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ORIGINAL RESEARCH

Relation of visual creative imagery manipulation to resting-state brain oscillations

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Abstract Visual creative imagery (VCI) manipulation is the key component of visual creativity; however, it remains largely unclear how it occurs in the brain. The present study investigated the brain neural response to VCI manipulation and its relation to intrinsic brain activity. We collected functional magnetic resonance imaging (fMRI) datasets related to a VCI task and a control task as well as pre- and post-task resting states in sequential sessions. A general linear model (GLM) was subsequently used to assess the specific activation of the VCI task compared with the control task. The changes in brain oscillation amplitudes across the pre-, on-, and post-task states were measured to investigate the modulation of the VCI task. Furthermore, we applied a Granger causal analysis (GCA) to demonstrate the dynamic neural interactions that underlie the modulation effect. We determined that the VCI task specifically activated the left inferior frontal gyrus pars triangularis (IFGtriang) and the right superior frontal gyrus (SFG), as well as the temporoparietal areas, including the left inferior temporal gyrus, right precuneus, and bilateral superior parietal gyrus. Furthermore, the VCI task modulated the intrinsic brain activity of the right IFGtriang (0.01–0.08 Hz) and the left caudate nucleus (0.2–0.25 Hz). Importantly, an inhibitory effect (negative) may exist from the left SFG to the right IFGtriang in the on-VCI task state, in the frequency of 0.01–0.08 Hz, whereas this effect shifted to an excitatory effect (positive) in the subsequent post-task resting state. Taken together, the present findings provide experimental evidence for the existence of a common mechanism that governs the brain activity of many regions at resting state and whose neural activity may engage during the VCI manipulation task, which may facilitate an understanding of the neural substrate of visual creativity.

Keywords Visual creative imagery (VCI) · Functional magnetic resonance imaging (fMRI) · General linear model (GLM) · Brain intrinsic activity · Left-over-right inhibition

Introduction

Visual creativity, which represents the production of novel and useful visual forms, is a primary component of multiple fields, such as painting, photography, sculpture, and architecture (Aziz-Zadeh et al. 2012; Palmiero et al. 2015). Neuroimaging studies have indicated that visual creativity tasks activate multiple brain regions (Aziz-Zadeh et al. 2012; Luo et al. 2013; Shah et al. 2013), and creativity performances are highly related to intrinsic brain activity characteristics (Q. Chen et al. 2014; Leonardi and Van De Ville 2013; Takeuchi et al. 2012). These observations may suggest the important roles of intrinsic brain activity and the subsequent neural changes in response to visual creativity. Previous studies have demonstrated the intimate interactions between specific task-induced brain activity and intrinsic brain activity (Lewis et al. 2009; Wang et al. 2015). Evidences have also shown that creativity tasks induced changes of intrinsic brain activity (Wei et al. 2014), and short-term training by creative tasks

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altered the brain activation (Saggar et al. 2016; Sun et al. 2016). However, the association of the neural response of a visual imagery manipulation process and the intrinsic brain activity remains unknown, which may facilitate an understanding of the neural basis of visual creativity.

Visual creativity is typically defined as breaking imagined combinations of familiar patterns and reconstructing practical and original patterns (Finke 1996, 2014), which has been documented to be complex and multifaceted (Arden et al. 2010; Dietrich 2004). The visual creative imagery (VCI) manipulation refers to the assessment of creative visual synthesis using mental imagery, which comprises a key component of visual creativity given that individuals are capable of making unexpected discoveries in imagery when mentally assembling or transforming a set of basic parts (Finke and Slayton 1988). Creative visual synthesis in imagery may be reliably induced under appropriate laboratory conditions; thus, VCI has been widely used to investigate visual creativity in many behavioral studies (Finke 1996; Kokotovich and Purcell 2000; LeBoutillier and Marks 2003; Verstijnen et al. 1998), as well as fMRI studies (Aziz-Zadeh et al. 2012; Palmiero et al. 2015; Palmiero et al. 2016). Multiple cognitive processes, such as working memory, attention, divergent thinking, and cognitive control, are involved during creative imagery processing (Guilford et al. 1978; Jung et al. 2010). According to the two fold process model, general creativity includes the idea generation and evaluation process (Basadur et al. 1982; Finke and Slayton 1988), which relies on the combinations of fundamental cognitive processes.

In particular, neuroimaging methods are widely used to investigate the neural basis of the creativity process, and the prefrontal cortex (PFC) is documented to provide the infrastructure to combine these complex cognitive functions by providing a buffer to retain information (Dietrich 2004). Consistently, many studies have indicated that the PFC, mainly including the inferior frontal gyrus (IFG), the superior frontal gyrus (SFG), and the middle frontal gyrus (MFG), is a consensus creativity-relevant brain region (de Souza et al. 2014). Moreover, previous studies have demonstrated activations of the left IFG (Benedek et al. 2014a, b; Zaidel 2014), the right IFG (Zhao et al. 2014), the right SFG (Dietrich and Kanso 2010; Saggar et al. 2015), and the left MFG (Benedek et al. 2014b; Cousijn et al. 2014) in creativity tasks. Nevertheless, controversial arguments remain regarding the hemispheric dominance of the previously described critical regions of visual creative tasks. Several studies have demonstrated that visual creativity was typically related to activity in the right hemisphere (Aziz-Zadeh et al. 2012; Saggar et al. 2015), which is different from the verbal creativity that has mainly been associated with the language-dominant left hemisphere (Shah et al. 2013). However, other studies have assessed the left hemispheric dominance during a creativity task regardless of verbal or visual creativity (Benedek et al. 2014a, b). Furthermore, brain lesion studies have also demonstrated that when patients had left frontal gyrus damage, they would suddenly manifest high-level creativity performance in terms of increasing the amount of their artworks or the creative artistic manifestation in their works, followed by evoked activity in the right brain hemisphere (Drago et al. 2009; Miller and Hou 2004). Thus, the limited activity of the left PFC would release the activity of the right PFC, which may be in favor of creative task performance. Consistent with this finding, Huang et al. (2013) proposed the existence of the spontaneous left-over-right inhibitory mechanism during figural creative thinking in healthy human non-artists. Thus, the activation of the right brain hemisphere was insufficient for detection and overwhelmed by the activation of the contralateral part, which may induce the underestimation of the role of the right brain hemisphere in the creativity process. In contrast to the hemispheric dominance notion, other researchers have emphasized the balance between the bilateral IFG (Goel and Vartanian 2005; N. Mayseless and Shamay-Tsoory 2015), and both are relative to an individual's performance of verbal or visual creativity (Abraham et al. 2012; Lotze et al. 2014). To attempt to understand this controversy, brain lesion studies may be appropriate; however, for healthy subjects, one potential detection approach may rely on the consideration of the intrinsic brain activity with the absence of task demands to discard the spontaneous left-over-right inhibition induced by the creativity process. Thus, we would shed light on the intrinsic brain activity, which has been tightly related to the creativity performance and the neural response to creativity, as well as the interaction between the intrinsic brain activity and the task-induced activation.

The human brain is a complex, dynamic system that generates a multitude of oscillatory waves, which are linked with various neural processes, including input selection, plasticity binding, and consolidation (Bianciardi et al. 2009), as well as cognitive functions, including salience detection, emotional regulation, attention and memory (Knyazev 2007). Intrinsic brain activity is considered predictive of task-induced activity (Liu et al. 2011; Tavor et al. 2016) and impacts subsequent behavior (Mennes et al. 2011); however, intrinsic brain activity may also be dynamically modulated by different specific tasks (Northoff et al. 2010; Tung et al. 2013). Thus, the neural response to a VCI task and its relation to intrinsic brain activity should be comprehensively investigated to identify the neural basis of visual creativity. In this study, we investigated the neural response to VCI manipulation and its relations with intrinsic brain activity in pre-, on-, and post-task stages.

