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Network Neuroscience of Creative Cognition: Mapping Cognitive Mechanisms and Individual Differences in the Creative Brain

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Abstract

Network neuroscience research is providing increasing specificity on the contribution of large-scale brain networks to creative cognition. Here, we summarize recent experimental work examining cognitive mechanisms of network interactions and correlational studies assessing network dynamics associated with individual creative abilities. Our review identifies three cognitive processes related to network interactions during creative performance: *goal-directed memory retrieval*, *prepotent-response inhibitio*n, and *internally-focused attention*. Correlational work using prediction modeling indicates that functional connectivity between networks—particularly the executive control and default networks—can reliably predict an individual's creative thinking ability. We discuss potential directions for future network neuroscience, including assessing creative performance in specific domains and using brain stimulation to test causal hypotheses regarding network interactions and cognitive mechanisms of creative thought.

Keywords

creativity; default network; divergent thinking; executive control network; functional connectivity; network neuroscience

The cognitive neuroscience of creativity has made considerable progress by mapping brain networks involved in creative cognition. In a recent review of studies examining creative cognition and artistic performance, we reported a consistent pattern of functional network connectivity that was characterized by interactions between the Default Network (DN) and the Executive Control Network (ECN; [1]). The DN is a set of midline and posterior inferior parietal brain regions that support self-referential and spontaneous thought processes such as mind wandering, episodic and semantic memory retrieval, and mental simulation [2,3]. The ECN consists of lateral prefrontal and anterior inferior parietal regions that support cognitive control processes such as response inhibition, goal maintenance, and attention control [4]. Our previous review [1] proposed that, during creative task performance, the interaction of

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Conflict of Interest
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the DN and the ECN may reflect goal-directed, self-generated cognition, with DN involved in idea generation and ECN in guiding, constraining, and modifying DN processes to meet creative task goals (cf. [5–8]).

Despite signs of convergence in the literature, important questions remain: (a) What are the specific cognitive mechanisms that underlie network interactions during creative cognition? and (b) How might network dynamics relate to individual differences in creative thinking ability? The current review aims to update and extend the literature in light of several studies that have begun to address these questions. This research can be broadly categorized into experimental and correlational investigations, with experimental work largely focused on linking brain network interactions to specific cognitive mechanisms. Correlational work is further categorized into studies (a) using prediction methods to estimate individual creative ability from patterns of brain connectivity and (b) reporting correlations between various network properties and creative ability. We conclude the review by offering suggestions for future research to further isolate cognitive mechanisms and individual differences in the creative brain.

Cognitive Mechanisms and Brain Networks of Creative Cognition

Increasing behavioral and neuroimaging evidence suggests that creative cognition involves some aspects of cognitive control, including *goal-directed memory retrieval*: the ability to strategically search episodic and semantic memory for task-relevant information. A recent fMRI study [9] examined brain networks supporting episodic retrieval during divergent thinking. The study manipulated the kind of retrieval process engaged during creative cognition via an episodic specificity induction (ESI): brief training in recalling details of a recent event, which can prime or facilitate the involvement of episodic retrieval mechanisms in subsequent tasks, including creativity and imagination tasks (for review, see [10]). A behavioral study previously showed that ESI enhances divergent thinking performance on the AUT [11]. Consistent with this work, in the fMRI study [9], participants generated more novel and appropriate uses (i.e., flexibility measure on the AUT) following ESI compared to a control induction. Critically, functional connectivity analysis revealed stronger coupling between a cognitive control network and a core (default) network comprised of memory-related brain regions (hippocampus) after ESI than after a control induction. In this context, DN-ECN coupling appears to reflect goal-directed retrieval processes recruited to strategically search, select, and combine elements of past experience during divergent thinking.

Another cognitive control function linked to creative cognition is *prepotent-response inhibition:* the ability to suppress interference from dominant or salient response tendencies [12] such as obvious concepts or ideas that come to mind during divergent thinking [13]. In contrast to convergent thinking—which involves the discovery of the correct solution to a problem—divergent thinking measures people's ability to generate several possible solutions to a problem or prompt, such as thinking of novel uses for common objects, as in the Alternate Uses Task (AUT)[1]. Behavioral work [12] has shown that divergent thinking ability is strongly correlated with performance on response inhibition tasks, suggesting that creative individuals may be better able to suppress interference from competing concepts during divergent thinking.

