



Research report

Neural representations for the generation of inventive conceptions inspired by adaptive feature optimization of biological species

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ABSTRACT

Inventive conceptions amount to creative ideas for designing devices that are both original and useful. The generation of inventive conceptions is a key element of the inventive process. However, neural mechanisms of the inventive process remain poorly understood. Here we employed functional feature association tasks and event-related functional magnetic resonance imaging (MRI) to investigate neural substrates for the generation of inventive conceptions. The functional MRI (fMRI) data revealed significant activations at Brodmann area (BA) 47 in the left inferior frontal gyrus and at BA 18 in the left lingual gyrus, when participants performed biological functional feature association tasks compared with non-biological functional feature association tasks. Our results suggest that the left inferior frontal gyrus (BA 47) is associated with novelty-based representations formed by the generation and selection of semantic relatedness, and the left lingual gyrus (BA 18) is involved in relevant visual imagery in processing of semantic relatedness. The findings might shed light on neural mechanisms underlying the inventive process.

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1. Introduction

As the source of human civilizations, creativity has brought forth science, technology, art, music and so on. At the same time, creativity is the most complex phenomenon in the mind. Mainly because there are a great number of creative products in multiple realms, such as Vincent Van Gogh's paintings, Albert Einstein's theory of relativity, fashion designs, and technical inventions. The issue has arisen whether the generation of these creative products shares the same mechanisms (Baer, 1998; Sternberg, 2005). An influential

theory states that creativity depends on divergent (numerous and varied responses) and convergent (one correct or conventional response) processing, especially its divergence (Guilford, 1967). Earlier studies of the neural substrates have found that damages in frontal cortex impair word or semantic fluency, particularly the left prefrontal cortex (Laine and Niemi, 1988; Luria, 1966; Perret, 1974). Recent neuroimaging studies have further reported that divergent thinking with different tasks involves prefrontal (e.g., Fink et al., 2009; Gibson et al., 2009; Goel and Vartanian, 2005; Green et al., 2010), parietal (Fink et al., 2009; Sieborger et al., 2007),

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temporal (Chavez-Eakle et al., 2007; Fink et al., 2009; Jung-Beeman et al., 2004), and visual regions (e.g., Howard-Jones et al., 2005). In the case of music, while trained pianists conduct improvisation with a piano, neural activity is different from studies of divergent thinking. Significant activation occurs in motor and pre-motor regions, dorsolateral prefrontal (Bengtsson et al., 2007; Berkowitz and Ansari, 2008), middle frontal polar cortex (Limb and Braun, 2008), temporoparietal (Limb and Braun, 2008), and fusiform (Bengtsson et al., 2007). However, neuroimaging studies of artists exhibit another different picture. For example, Kowatari et al. (2009) have found that creativity in designing a pen is correlated with the degree of dominance of the right prefrontal over that the left one. In these studies, the task diversity makes it impossible to have an overlap of activation regions of the brain across studies of creativity (Arden et al., 2010). “To make creativity tractable in the brain, it must be further subdivided into different types that can be meaningfully associated with specific neurocognitive processes” (Dietrich and Kanso, 2010). That is, a best way to investigate creativity is to capture a facet of creative cognition and separate neural components from the brain, rather than creativity writ large.

Invention refers to the creation of a device that did not exist before, which helps humankind to live better or easier (Britannica encyclopedia, 2012; The world book encyclopedia, 1990). The inventive product is about physical objects or devices created in a novel way for practical uses. It is different from scientific, artistic, or literary creativity. Generally, inventive conception of the inventive product means creative ideas for designing devices in the category of technical inventions, rather than a broad category like creativity. It is obvious that the emphasis of inventive conceptions is conducive to elucidate neural mechanisms of the inventive process. Moreover, such exploration may extend the body of knowledge on neuroscience of creativity.