Using a specific experimental design, we identified the brain regions that were activated by the VCI task. We then further applied the amplitude of fluctuation (AF) on different frequency domains (0–0.05, 0.01–0.08, 0.05–0.1, 0.1–0.15, 0.15–0.2, and 0.2–0.25 Hz) to determine the spontaneous brain activity, the modulation effect of the VCI task on the pre-task resting state, and whether the modulation effect could last during the post-task resting state. In addition, we applied the Granger causality analysis (GCA) which is an operative approach basing on the simple idea that causes both precede and help predict their effects to measures the causal influence and the flow of information related to the dynamic neural interactions that underline the modulation effects.

Materials and methods

Participants

We recruited 16 right-handed, healthy undergraduates (8 M/8F, 20 ± 1.34 years) for this study from South China Normal University (SCNU), Guangzhou, China. All participants had normal or corrected-to-normal vision, and none of the participants had a history of neurological or psychiatric disease, according to self-reports. Written informed consent was obtained from each participant, and this study was conducted in accordance with the Declaration of Helsinki and approved by the Institutional Review Boards at SCNU.

Experimental design and procedure

The experiment comprised 3 sections, i.e., the pre-task resting-state fMRI (R-fMRI) scan, the task-fMRI (T-fMRI) scan, and the post-task R-fMRI scan (Fig. 1a). The pre-task R-fMRI scan lasted for 6 min, in which all participants were asked to lie in the scanner in a supine position with their eyes fixated at the black cross on the screen. The T-fMRI scan contained two 12-min stimuli, in which the participants were asked to complete a VCI task and a contrast control task. The two tasks were randomly matched among the participants, and each task contained 18 trials. The post-task R-fMRI scan also lasted for 6 min, in which the participants performed the same protocol as the pre-task R-fMRI scan.

Stimuli and tasks

In the VCI task, we used 18 simple pictures, which had been employed by Finke and Slayton (1988). Each picture contained 3 simple line-shape items, such as a cuboid, cylinder, annulus, and cone. The participants were required to create unique and valuable products that belonged to one of 6 categories (e.g., toys, office supplies, furniture, sports goods, accessory, and building) using 3 of the previously described items. Each category was repeated 3 times; however, the raw items were distinct each time. All pictures were presented with a black line in a white background at a size of 680 × 400 pixels. Each picture was presented only one time (Fig. 1b).

The stimuli of the control task were the same as Aziz's study (Aziz-Zadeh et al. 2012). Eighteen pictures were synthesized by decomposing 3 normal shapes (e.g., triangle, square, and rectangle) into 3 parts, thereby rotating each part to angles based on each fixed peak of the part. Each original

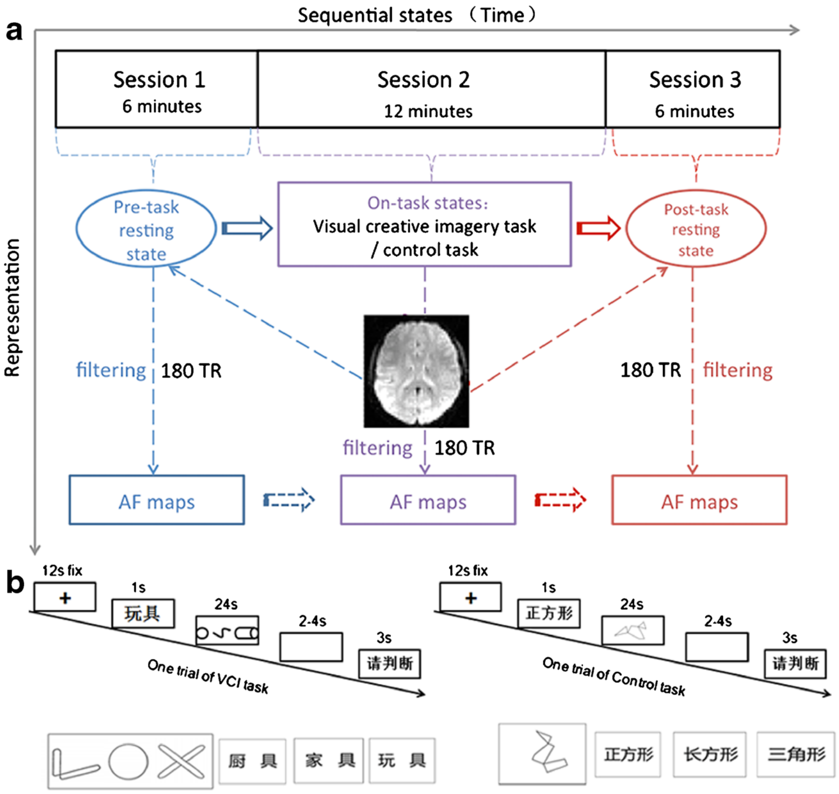

Fig. 1 Experimental procedure **a** task design and task materials **b**. Samples of the experimental materials and categories in the VCI task (*left button*) and control task (*right button*). Three sessions were conducted in this study, i.e., the pre-task resting state, two on-task states, and two post-task resting states. After data preprocessing, we extracted the last 180 time points from the two on-task states, together with the pre-task resting state and the two post-task resting states to calculate the maps of AF. This study implemented a within-participant paradigm that utilized a single event-related design in which all conditions (VCI, control, rest/fixation cross, waiting and assessment) were evenly distributed across two task fMRI runs

shape was transformed to 6 irregular forms according to congruent and incongruent conditions. Therefore, there were 18 transformed pictures presented to the participants in the control task.

In all experiments, the participants laid supine on the scanner bed and viewed visual stimuli back-projected onto a screen through a mirror attached onto the head coil. Foam pads were used to minimize the head motion. The stimulus presentation and timing of all stimuli were achieved using E-prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA). The participants were provided with task instructions and performed practice sessions on a laptop prior to the imaging session to ensure that they understood the detailed tasks and performed most tasks correctly. They were also informed that they needed to recall and portray the products they generated in the scanner for each task trial during the outside feedback session following the fMRI scanning session. In the scanning session, a trial presentation order that included a fix rest (12 s), followed by a VCI or control task cued category (0.8–1 s) and stimuli presentation (24 s), a jittered blank interval (2–4 s), and an assessment period (3 s) were maintained in both the VCI and control tasks. Each functional run included 18 trials and lasted for 770 s (385 TRs). The run order was randomly matched across the participants (Fig. 1b).

When the 3 simple items were viewed, the participants were asked to imagine types of creative goods that pertained to the category that was presented prior to the stimuli picture (cue start). For example, with the cue start of the category of “toy” followed by a 24-s viewing of three items of cylinder, wave, and circle, the participants would invent unique items that belonged to the “toy” category in their minds. They subsequently assessed the novelty and creativity level of the goods they invented by pressing the keys “1”, “2” on the left finger or “3”, “4” on the right side. Of note, “1–4” represented the lowest-level creative to a very creative degree. Accordingly, in the control task, the cue start was replaced with “rectangle”, “triangle”, or “square” with the corresponding decomposed line-shape pictures. When viewing these transformed shapes, the participants should rotate and reverse them in their minds to determine whether these ill-formed shapes may constitute the original shapes. If the reversed shape in mind was judged to be congruent with the cued category, the subjects should press the “1” key on the left finger; otherwise, key “4” was pressed on the right finger. The congruent and incongruent trials were balanced.