In a recent fMRI experiment of pre-potent response inhibition [14], we examined brain networks underlying semantic interference in the context of the classic verb generation task. During the initial phase, participants studied a list of noun and verb pairs; during the second phase, participants were presented with studied ("high-constraint") and unstudied ("low-constraint") nouns and asked to "think creatively" while searching for uncommon verbs to relate to each noun [15]. We found that the semantic distance between nouns and verbs, assessed computationally via latent semantic analysis, was greater in the low-constraint compared to the high-constraint condition, likely due to greater interference from the prepotent (studied) verb response disrupting remote conceptual combination in the high-constraint condition. Critically, functional connectivity analyses revealed stronger functional coupling of anterior DN and left ECN regions in the high- than the low-constraint condition. These findings highlight another mechanism of DN-ECN coupling: the activation of a prepotent, automatic response via the DN (cf. [16]) and its inhibition via the ECN.

Creative cognition has recently been hypothesized to invoke a state of *internally-focused attention*: the focusing of attention on self-generated thought processes and the shielding of internal processes from external interference [17]. A recent study [18] sought to dissociate neural circuits supporting external vs. internal attention and divergent vs. convergent thinking. The direction of attention was manipulated by controlling how stimuli were presented during divergent and convergent thinking tasks. In one condition, stimuli were visible for the duration of a trial, allowing participants to continuously view the stimulus (i.e., "external attention" condition); in another condition, stimuli were presented very briefly at the beginning of the trial and thus required internal maintenance ("internal attention" condition). Compared to external attention, divergent thinking requiring internal attention was related to increased activity of the right anterior inferior parietal lobule (IPL), corresponding to a posterior hub of the ECN. Functional connectivity analyses further revealed stronger coupling between the right IPL and visual cortex in the internal condition. Thus, posterior ECN regions may play a role in directing attentional resources during divergent thinking by attenuating sensory input and focusing attention to internally-directed cognitive processes.

In sum, network neuroscience methods are beginning to provide insight into specific cognitive mechanisms related to network interactions during creative cognition. Figure 1 depicts the network interactions and corresponding cognitive mechanisms identified in the literature thus far. This work has demonstrated that DN-ECN coupling reflects both goal-directed episodic memory retrieval [9] and prepotent-response inhibition of semantic information [14]. Moreover, posterior ECN regions can interact with sensory cortices to attenuate external input and shield internal thought processes during idea generation [18]. Future research should continue to employ experimental paradigms to elucidate specific mechanisms underlying other modes of creative thought (e.g., figurative language

[1]AUT responses are commonly coded for fluency (i.e., total number of ideas), flexibility (i.e., total number of conceptual categories of ideas), and originality (i.e., creative quality of ideas).

production; [19]) and extend correlational findings using causal modeling to determine the direction of between-network information flow (cf. [20]).

Individual Differences in Brain Connectivity and Creative Ability

The past few years have seen a substantial increase in the number of studies examining how individual creative ability relates to variation in brain network connectivity. Table 1 lists the individual differences work conducted within the last two years (i.e., 2017–2018). New connectomic methods have been developed to characterize individual differences in personality and cognitive ability, such as connectome-based predictive modeling (CPM), which uses whole-brain connectivity patterns to predict individual traits and cognitive abilities [21–26]. CPM was recently used to identify functional connections correlated with high and low creative ability in a sample of 163 participants engaged in divergent thinking during fMRI [21]. A “high-creative” network consisted of default, salience, and executive network hubs; a “low-creative” network consisted of default, sensory, and cerebellar nodes (see Figure 2). Critically, the high-creative network generalized to predict divergent thinking ability in three independent samples of participants whose data were not used in model construction. Participants with stronger functional connections in this network thus tended to produce more original ideas.

Other work using similar prediction methods [27] has combined resting-state fMRI and genetic data to predict figural divergent thinking ability (i.e., visual-spatial; e.g., drawing). A model including both fMRI and genetic data showed better prediction of divergent thinking than models with separate fMRI and genetic data, and findings generalized to an independent sample of participants. Notably, although the “high-creative” network reported in this study showed some overlap with the high-creative network of the task-based CPM study noted above [21], the networks also showed considerable differences, likely due to variation in divergent thinking assessment (figural vs. verbal) and the type of imaging data (rest vs. task). Prediction modeling has also been used in longitudinal research to estimate future divergent thinking ability from structural brain networks [28]: executive network maturation, assessed via changes in grey-matter density, tracked improvements in divergent thinking ability three years later.

