls, E.T., Sun, J., Zhang, K., Jiao, Z., Chen, Q., Zhang, J., Qiu, J., 2018. Neural and genetic determinants of creativity. *Neuroimage* 174, 164–176.
- Long, H., 2014. More than appropriateness and novelty: judges' criteria of assessing creative products in science tasks. *Think. Skills Creat.* 13, 183–194.
- Lotze, M., Erhard, K., Neumann, N., Eickhoff, S.B., Langner, R., 2014. Neural correlates of verbal creativity: differences in resting-state functional connectivity associated with expertise in creative writing. *Front. Hum. Neurosci.* 8, 516.
- Madore, K.P., Addis, D.R., Schacter, D.L., 2015. Creativity and memory: effects of an episodic-specificity induction on divergent thinking. *Psychol. Sci.* 26, 1461–1468.
- Madore, K.P., Szpunar, K.K., Addis, D.R., Schacter, D.L., 2016. Episodic specificity induction impacts activity in a core brain network during construction of imagined future experiences. *Proc. Natl. Acad. Sci. U.S.A.* 113, 10696–10701.
- Martin, R.C., Cheng, Y., 2006. Selection demands versus association strength in the verb generation task. *Psychon. Bull. Rev.* 13, 396–401.
- Maysless, N., Aharon-Peretz, J., Shamay-Tsoory, S., 2014. Unleashing creativity: the role of left temporoparietal regions in evaluating and inhibiting the generation of creative ideas. *Neuropsychologia* 64, 157–168.
- Maysless, N., Shamay-Tsoory, S., 2015. Enhancing verbal creativity: modulating creativity by altering the balance between right and left inferior frontal gyrus with tDCS. *Neuroscience* 291, 167–176.
- McCallum, R.S., Glynn, S.M., 1979. Hemispheric specialization and creative behavior. *J. Creat. Behav.* 13, 263–273.
- Mihov, K.M., Denzler, M., Förster, J., 2010. Hemispheric specialization and creative thinking: a meta-analytic review of lateralization of creativity. *Brain Cogn.* 72, 442–448.
- Miller, B.L., Boone, K., Cummings, J.L., Read, S.L., Mishkin, F., 2000. Functional correlates of musical and visual ability in frontotemporal dementia. *Br. J. Psychiatry* 176, 458–463.
- Miller, B.L., Hou, C.E., 2004. Portraits of artists: emergence of visual creativity in dementia. *Arch. Neurol.* 61, 842–844.
- Miroux, H.J., Beeman, M., 2012. Bilateral processing and affect in creative language comprehension. *Handb. Neuropsychol. Lang.* 319–341.
- Moore, D.W., Bhadelia, R.A., Billings, R.L., Fulwiler, C., Heilman, K.M., Rood, K.M., Gansler, D.A., 2009. Hemispheric connectivity and the visual-spatial divergent thinking component of creativity. *Brain Cogn.* 70, 267–272.
- Pinho, A.L., de Manzano, Ö., Fransson, P., Eriksson, H., Ullén, F., 2014. Connecting to create: expertise in musical improvisation is associated with increased functional connectivity between premotor and prefrontal areas. *J. Neurosci.* 34, 6156–6163.
- Pinho, A.L., Ullén, F., Castelo-Branco, M., Fransson, P., de Manzano, Ö., 2015. Addressing a paradox: dual strategies for creative performance in introspective and extrospective networks. *Cerebr. Cortex* 26, 3052–3063.
- Raemaekers, M., Schellekens, W., Petridou, N., Ramsey, N.F., 2018. Knowing left from right: asymmetric functional connectivity during resting state. *Brain Struct. Funct.* 223, 1909–1922.
- Rubinov, M., Sporns, O., 2010. Complex network measures of brain connectivity: uses and interpretations. *Neuroimage* 52, 1059–1069.
- Runco, M.A., Jaeger, G.J., 2012. The standard definition of creativity. *Creativ. Res. J.* 24, 92–96.
- Saggar, M., Quintin, E.-M., Kienitz, E., Bott, N.T., Sun, Z., Hong, W.-C., Chien, Y.-h., Liu, N., Dougherty, R.F., Royalty, A., 2015. Pictionary-based fMRI paradigm to study the neural correlates of spontaneous improvisation and figural creativity. *Sci. Rep.* 5, 10894.
- Seeley, W.W., Matthews, B.R., Crawford, R.K., Gorno-Tempini, M.L., Foti, D., Mackenzie, I.R., Miller, B.L., 2007. Unravelling Boléro: progressive aphasia, transmodal creativity and the right posterior neocortex. *Brain* 131, 39–49.
- Shamay-Tsoory, S., Adler, N., Aharon-Peretz, J., Perry, D., Maysless, N., 2011. The origins of originality: the neural bases of creative thinking and originality. *Neuropsychologia* 49, 178–185.