MRI acquisition

All imaging data were acquired on a 3.0 T Siemens Trio Tim scanner in the MRI Center at South China Normal University. A single-shot T2*-weighted gradient-echo, echo planar imaging (EPI) sequence was used for the functional imaging acquisition with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle =90°, field of view (FOV) = 224 × 224 mm^2, matrix =64 × 64, 32 slices, slice thickness = 3.5 mm, and voxel size =3.5 × 3.5 × 3.5 mm^3. Individual high-resolution brain structural images were acquired with a 3D multi-echo magnetization-prepared gradient echo (MP-RAGE) sequence.

Data preprocessing

The preprocessing of the task state imaging data was performed using SPM8 (Statistical Parametric Mapping, http://www.fil.ioin.ucl.ac.uk/spm). The first 5 volumes of the functional images were discarded to account for signal equilibrium and participant adaptation to the immediate environment. The remaining 380 images were preprocessed, which included slice timing, head motion correction and spatial normalization using the EPI template in a standard Montreal Neurological Institute (MNI) space (voxel size =3 × 3 × 3 mm^3), and smoothed with a 4-mm full-width at half- maximum (FHWM) Gaussian kernel. The data were high-pass filtered (1/128 s) to account for the effects of scanner drift.

The two R-fMRI scans, as well as the last 180 time points of the two T-fMRI scans underwent preprocessing using the Resting-State fMRI Data Analysis Toolkit (REST, http://www.restfmri.net) (Song et al. 2011) with the following steps: slice timing, realignment, normalization (using the EPI template), smoothing (6-mm FWHM), temporal filtering, detrending and regressing out of white matter signal as well as cerebrospinal fluid signal. The time course of head motions was obtained by estimating the translations in each direction and the rotations in each axis. All subjects included in this study met the criteria of the head motion less than 1.5 mm of displacement and 1.5 of rotation in any direction. Of note, a frequency domain analysis was used in the temporal filtering step. The entire frequency band below the Nyquist frequency was examined in the frequency domain analyses. The Nyquist frequency represents the highest frequency of a sampled signal that is reliably recorded and is equal to half the sampling frequency of the signal (Nyquist 1928). Here, this value is (1/2) × (1/TR) = 0.25 Hz. We thus divided the entire frequency band into five sub-frequency domains: 0–0.05, 0.05–0.1, 0.1–0.15, 0.15–0.2 and 0.2–0.25 Hz and then additionally included the domain 0.01–0.08 Hz due to previous groups having explicitly studied it (Boccia et al. 2015; Yuan et al. 2014).

AF calculation

We computed the AF in the 6 sub-frequency bands using Rest (http://www.restfmri.net). The AF calculation procedure was the same as previous studies (Yan et al. 2009; Yang et al. 2007; Yu-Feng et al. 2007). For the calculation, the time course of each voxel was initially converted to the frequency domain using a Fast Fourier Transform (FFT), and the power spectrum was obtained. Since the power of a given frequency is proportional to the square of the amplitude of this frequency component in the original time series in time domain, the power spectrum obtained by FFT was square rooted and subsequently averaged across the predefined frequency interval at each voxel. This averaged square root was referred to as the AF at the given voxel and was further divided by the mean AF value within a brain mask for normalization purposes. The brain mask utilized comprised the normalized whole brain mask inset in the package of REST software of BrainMask_05_61 x73x61.

Granger causality analysis (GCA)

In this study, we performed a voxel-wise GCA on the signed-path coefficient-based *F* (H. Chen et al. 2009), using GCA (Zang et al. 2012) integrated on REST (Song et al. 2011), to investigate the directed "information flow" (Seth et al. 2015) between the region of interest (ROI) and all other voxels in the brain in each subject for the pre-, on- and post-task states of the VCI task, respectively.

The data preprocessing of these states was the same as the AF calculation; however, it only filtered on the frequency bands of interest. That is, the data preprocessing procedure of these states was the same as the AF calculation except for the filtering step. In the frequency domain analysis, we filtered the data with all six sub-domains, whereas GCA was only performed upon the frequency bands with significant modulation effect (0.01–0.08 Hz and 0.2–0.25 Hz in this study). A spherical ROI was placed at the modulated region (for instance, the right IFGtriang in the frequency band of 0.01–0.08 Hz), centered at x = 54, y = 27, and z = 12 with a radius = 5 mm. The preprocessed mean time course of the ROI was defined as the seed time series x, and the time series y denotes the time series of all voxels in the brain. The linear direct influence of x on y ($F_{x \rightarrow y}$) and the linear direct influence of y on x ($F_{y \rightarrow x}$) were calculated voxel by voxel in the brain (Hamilton et al. 2011; Liao et al. 2011). Thus, 2 Granger causality maps were generated based on the influence measures for each subject. The autoregressive order was one, and no covariate was used. The coefficients of the models were calculated using a standard least squares optimization.

Statistical analysis

Task activation

The general brain activation related to the VCI and control tasks was analyzed with the contrast of each condition against the implicit baseline, respectively: VCI > 0 and Control >0. At the second level, a random effects analysis was performed via the computation of a one-sample *t*-test for the subject-specific statistical parametric maps obtained at the first level. All reported activations were family-wise-error (FWE) corrected for multiple comparisons at the cluster level with an intensity threshold of $p < 0.05$ and an extent voxel size threshold of 30 voxels. The FWE correction procedure was performed using the formula integrated in SPM, which threshold the resulting T-statistic images by using the minimum given by a Bonferroni correction and Random Field Theory (RFT).

To generate the VCI task-specific brain activation related to the control task, we computed the contrast of the VCI and control tasks: VCI > control. The voxel-based results for this specific task effect are reported using a conservative criterion, i.e., for clusters with a cluster size of k > 30, the data were significant at a level of $p < 0.05$ (FDR corrected).

Modulation effect of VCI tasks

For each state, AF maps for each participant were computed according to the different frequency bands. A paired *t*-test was performed to determine the AF difference between the on-task state and pre-task state in 6 frequency bands, respectively, (VCI task state) - (pre-task resting state). The resultant statistical maps were set at a combined threshold of $p < 0.05$ (FWE corrected), and the minimum cluster size was 30 voxels. To determine the AF difference between the two conditions, we conducted paired *t*-tests between the two task states: VCI - control. Furthermore, paired *t*-tests between the pre- and post-task resting states were also taken into consideration to assess whether the task modulation effect would last in the post-task resting states: (post-VCI task resting state) - (pre-task resting state). For the paired *t*-tests, we adopted a small volume correction (SVC), in which the voxels with an intensity threshold of $p < 0.05$ and an extent voxel size threshold of 10 voxels were considered significantly different between the two conditions (FWE corrected). The modulated region derived from the paired *t*-test between on-task state and pre-task resting state was masked to perform the SVC.

GCA maps of three states of the VCI task

Six group-level Granger causality maps were obtained as 2 conditions multiplied by 3 states, i.e., the right IFGtriang with $F_{x \rightarrow y}$ and $F_{y \rightarrow x}$ for the pre-, on- and post-task states of the VCI task. Prior to performing statistical tests, a z-transformation was performed to the coefficient-based *F* individually. One sample *t*-tests against zero were subsequently performed on the *Z* score on a voxel level, and the significance threshold was corrected for a two-tailed false discovery rate (FDR, $p < 0.05$, a minimum cluster size of 30 voxels).