Several correlational studies have further investigated large-scale network characteristics associated with individual differences in creative thinking ability. Building on earlier seed-based studies reporting correlations between divergent thinking ability and resting-state functional connectivity (RSFC; e.g. [29–32]), a recent study [33] found that divergent thinking ability was related to increased RSFC between the left inferior frontal gyrus (IFG) of ECN and medial prefrontal cortex (MPFC) of the DN. This finding is consistent with earlier work [29] showing increased coupling between left IFG and MPFC in a high divergent thinking group. Several studies applied graph theoretical metrics such as global efficiency (i.e., the average shortest number of paths needed to traverse a given pair of brain regions) to assess information processing between network nodes. Other related work [34] found that a high divergent thinking group showed greater global efficiency within a resting-state network of executive and default nodes, similar to previous task-based research reporting a positive correlation between divergent thinking ability and global efficiency within a network of executive, salience, and default nodes [35]. The correspondence between resting-state and task-based networks was recently investigated in another study [36] that found executive-default coupling at rest predicted executive-default during divergent thinking, highlighting a link between network connectivity at rest and during task performance.

Dynamic connectivity research has complemented static connectivity findings by examining how network connectivity patterns shift over short time scales. One study [37] found that temporal variability of functional connectivity among executive (DLPFC) and default (precuneus and parahippocampal gyrus) network regions assessed at rest correlated with verbal creative thinking ability. The authors report several additional analyses examining within- and between-network variability and show that verbal creativity relates to between-network variability of other canonical networks beyond the DN and ECN (see Figure 3). Interestingly, of the 13 networks assessed in this study, only DN within-network variability correlated with creativity scores, highlighting a possible correspondence between neural variability within the DN and thought variability relevant to creative cognition.

Another recent study of connectivity dynamics [38] assessed network transitions in high and low divergent thinking groups and found that high divergent thinking ability was characterized by more frequent transitions between different brain connectivity “states” (i.e., recurring patterns of correlation between cortical networks), suggesting that flexible thinking may be marked by a more plastic brain. A related study exploring dynamic connectivity linked to Openness to Experience—a personality trait associated with creative thinking and default network functioning [39]—found that high Openness was related to increased time spent in a brain state characterized by positive correlations among the default, salience, executive, and dorsal attention networks [40]. Taken together with dynamic connectivity findings [37,38], it appears creative individuals benefit from an ability to dynamically shift between different patterns of brain connectivity.

Other studies have assessed variation in structural brain network connectivity in relation to creative thinking ability [41–44]. One such study [41] used network-based lesion-deficit mapping in a patient sample and found that MPFC lesions within the DN impaired remote concept generation, pointing to a role for the DN in spontaneous idea production; conversely, left rostrolateral prefrontal lesions within the ECN spared concept generation ability but impaired concept combination, consistent with role of ECN in higher-order control processes. Other recent work using network control theory analysis of white matter tracts has reported a correlation between divergent thinking ability and “modal controllability” in the right DLPFC of the ECN [42], suggesting that divergent thinking ability is characterized by an ability to “drive” the brain into difficult-to-reach cognitive states via the right DLPFC.

Notably, recent evidence suggests that correlations between creativity and structural brain connectivity vary as a function of sex. One study [43] found correlations between regional white matter volume and divergent thinking across diverse brain regions, but only in women. Other work [44] has reported decreased global network connectivity and clustering in women. Together, these findings highlight the importance of considering sex differences when assessing individual differences in creative thinking and brain network connectivity.

Summary and Future Directions

The cognitive neuroscience of creativity has benefited from recent innovations in network neuroscience methodology. This research is providing an increasingly sophisticated understanding of the complex mechanics of the creative brain, mapping neural dynamics to specific cognitive mechanisms and predicting individual creative abilities from patterns of brain connectivity. The literature has identified network dynamics supporting several cognitive processes relevant to creative thought (Figure 1), including goal-directed memory retrieval (executive-default; [9]), prepotent-response inhibition (executive-default; [14]), and internally-focused attention (executive-visual; [18]). Connectome prediction methods have been applied to estimate creative thinking ability from unique patterns of brain connectivity assessed both at rest [27] and during task performance [21], suggesting that variation in brain-network connectivity provides a reliable biomarker of creative thinking ability.