- Shi, L., Sun, J., Xia, Y., Ren, Z., Chen, Q., Wei, D., Yang, W., Qiu, J., 2018. Large-scale brain network connectivity underlying creativity in resting-state and task fMRI: Cooperation between default network and frontal-parietal network. *Biol. Psychol.* 135, 102–111.
- Siegel, J.S., Ramsey, L.E., Snyder, A.Z., Metcalf, N.V., Chacko, R.V., Weinberger, K., Baldassarre, A., Hacker, C.D., Shulman, G.L., Corbetta, M., 2016. Disruptions of network connectivity predict impairment in multiple behavioral domains after stroke. *Proc. Natl. Acad. Sci. U.S.A.* 113, E4367–E4376.
- Solso, R.L., 2001. Brain activities in a skilled versus a novice artist: an fMRI study. *Leonardo* 34, 31–34.
- Sternberg, R.J., Lubart, T.I., 1996. Investing in creativity. *Am. Psychol.* 51, 677–688.
- Sun, J., Chen, Q., Zhang, Q., Li, Y., Li, H., Wei, D., Yang, W., Qiu, J., 2016. Training your brain to be more creative: brain functional and structural changes induced by divergent thinking training. *Hum. Brain Mapp.* 37, 3375–3387.
- Swan, L., 2001. Unilateral spatial neglect. *Phys. Ther.* 81, 1572–1580.
- Takeuchi, H., Taki, Y., Sassa, Y., Hashizume, H., Sekiguchi, A., Fukushima, A., Kawashima, R., 2010. White matter structures associated with creativity: evidence from diffusion tensor imaging. *Neuroimage* 51, 11–18.
- Takeuchi, H., Taki, Y., Hashizume, H., Sassa, Y., Nagase, T., Nouchi, R., Kawashima, R., 2012. The association between resting functional connectivity and creativity. *Cerebr. Cortex* 22, 2921–2929.
- Tipping, M.E., 2001. Sparse Bayesian learning and the relevance vector machine. *J. Mach. Learn. Res.* 1, 211–244.
- Toga, A.W., Thompson, P.M., 2003. Mapping brain asymmetry. *Nat. Rev. Neurosci.* 4, 37–48.
- Torrance, E.P., 1982. Hemisphericity and creative functioning. *J. Res. Dev. Educ.* 15, 29–37.
- Volle, E., de Lacy Costello, A., Coates, L.M., McGuire, C., Towgood, K., Gilbert, S., Kinkingnehun, S., McNeil, J.E., Greenwood, R., Papps, B., 2011. Dissociation between verbal response initiation and suppression after prefrontal lesions. *Cerebr. Cortex* 22, 2428–2440.
- Wang, D., Buckner, R.L., Liu, H., 2014. Functional specialization in the human brain estimated by intrinsic hemispheric interaction. *J. Neurosci.* 34, 12341–12352.
- Wang, J., Tian, Y., Wang, M., Cao, L., Wu, H., Zhang, Y., Wang, K., Jiang, T., 2016. Brain Imaging Behav 10, 1029–1037.
- Wei, D., Zhuang, K., Ai, L., Chen, Q., Yang, W., Liu, W., Wang, K., Sun, J., Qiu, J., 2018. Structural and functional brain scans from the cross-sectional Southwest University adult lifespan dataset. *Sci. data* 5.
- Wheatley, G.H., 1977. The right hemisphere's role in problem solving. *Arith. Teach.* 25, 36–39.
- Wu, X., Yang, W., Tong, D., Sun, J., Chen, Q., Wei, D., Zhang, Q., Zhang, M., Qiu, J., 2015. A meta-analysis of neuroimaging studies on divergent thinking using activation likelihood estimation. *Hum. Brain Mapp.* 36, 2703–2718.
- Xia, M., He, Y., 2017. Functional connectomics from a “big data” perspective. *Neuroimage* 160, 152–167.
- Yan, C.-G., Wang, X.-D., Zuo, X.-N., Zang, Y.-F., 2016. DPABI: data processing & analysis for (resting-state) brain imaging. *Neuroinformatics* 14, 339–351.
- Ye, R., Hong, D., Torrance, P.E., 1988. Cross cultural comparison of creative thinking between Chinese and American students using Torrance Test. *Chin. J. Appl. Psychol.* 3, 22–29.
- Zalesky, A., Fornito, A., Harding, I.H., Cocchi, L., Yücel, M., Pantelis, C., Bullmore, E.T., 2010. Whole-brain anatomical networks: does the choice of nodes matter? *Neuroimage* 50, 970–983.

Zhao, Q., Zhou, Z., Xu, H., Fan, W., Han, L., 2014. Neural pathway in the right hemisphere underlies verbal insight problem solving. *Neuroscience* 256, 334–341.

Zhong, S., He, Y., Shu, H., Gong, G., 2016. Developmental changes in topological asymmetry between hemispheric brain white matter networks from adolescence to young adulthood. *Cerebr. Cortex* 27, 2560–2570.

Zhu, W., Chen, Q., Xia, L., Beaty, R.E., Yang, W., Tian, F., Sun, J., Cao, G., Zhang, Q., Chen, X., 2017. Common and distinct brain networks underlying verbal and visual creativity. *Hum. Brain Mapp.* 38, 2094–2111.