Validation analysis

To determine whether the control task also exhibited modulation effects, namely, to test the specificity of the VCI task modulation effect, we repeated all data analyses regarding the VCI task for the control task. Paired *t*-tests were performed to determine the AF difference between the on-task state and pre-task state (FWE corrected, $p < 0.05$, $k > 30$), as well as the pre- and post-task resting states of the control task in 6 frequency bands (SVC, $p < 0.05$, $k > 10$). In addition, we also investigated whether the modulation effect of the VCI task in the low frequency band was also demonstrated in the high frequency band, i.e., the specificity of the frequency band.

Results

VCI task-related brain activity

The VCI task manifested its activation in the left MFG, the left superior parietal gyrus (SPG), the left middle occipital gyrus (MOG), the left lingual gyrus (LING), the right cerebellum cortex, and the right calcarine fissure and surrounding cortex (Table 1 & Fig. 2a) (Farah et al. 1988). In contrast, the control task mainly activated the right CAL, the right MOG, the right inferior parietal lobe (IPL), and the bilateral SPG (Table 1 and Fig. 2b). Compared with the control task, the VCI task specifically activated the left IFGtriang, the right SFG in the PFC, and the temporoparietal areas, including the left superior temporal gyrus (STG) and the left inferior temporal gyrus (ITG), as well as the bilateral SPG, the right precuneus, the left postcentral gyrus, and the left supramarginal gyrus (SMG) (Table 1 & Fig. 2c). Furthermore, we identified the co-activation pattern of the occipital (left IOG, right CAL) cortex and the parietal cortex (right SPG, left IPL), as well as the PFC (left SFG) in the conjunction analysis (Table 1 & Fig. 2d).

The VCI task modulation on pre-task resting state

A subtraction analysis on the AF between the VCI task state and the pre-task resting state was implemented to investigate the significant modulation effect of the VCI task in the pre-task resting state (FWE corrected, $p < 0.05$, Fig. 3a). For the VCI task, significantly increased AFs in the on-task state were identified in the right IFGtriang in all three low-frequency bands (< 0.1 Hz), i.e., the amplitude of low-frequency fluctuation (ALFF). Significantly increased AFs were also identified in the right SMG and the left angular gyrus (ANG) in the frequency band of 0.01–0.08 Hz. Furthermore, a salient modulation effect was identified in the frequency bands of 0.2–0.25 Hz, in which significantly increased AFs were detected in the left caudate nucleus (CAU) in the VCI task state.

ALFF difference between two on-task states

A significantly increased AF in the right IFGtriang was identified in the VCI on-task state compared with the control task in the frequency band of 0.01–0.08 Hz (FWE corrected, $p < 0.05$, SVC). The right SMG and the left ANG were also the modulated regions of the VCI task in this frequency band. Furthermore, we also performed the subtraction analysis between the VCI task and the control task on the frequency band of 0.2–0.25 Hz. As a result, the VCI task exhibited significantly increased AFs in the right IFGtriang and the left CAU compared with the control task (FWE corrected, $p < 0.05$, SVC; Fig. 4).

Post effect of modulation

We performed a comparison between the post- and pre-VCI task resting states. The same reliable result was demonstrated as previously described in the VCI task, namely, the post-task resting state exhibited significantly increased AF in the right IFGtriang in the low frequency band of 0.01–0.08 Hz and the left CAU in the high frequency band of 0.2–0.25 Hz (FWE corrected, $p < 0.05$, SVC)(Fig. 4). Nevertheless, the previously described findings were not demonstrated in the comparison between the pre-task resting state and the post- resting states of the control task.

GCA results

The result of the one sample *t*-test on the signed-path coefficients of the different states in the frequency of 0.01–0.08 Hz is presented in Fig. 5. In the pre-task resting state, the right IFGtriang exhibited increased effective connectivity with the right cerebellum crust, the right ITG and the right precuneus lobule, as well as decreased effective connectivity with the right cerebellum crust (Fig. 5a). Furthermore, the right IFGtriang manifested a significantly positive causal effect on the left SFG and the right cerebellum crust in the on-VCI task state. However, the left MFG and the right SFG median part (SFGmed) exhibited a significantly negative causal effect on the right IFGtriang (Fig. 5b). In the post-VCI task resting state, the right IFGtriang exhibited significantly positive casual effects on the left MTG and the left SFG in contrast to a significantly negative effect on the right Cerebellum crust (Fig. 5c).

Validation findings

We validated the specificity of the stable modulation effect of the VCI task by determining whether the modulation effect also occurred and was steadily effective in the on-task state and post-task resting state of the control task. Compared with

Table 1 Brain regions activated by the VCI and control tasks and their relations

Regions		Broadman Area	Peak MNI coordinate			*t* value
			x (mm)	y (mm)	z (mm)	
I - F (FWE, $p < 0.05$, k ≥ 30)						
Cerebellum	Cerebelum_CruR	0	36	-57	-33	10.87
Occipital	Lingual_L	18	-12	-87	-12	12.05
	Calcarine_R	18	15	-93	0	12.08
	Occipital_Mid_L	19	-27	-84	30	10.12
Parietal	Parietal_Sup_L	7	-21	-63	45	12.08
Prefrontal	Frontal_Mid_L	6	-24	0	57	10.31
C - F (FWE, $p < 0.05$, k ≥ 30)						
Occipital	Calcarine_R	17	12	-93	0	13.95
	Occipital_Mid_R	18	30	-90	12	10.33
Parietal	Parietal_Inf_R	2	45	-33	45	12.46
	Parietal_Sup_L	7	-24	-66	54	12.83
	Parietal_Sup_R	7	21	-66	51	14.07
I - C (FDR, $p < 0.05$, k ≥ 30)						
Occipital	Lingual_L	18	-12	-72	-9	8.42
	Calcarine_L	30	-3	-54	6	7.10
Temporal	Temporal_Inf_L	48	-42	-12	-3	6.14
	Temporal_Sup_L	32	-42	-12	-3	8.03
Subcortical	Insula_R	48	36	6	3	6.99
	SupraMarginal_L	32	-48	-30	24	8.04
Parietal	Precuneus_R	79	24	-45	0	10.83
	Parietal_Sup_R	103	24	-54	60	15.94
	Parietal_Sup_L	202	-15	-78	48	19.26
	Postcentral_L	80	-33	-36	66	13.30
Prefrontal	Frontal_Inf_Tri_L	6	-39	27	6	9.37
	Frontal_Sup_R	133	24	-9	66	10.83
I ∩ C (FWE, $p < 0.05$, k ≥ 30)						
Occipital	Occipital_Inf_L	37	51	-66	-15	7.86
	Calcarine_R	18	15	-93	0	11.13
	Occipital_Mid_L	17	-15	-102	3	10.30
Subcortical	Pulvinar	-	24	-27	6	8.90
Parietal	Parietal_Sup_R	7	21	-66	51	9.25
	Parietal_Inf_L	40	-39	-45	48	10.78
Prefrontal	Frontal_Sup_L	6	-21	0	57	8.42

I-F, the subtraction analysis between the VCI task and basic fixation condition ("imagery" – "fixation"); C-F, the subtraction analysis between the control task and basic fixation condition ("control" – "fixation"); I-C, the subtraction analysis between the VCI task and control task ("imagery" – "control"); I ∩ C, the conjunction analysis between the VCI task and control task ("imagery" ∩ "control"). L, left hemisphere; R, right hemisphere

the pre-task resting state, the left MOG exhibited a significantly increased AF in the frequency band of 0.01–0.08 Hz, whereas the left SPG demonstrated a significantly increased AF in the frequency band of 0.05–0.1 Hz in the on-task state. In addition, in the frequency band of 0.2–0.25 Hz, a significantly increased AF in the right cerebellum cortex was identified (FWE corrected, $p < 0.05$, Fig. 3b).