Future research should continue to map specific cognitive processes and individual differences supporting creative cognition. Network neuroscience methods provide a powerful approach, but activation studies continue to provide important insights into key cognitive mechanisms, including dissociating brain regions involved in generating “new” vs. “old” ideas [45], identifying neural correlates of remote conceptual combination [15] and expansion [46], and characterizing spontaneous cognitive processes related to DN activity and creative thought [47]. Moreover, research has thus far largely relied on correlational methods, so it is unclear whether connectivity patterns are causally related to creative performance. To address this issue, future research could employ new techniques in brain stimulation, such as transcranial alternating current stimulation, to causally manipulate interactions between large-scale brain networks. Although brain stimulation has already shown promise in identifying brain regions supporting creative thinking [48,49], an interesting next step would be to modulate interactions between these regions, particularly nodes within DN and ECN. Moreover, future individual differences research could examine whether connectivity patterns predictive of domain-general creative thinking (e.g., divergent thinking; [50]) extend to predict domain-specific creative performance [51,52], such as improvisation [53–58], poetry composition [59], visual creativity [5,60], or creative writing [61,62]. These are only a few potential directions for neuroscience research in what promises to be an exciting pursuit for the foreseeable future in mapping the creative brain.

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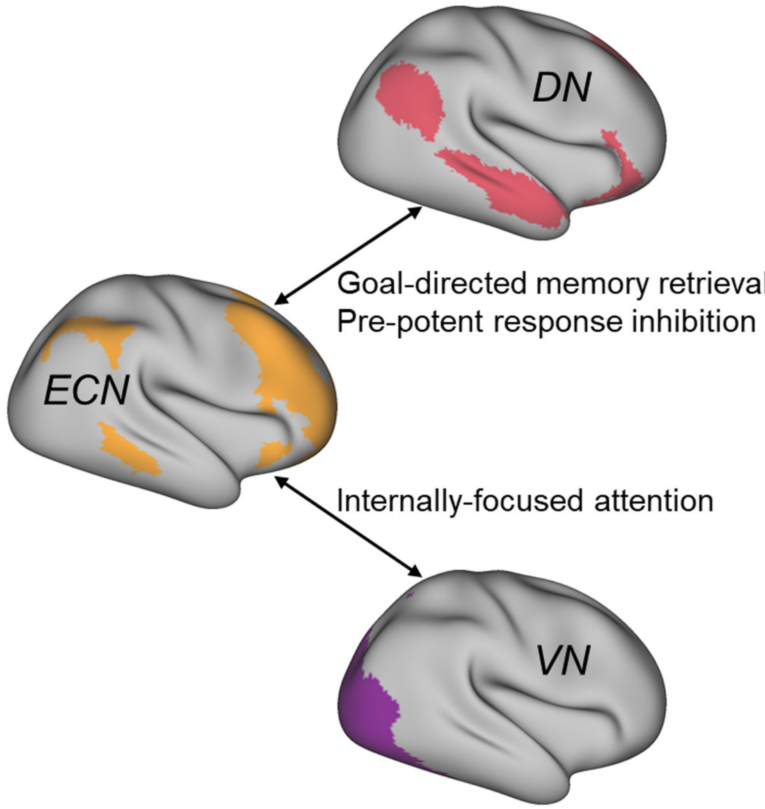

Figure 1. Cognitive mechanisms of brain network interactions during creative cognition.
Notes. DN = default network; ECN = executive control network; VN = visual network.