We validated the frequency domain specificity of the VCI task modulation effect by determining whether the modulated region in the high frequency (i.e., the left CAU) also constructed effective connectivity within the whole brain. We utilized the left CAU as the seed with the coordinate centered at $x = -6$, $y = 6$ and $z = -3$ and a radius = 5 mm to conduct the sigh-path voxel-wise GCA. However, there was no significant effective connectivity among the left CAU and the other voxel in the brain with the same threshold of $p < 0.05$ and the minimum voxel size of 30 voxels (FDR corrected) as performed in the low frequency band analysis.

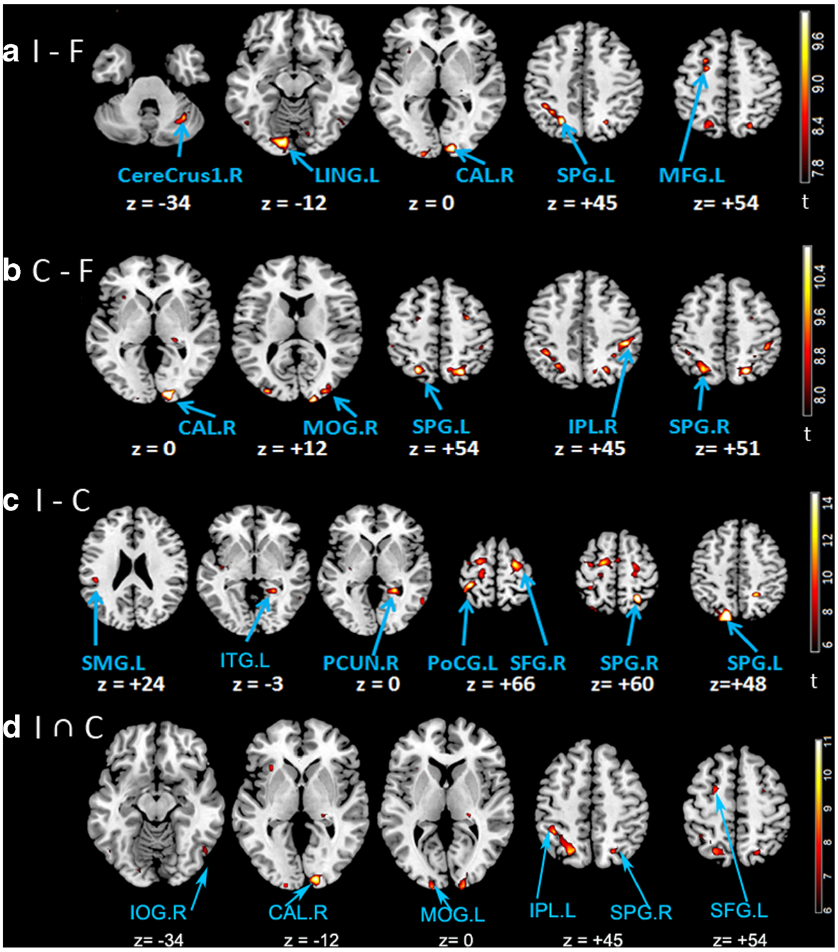

Fig. 2 Overview of the cortical activation maps. Panel **a** the main effect of the VCI task projected on the MNI-brain with a threshold of $p < 0.05$, FWE corrected. Panel **b** the same as panel A but for the control task. Panel **c** the results of the contrast "VCI task – control task" with $p < 0.05$, FDR corrected, one-tailed. Panel **d** the conjunction results of the VCI task and control task ($p < 0.05$, FWE corrected). I-F, the subtraction analysis between the VCI task and basic fixation condition ("imagery" – "fixation"); C-F, the subtraction analysis between the control task and basic fixation condition ("control" – "fixation"); I-C, the subtraction analysis between the VCI task and control task ("imagery" – "control"); I ∩ C, the conjunction analysis between the VCI task and control task ("imagery" ∩ "control"). L, left hemisphere; R, right hemisphere

Discussion

In this study, we adopted a VCI task to investigate the neural response to visual creativity and its relation to intrinsic brain fluctuations in the resting state. The main findings may be summarized as follows: (1) the VCI task specifically activated the PFC (i.e., the left IFGtriang and the right SFG) and temporoparietal areas (i.e., the left STG & ITG, the bilateral SPG, and the right precuneus); (2) the VCI task significantly modulated the intrinsic brain fluctuation amplitude of the right IFGtriang and the left caudate nucleus, and the modulation effect was frequency dependent; (3) an inhibitory effect (negative correlation) may exist from the left SFG to the right IFGtriang in the on-VCI task state, whereas this effect shifted to an excitatory effect (positive effect) in the post-VCI task state.

Brain response to VCI manipulation task

The present study identified the activation patterns of the VCI task compared with the control task. First, we determined that both the VCI and control tasks activated the brain regions associated with visuospatial processing and mental imagery, including the bilateral SPG, the insula and the occipital cortexes. These regions have been implicated in mental rotation tasks (Ng et al. 2001). Specifically, the activation of the left SPG and the right calcarine sulcus has been associated with simple mental imagery and the visuospatial synthesis of objects (Milivojevic et al. 2009). These findings were consistent with the essence of the present task manipulation demands. Furthermore, by contrasting the VCI and control tasks, we further demonstrated that the VCI task specifically activated the right SFG and left IFGtriang of the PFC and the temporoparietal areas (i.e., the left STG & ITG, the left SMG, the left postcentral cortex, the right precuneus and the bilateral SPG) (Table 1 and Fig. 2). These regions, nearly all of which involved the temporoparietal cortex, belong to the default mode network (DMN), which involves the left ITG, the left SMG, the right precuneus, the left postcentral gyrus (Raichle and Snyder 2007) and the bilateral SPG (Roger E. Beaty et al. 2014). The DMN is characterized by its deactivation during task performance; however, previous studies have demonstrated that the DMN was tightly associative with mental

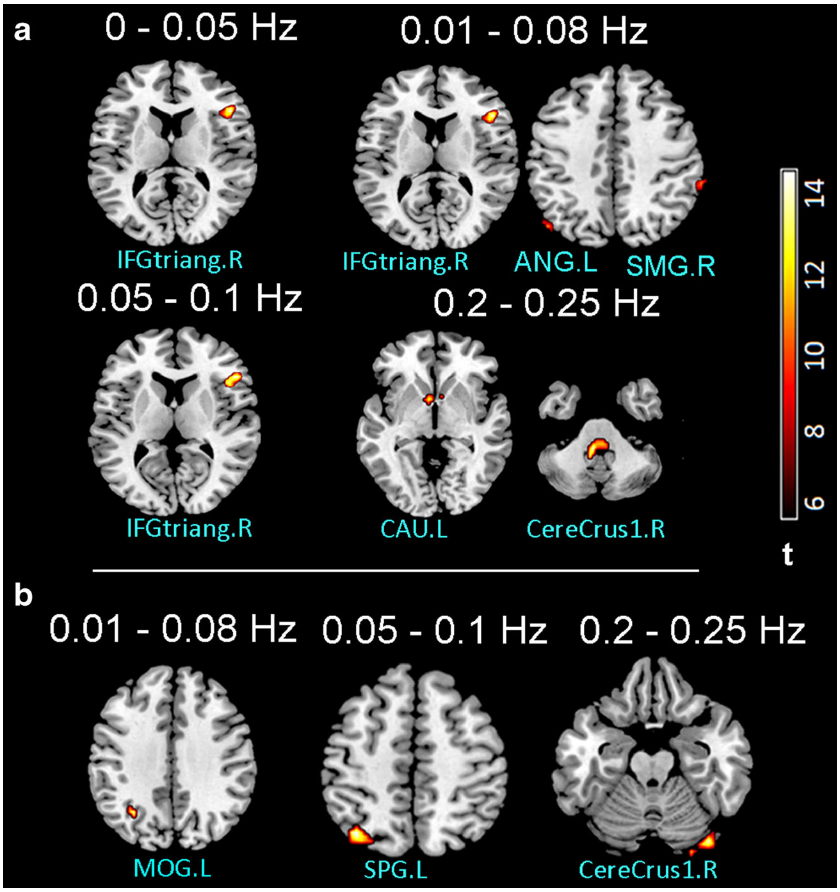

Fig. 3 Modulation effect on AF of the VCI task state **a** and control task state **b** in the pre-task resting state that pertained to different frequency domains. FWE corrected, $p < 0.05$, cluster size >30 voxels. L, left hemisphere; R, right hemisphere

phenomena, including episodic future thinking (Schacter et al. 2012), perspective-taking (Andrews-Hanna 2012), and mind wandering (Buckner and Carroll 2007). In addition, we also demonstrated that the activation of the left temporoparietal regions (which mostly belonged to the DMN) for the specific VCI task was consistent with previous studies, which highlighted the substantial function of idea generation of the DMN in creativity (Roger E Beaty et al. 2015; Roger E. Beaty et al. 2014; Naama Mayseless et al. 2014). Furthermore, another observation was that the PFC was significantly activated by the VCI task. The PFC has been implicated in higher cognitive functions, such as planning, problem solving and cognitive flexibility (Boccia et al. 2015; Q. Chen et al. 2014; H. R. Park et al. 2015). As a part of a control network, the PFC is well poised to facilitate the evaluation and judgment of the appropriateness of a novel idea, as well as the implementation of goal-directed plans (Dietrich 2004), which was involved in the VCI task and has been documented in many previous studies (Michael W Cole et al. 2013; de Souza et al. 2014; Gonen-Yaacovi et al. 2013). Together, regarding the brain activation aspect, the present study demonstrated the broad involvement of high-level brain regions related to visuospatial switching and cognition control/evaluation in the VCI manipulation task. This finding may be supported by the twofold processes of creativity, namely, the idea generation and evaluation processes (Basadur et al. 1982; Finke et al. 1992), which are widely considered a considerable model to explain the creativity process by many researchers (Cassotti et al. 2016; Pan and Yu 2016; Sowden et al.

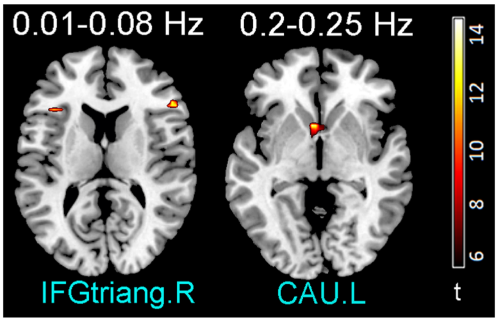

Fig. 4 Results of contrasting VCI task with control task on the AF in the frequency bands of 0.01–0.08 and 0.2–0.25 Hz. Z1 and Z3: the AF maps were significantly different between the on-VCI and control tasks at 0.01–0.08 and 0.2–0.25 Hz, respectively; Z2 and Z4: the AF maps were significantly different between the post- and pre-VCI task resting state at 0.01–0.08 and 0.2–0.25 Hz, respectively. The MNI coordinates of Z1, Z2, Z3, and Z4 are (51, 30, 12), (54, 27, 12), (−6, 12, −3), and (−6, 9, −3), respectively. FWE corrected, $p < 0.05$, cluster size >10, SVC. L, left hemisphere; R, right hemisphere

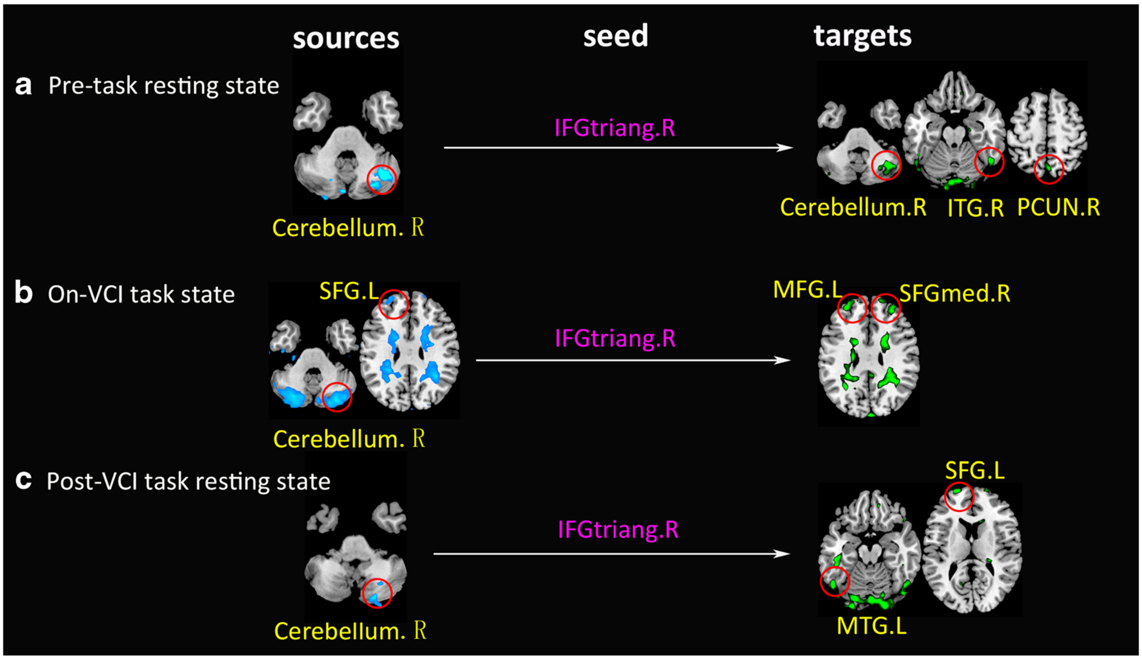

Fig. 5 GCA results regarding the 3 states of the VCI task. Regions in *blue* indicate the sources of the information flow (negative causal effect), whereas regions in green indicate the targets of the information flow (positive causal effect). The right IFGtriang in pink indicates the seed region. Panel **a** represents the influence flow in the pre-task resting state, panel **b** represents the On-VCI task state, and panel **c** represents the post-VCI task resting state

2015). Thus, these findings indicated the appropriateness and rationale of the VCI manipulation design to reflect the visual creativity process.