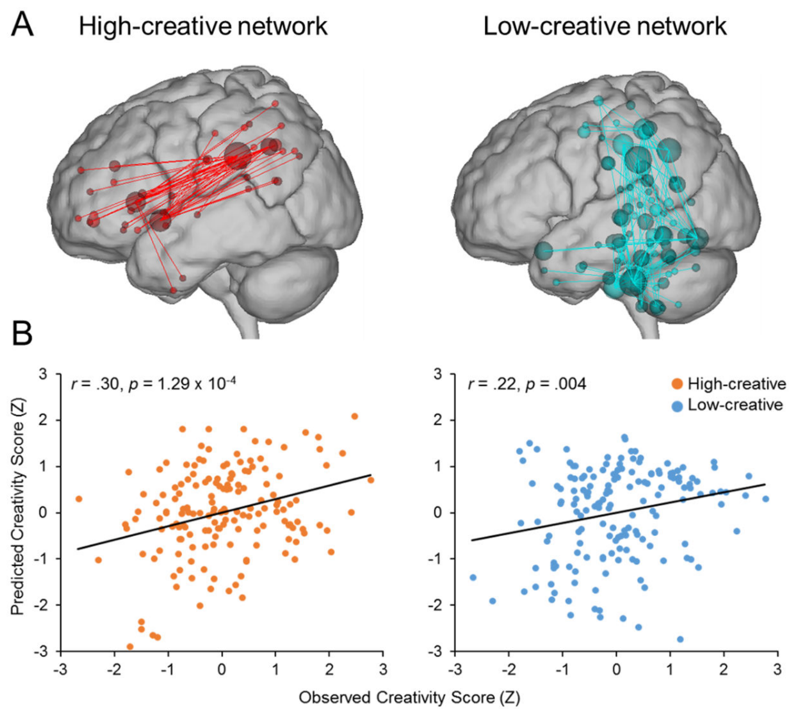

Figure 2. Functional networks predictive of verbal divergent thinking ability identified via connectome-based predictive modeling.

Notes. Task-related fMRI data were acquired from participants ($n = 163$) engaged in an alternate uses divergent thinking task. (A) Functional networks were defined by extracting a latent factor of originality ratings, correlating these values with all possible connections (i.e., edges) in a whole-brain network (total possible edges = 35,778), and thresholding edges ($p < .01$) to retain the most significant edges, resulting in a "high-creative network" (224 edges) and a "low-creative" network (603 edges). (B) Scatterplots depicting correlations between observed creativity scores (x-axis) and model-predicted creativity score (y-axis) for the high- and low-creative networks. Adapted from [21].

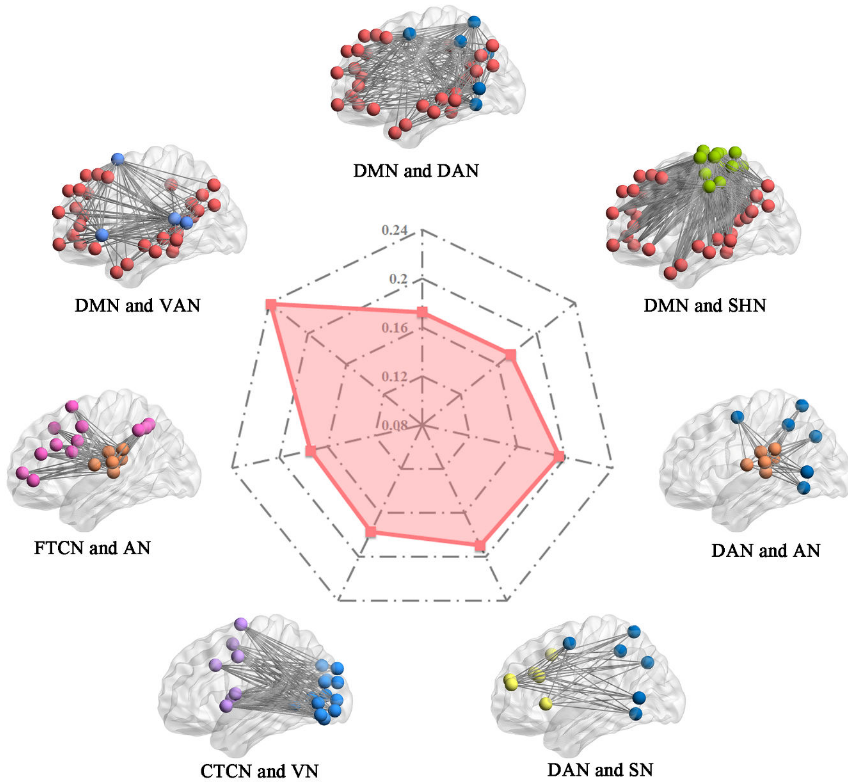

Figure 3. Resting-state between-network variability correlated with figural divergent thinking.