VCI task modulates the intrinsic brain activity

By investigating the alteration of the brain activity between the VCI task state and resting states, we attempted to identify the neural relation of the brain response to the VCI task and the intrinsic brain activity because the neural activity evoked by the VCI task was based on the spontaneous brain activity. Our results demonstrated that the VCI task specifically modulated the amplitude of fluctuation of the right IFGtriang in the frequency band of 0.01–0.08 Hz and the left caudate nucleus in the frequency band of 0.2–0.25 Hz (Fig. 3a). In addition, the modulation effects were different between the VCI and control tasks, which suggests the specificity of the modulation effect of the VCI task on the intrinsic brain activity. More importantly, the modulation effect of the VCI task was strongly and stably maintained in the post-task resting state (Fig. 4), which was not identified in the control task states. Nevertheless, the validation results supposed that the modulation effect of the control task did not exhibit the stableness between the different frequency domains or the post effect. Notably, the present study indicated that the right IFGtriang, the key sub-region of the PFC, was a modulated region of the VCI task in the pre-task resting state. In contrast, we identified vigorous activity in the left IFGtriang in the VCI-specific activation pattern (Table 1 & Fig. 2). Some studies may support the predominantly left-hemisphere activation, specifically the left IFG, of visual creativity (Aziz-Zadeh et al. 2012; Roger E Beaty et al. 2015; Roger E. Beaty et al. 2014); however, a recent meta-analysis of neurological research on creativity pointed towards general right hemispheric superiority in visual creative thinking and idea generation (Mihov et al. 2010). More specifically, the right IFG has been implicated in figural creativity (Benedek et al. 2014b; Shah et al. 2013; Zhao et al. 2014). Consistent with recent findings, the present study provided further evidence for the important role of the right IFGtriang in visual creativity performance. In addition, the basal ganglia was also demonstrated to be vital in creative cognition, which may modulate the association between creativity and the dopaminergic systems (Reedijk et al. 2013; Takeuchi et al. 2013).

An important finding of the present study was that the modulation effect was frequency dependent. Specifically, the modulation effect of the VCI task on the cerebral cortex (e.g., the right IFGtriang) was identified in the low-frequency band (< 0.08 Hz), whereas the effect of the sub-cortex (i.e., the left caudate nucleus) was sensitive to the high-frequency bandwidth (0.2–0.25 Hz). Furthermore, the validation analysis demonstrated the low frequency-dominance of the modulation effect. It is easy to interpret the modulation effect of the cerebral cortex identified in the low-frequency band because many previous studies have demonstrated that the neural signals carried in the low-frequency band are informative and vital to both the resting state and task state (Michael W. Cole et al. 2014; Tavor et al. 2016). Ongoing, large-scale neural activity in the low-frequency band is no longer considered noise; instead, it comprises a highly structured activity that may shape stimulus-evoked neural responses (Arieli et al. 1996; He 2013) and perceptual performance (Boly et al. 2007; H.-D. Park et al. 2014; H. R. Park et al. 2015; Sadaghiani and Kleinschmidt 2013). Adversely, the resting state pattern may be modulated or reshaped by specific task-evoked activity (Cousijn et al. 2014; Pyka et al. 2009). Moreover, this study demonstrated that the modulation effect of the VCI was also present in the left caudate nucleus in the frequency band of 0.2–0.25 Hz; consistent with this finding, previous studies have indicated that the signal power of the limbic and paralimbic regions (i.e., the caudate nucleus) is mainly located in high-frequency bands (Baria et al. 2011; Zuo et al. 2010). Furthermore, high-frequency fluctuations of resting state fMRI signals may be modulated by different states and may thus be of physiological importance (Yuan et al. 2014). Therefore, the current findings may also indicate that the VCI task modulation effect is not related to a single frequency band but rather a distinct oscillatory activity.

Inter-hemisphere effective connectivity

GCA provides a powerful and generic statistical tool for characterizing directed functional interactions from time-series data, and it has the potential to shed directive light on the functional circuits that underlie perception, cognition and behavior (Seth et al. 2015). GCA is one methodology used to calculate the effective connectivity, which explicitly refers to the influence that one neural system exerts over another system at a synaptic or population level (Friston 1994, 2011). Thus, the effective connectivity may indicate the relationship of modulating or being modulated between two neural systems. Thus, we performed the GCA procedure with the right IFGtriang as the seed because of the observation of its modulation effect in the low frequency band. As shown in Fig. 5, during the on-VCI task state, the influence exhibited negative effective connectivity between the left SFG and the right IFGtriang; however, positive effective connectivity with the right IFGtriang was identified in the left MFG and the right SFGmed. The excitatory and inhibitory effects may constitute a feedback circuit, considering the positive causal effect could be interpreted as an excitatory effect and the negative causal effect comprised an inhibitory effect (Hamilton et al. 2011). Of note, these activated regions are task-related, i.e., the left SFG comprised the co-activated region detected in the conjunction analysis, whereas the left MFG was activated when contrasting the VCI task with the fixation condition and the right SFG demonstrated in the activation pattern of the VCI contrast control task. In addition, the excitatory effect may suggest a modulation effect from the right IFGtriang to both the left MFG and the right SFGmed, which may explain their activations during task performance. However, with the help of the GCA procedure, we identified the underlying functional circuit of the VCI task that may depend on the right IFGtriang as the information transfer station. In the subsequent post-task resting state, information flows exhibited an excitatory effect from the right IFGtriang to the left SFG, which was in contrast to the inhibitory effect in the on-VCI task state and formed an intact circuit. This result may be further interpreted that, to a certain degree, the left SFG "released" its inhibitory control on the right IFGtriang following the VCI task. Thus, reconfiguration of the post-task resting state brain oscillation occurred related to the VCI manipulation. It is also likely the consequence of the task modulation towards the resting state, namely, the VCI task may alter the spontaneous left-over-right inhibitory mechanism originally in the resting state. Nevertheless, in the pre-task resting state, the influence circuit only interacted in the right hemisphere between the regions of the right cerebellum, the right MTG and the precuneus. These observations would further confirm our former result regarding the important role of the right IFGtriang for visual creativity, whereas the left PFC exhibited the role for inhibitory control.

Lesion studies that involved creativity tasks have indicated that brain damage in the left hemisphere, particularly the left PFC, has been associated with increased creativity (Naama Mayseless et al. 2014; Shamay-Tsoory et al. 2011). These reports indicate that damage to the left frontal area, including the left IFG, may have a "releasing effect" on creative production, which suggests that these regions are implicated in creativity and may actually "inhibit" creativity, potentially by imposing inhibitory control over the process. Considering its positive activation during task performance, the left IFGtriang comprises a potential source of the inhibitory control, which has been reported in a previous study (Swick et al. 2008). The paradoxical effect that brain damage onset to the left PFC cortex may increase creativity has been referred to as paradoxical functional facilitation (PFF) by Kapur et al. (1996, 2013). The authors proposed that the PFF may be attributed to an inhibitory mechanism based on the completion among different brain regions or a compensation enhancement that results from neural plasticity. Under the inhibitory mechanism, the right hemisphere predominance in creative thinking may be inhibited by the contralateral hemisphere region in normal individuals; however, it may be disinhibited after damage to the left brain regions (Zaidel 2014). Under the compensation enhancement, regions of the right hemisphere may subsume the functions of the damaged areas, which causes more information flow in localized brain areas and thereby boosts the original right brain functions. The spontaneous left-over-right inhibition mechanism would bias the real activation pattern result in the underestimation of the right hemisphere in visual creativity. Therefore, we suggest that it was far from comprehensive and appropriative to unfold the neural mechanism of creativity in normal individuals using a simple task activation analysis.

Transcranial direct current stimulation (tDCS), a noninvasive procedure that facilitates safe and transient alterations in neuronal firing, has been suggested to alter neuronal membrane potentials (Zheng et al. 2011); anodal tDCS induced increased cortical excitability, whereas cathodal tDCS has been associated with decreased cortical excitability (Nitsche et al. 2003; Nitsche and Paulus 2001). Mayseless and Shamay-Tsoory (2015) used tDCS to modulate the activity of the right and left IFG in verbal and figural creativity-related tasks; they determined that increased creativity in verbal divergent thinking tasks was present only when cathodal stimulation was implemented over the left IFG coupled with anodal stimulation of the right IFG. However, no effect on divergent thinking was identified using the opposite montage. Furthermore, they conducted a second experiment to investigate the effect of cathodal stimulation over the left IFG alone, as well as the effect of right IFG anodal stimulation alone. The findings indicated that stimulation that independently targeted the left or right IFG did not result in changes in creativity, which verified that altering creativity requires both decreased activity in the left IFG and increased activity in the right IFG. This study provided an externally operational interference to help better understand the relationship between the left and right IFG to identify the mechanism of creativity. We considered that our result could be explained and supported by the spontaneous left-over-right inhibitory mechanism because we determined that the left IFGtriang was activated when contrasting the VCI task with the control task; however, the VCI task only modulated the right IFGtriang in the resting state.

Further consideration and future directions

There were several considerations to interpret the present findings. This study recruited sixteen undergraduates to take part in the VCI task mainly with the following considerations. Undergraduates are the majority who exhibited preferable creativity behavior, and the ability of creative thinking is important either to their current studies or future careers. It is valuable to detect the neural mechanism of visual creativity and to search for some effective training. As we expected, the present findings indicate the tight linkage of the visual creativity imagery manipulation task with intrinsic brain activity, which may facilitate an understanding of the neural substrate of visual creativity. This study may enrich the research field about the interaction and the modulation effect between specific task-induced brain neural patterns and the intrinsic brain activity. It is insightful and valuable to help understand human visual creativity and to give a hint about oriented training or teaching direction in high education. Of course, we also realized that the present findings should be further validated on other populations such as the children and elders, to figure out the generality and specificity of the present findings. This study is a preliminary study regarding creativity researches to investigate the neural activity of this type of task and its relationship with the intrinsic brain activity.

The present study is limited in term of the inability to capture participant responses in the scanner, which would have shed light on task compliance and further permitted parametric analysis of brain activity related to the creative quality of response. Yet the high consistency between the present findings of this study and previous studies, suggests that participants were indeed engaged in visual creative imagery during the task. This study was also limited to the use of a single assessment (the VCI task) to indicate a rather broadly defined construct (visual creativity). Future research should examine amplitude of fluctuation among brain regions during other creative thinking tasks and in relation to creative performance in specific domains, such as musical improvisation (auditory creativity) and creative writing (verbal creativity). This approach would shed light on whether the left-over-right inhibitory mechanism is exclusive to visual creativity, or whether such an inhibition effect reflects a domain-general mechanism underlying a range of creative thought processes.

To the best of our knowledge, the existence of a relationship between mental imagery and visual creativity has been suggested by many studies (Daniels-McGhee and Davis 1994; Le Boutillier 1999; LeBoutillier and Marks 2003). Some studies have investigated the relationship between creativity and spatial visualization ability (i.e., performance on tests that measure the ability to transform and manipulate spatial images) (Blazhenkova and Kozhevnikov 2010), as well as the ability to present pictorially visual images (e.g., vividness of imagery) (Kosslyn 1980; Kozhevnikov et al. 2013), whereas several studies have focused on the variance of the verbalizer-visualizer cognitive style (Palmiero et al. 2015; Palmiero et al. 2016). The current findings indicated the involvement of the mental rotation task-related regions in the VCI task; however, the detailed role of the mental imagery process in the VCI warrants further investigation. Future research should attempt to clarify whether visual creative cognition differs from other imaginative processes in terms of visual-spatial and executive involvement.

Many previous studies have shown the tight relationship between brain intrinsic activity and task performance, and these studies usually performed it within the low frequency domain of 0.01–0.08 Hz. Meanwhile, many studies also showed the functional implication of the different frequency bands of the intrinsic brain activity, such as the slow-4 and slow-5 (Han et al. 2011; Hou et al. 2014). In this study, we applied the amplitude of low frequency fluctuation (ALFF) metric which was usually defined within the low frequency domain of 0.01–0.08 Hz to explore the relation of brain intrinsic activity to the creativity task. Considering that the brain activities evoked by tasks are sensitive according to different frequency domains; cortical activity usually exhibited in low frequency while subcortical activity more sense in high frequency (Yuan et al. 2014). Therefore, we divided into six subfrequency bands to study neural mechanism in the whole frequency band to have a comprehensive observation of the cognitive process of visual creative imagery. A recent research study indicated that creativity is increased by enhancing alpha power using 10 Hz transcranial alternating current stimulation (10 Hz-tACS) of the bilateral frontal cortex when performing the TTCT-figural task (Lustenberger et al. 2015). The present study demonstrated that the modulation effect was frequency dependent; however, the modulation effect on the other frequency bands (> 0.25 Hz) remains largely unknown. Thus, other imaging techniques, such as EEG and MEG, should be employed to investigate this issue. Also, the resting state and the task state were combined to assess the modulation effect using the frequency analysis approach. Many previous studies have demonstrated that the long continuous task state, such as the resting state, was available for frequency analysis. They assessed that to acquire the low-frequency information, a prolonged continuous state (e.g., an event-related design) and a fixed inter-stimulus interval (ITI) should be used in the experimental design. However, most fMRI studies have used random or pseudo-random ITIs to optimize the event-related fMRI design. In the block design, a scanning session has an intrinsic periodicity caused by the alternating blocks (e.g., task blocks and rest blocks presented every 24 s). Therefore, it is difficult to investigate the low-frequency components of fMRI signals in most conventional fMRI designs. Nevertheless, in our study, we used a within-participant paradigm that implemented a prolonged event-related design in which all conditions (VCI, control, fixation and assessment) were evenly distributed across two task fMRI runs. Both the VCI and control tasks lasted for 24 s and the fixation phrase lasted for 12 s in one trial, which were relatively prolonged compared with the conventional event-related design. In addition, to ensure the state for frequency analysis was a completely continuous phrase, we selected the last 180 TRs from the two task states to perform the frequency domain analysis, which also guaranteed the stability of the tasks. Furthermore, we believed that the mental state during creative imagery is quite similar to the resting state considering their shared characteristics of relaxation and mind wandering. Thus, in this study, we further investigated the different modulation effects of the task states to resting states in various frequency domains and determined that the low frequency fluctuation was the most sensitive band to the task-induced effect. The results indicated that the right IFGtriang modulated the on- and post-VCI task states in the low frequency band, which shed light on the cognitive necessity of the right IFGtriang in visual creativity from the perspective of the stimulus-rest interaction. However, further exploration is warranted for validation and reproducibility studies concerning alternative data processing and statistics analysis procedures.

Conclusions

This study investigated the brain response to a VCI manipulation task and its relation to intrinsic brain activity. The results indicated that the VCI task specifically activated the regions of the PFC and temporoparietal areas. Furthermore, the activation of the VCI task was significantly related to the intrinsic oscillations in the brain within a distinct frequency band. More importantly, the intrinsic dynamic interaction of the right IFGtriang may build the neural baseline of the VCI manipulation. These observations may facilitate an understanding of the neural essence of visual creativity performance.

Compliance with ethical standards

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Conflict of interest The authors declare that they have no competing financial interests.

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