Notes. Resting-state fMRI data were acquired from participants (*n* = 574) who completed a battery of verbal divergent thinking tasks outside the scanner. The radar plot in the middle displays correlations between pairs of functional networks whose resting-state signal variability significantly relates to verbal divergent thinking scores. AN = auditory network; CTCN = cingulo-opercular task control network; DAN = dorsal attention network; DMN = default mode network; FTCN = fronto-parietal task control network (executive control network); SHN = sensory/somatomotor hand network; SN = salience network; VAN = ventral attention network; VN = visual network.

Table 1.

Correlational studies of individual differences in creative ability and functional connectivity (2017-2018)

Study	Sample Size	MRI Data	Creativity Task(s)	Network Analysis	Results
Beaty *et al.* (2018)	*n* = 163	Task fMRI	AUT (originality)	Connectome-based predictive modeling	Network connectivity strength predicted verbal creativity in 4 datasets
Liu *et al.* (2018) *	*n* = 236	Resting-state fMRI (and genetic data)	TTCT-V (composite)	Connectome-based predictive modeling	Network connectivity strength predicted verbal creativity in 2 datasets
Chen *et al.* (2018) *	*n* = 159	Structural MRI (2-3 timepoints)	TTCT-V (composite)	Longitudinal VBM	ECN and FTN gray matter maturation predicted future verbal creativity
Zhu *et al.* (2017) *	*n* = 282	Resting-state fMRI	TTCT-V (composite) and TTCT-F (composite)	ICA (mediation)	ECN mediated relation between DN and verbal, figural creativity
Sun *et al.* (2018) *	*n* = 574	Resting-state fMRI	TTCT-V (composite)	Temporal variability of FC	DN between- and within-network FC variability correlated with verbal creativity
Bendetowicz *et al.* (2018)	*n* = 29 frontal patients, *n* = 54 controls	Structural MRI (lesion mapping)	CAT-V and FGAT	Voxel-based lesion-deficit mapping; disconnection-deficit mapping; network-based lesion deficit	MPFC (DMN) lesion disrupted remote concept generation; RLPFC (ECN) lesion disrupted remote concept combination but not generation
Gao *et al.* (2017) **	*n* = 22 HCG, *n* = 22 LCG	Resting-state fMRI	TTCT-F (composite)	Voxel-wise whole-brain FCS; seed-to-voxel; graph theory	HCG showed greater FCS across regions of multiple networks; network efficiency correlated with figural creativity score
Kenett *et al.* (2018)	*n* = 416	DTI	TTCT-V (composite)	Network Control Theory	Network controllability of DLPFC (ECN) and other regions correlated with verbal creativity score
Li *et al.* (2017) **	*n* = 22 HCG, *n* = 22 LCG	Resting-state fMRI	TTCT-F (composite)	ICA; Dynamic FC	HCG showed more frequent transitions between brain states
Takeuchi *et al.* (2017)	*n* = 1277	Resting-state fMRI	S-A creativity test	ReHO; seed-to-voxel; fALFF	Creativity score in females

Study	Sample Size	MRI Data	Creativity Task(s)	Network Analysis	Results
					correlated with ReHo of MTG (DMN); RSFC between MPFC (DMN) and IFG (ECN); and fALFF in precuneus (DMN), MTG (DMN), and other regions

Notes. * = data from the Southwest University Longitudinal Imaging Multimodal (SLIM) Brain Data Repository (http://fcon_1000.projects.nitrc.org/indi/retro/southwestuni_qiu_index.html);

** = data from the same subset of 180 undergraduates used to form the HCG and LCG. CAT-V = Combined Associates Task; DN = default network; DTI = diffusion tensor imaging; ECN = executive control network; fALFF = fractional amplitude of low frequency fluctuations; FC = functional connectivity; FCS = functional connectivity strength; FGAT = Free Generation of Remote Associates Task; fMRI = functional magnetic resonance imaging; FTN = fronto-temporal network; HCG = high-creative group; IFG = inferior frontal gyrus; ICA = independent components analysis; LCG = low-creative group; MPFC = medial prefrontal cortex; MTG = middle temporal gyrus; RLPFC = rostrolateral prefrontal cortex; TTCT-F = Torrance Test of Creative Thinking - Figural; TTCT-V = Torrance Test of Creative Thinking - Verbal; ReHo = regional homogeneity; SN = salience network; VBM = voxel-based morphometry.