Inventive conceptions involve creative ideas for designing devices that are both original and useful. The generation of inventive conceptions relies on the formation of novelty-based representations in the mind for inventive devices or machines (Finke, 1990; Henderson, 2004; Royce, 1998; Simon, 1983). That a blade with sharp teeth along one edge could cut wood, for example, must have been generated in one’s mind for invention of a saw. Such novelty-based representation has been considered to be essential to the inventive process, although physical objectification is subsequently conducted (Fagerberg, 2004; Wiener, 1993). Previous studies of invention have focused on cognitive mechanisms and computational models of novelty-based representations in the inventive process (Dyer and Hodges, 1986; Hampton, 1997; Ward et al., 1999). However, there has been no study aimed at neural substrates of the inventive process. Are there specific regions of the brain that mediate novelty-based representations in the inventive process? The purpose of the present study is to elucidate whether and what regions of the brain are specialized for the generation of inventive conceptions.

Many significant inventions in history are inspired by adaptive feature optimization of biological species (Argentina et al., 2007; Bar-Cohen, 2005; Dickinson, 1999; Vogel, 1998). In nature, these diverse features of living beings are highly

optimized, which are efficiently acquired from million years of evolution (Darwin, 1859). It has sparked our novelty-based representations for artificial devices and machines in the inventive process, such as an oar based on fins of a fish, a fishnet based on the spider’s web, and an early flying machine based on the bird (Chanute, 1997). Even in modern times, inventions have still been inspired by adaptive optimization. The surface design of some vehicles and buildings with non-stick surfaces was triggered by the lotus effect (Barthlott and Neinhuis, 1997), and the development of robot scientist “Adam” was based on thinking and reasoning (King et al., 2009). Much evidence demonstrates that enlightenment from adaptive feature optimization of biological species is one of the most important paradigms in inventions.

A functional feature association approach restricted to adaptive feature optimization of biological species inspires the generation of inventive conceptions for new devices (Bar-Cohen, 2005; Dickinson, 1999; Vogel, 1998), because the essential core of this paradigm for inventions is involving novelty-based representations formed by novel semantic relatedness. In such tasks biological features and artificial devices are not related semantically and never connected before. To establish their connection, a concept related to biological features at a node activates and spreads in various directions so that a novel idea related to a non-existent device is found among different associations (Estes and Ward, 2002; Guilford, 1967; Koestler, 1964; Mobley et al., 1992; Torrance, 1962). In other words, these unusual links can initiate original representation and novelty response for new devices in the inventive process (Beeman and Bowden, 2000; Mednick, 1962; Razumnikova, 2007). Conversely, processing of familiar semantic relatedness mainly involves retrieval of information about prior semantic relatedness in long-term memory. Thus, this one or very few specific connection drives automatic response among few alternatives, making it harder to find an original idea or solution. Therefore, in the present experiment we employed two types of functional feature association tasks to investigate neural activity underlying the generation of invention conceptions: biological functional feature association tasks (BFFAT) embodying novel semantic relatedness to stimulate the generation of inventive ideas, and non-biological functional feature association tasks (NBFFAT) embodying familiar semantic relatedness to stimulate the generation of ordinary ideas.

BFFAT and NBFFAT might be represented in different regions of the brain, and the neural activity pattern from direct contrast between the two types of tasks might be a measure for crucial components of neural networks underlying novelty-based representations in the generation of inventive conceptions. Previous patient studies have revealed the generation of ideas in divergent thinking is impaired with the left ventral prefrontal lesions (Janowsky et al., 1989; Laine and Niemi, 1988; Luria, 1966; Perret, 1974; Stuss et al., 1998). Neuroimaging data have revealed further that not only generation of ideas but also selection of a certain idea are associated with the left inferior frontal gyrus (Chavez-Eakle et al., 2007; Dapretto and Bookheimer, 1999; Fink et al., 2009; Goldberg et al., 2007; Jung-Beeman, 2005). Based on these studies, we hypothesized that the left ventral prefrontal cortex might be

responsible for novelty-based representations that relates to the generation of inventive conceptions.

2. Materials and methods

2.1. Participants

Eighteen college students (eight males and ten females, mean age 20.3 years, range 17–23 years) fully right-handed were paid for their participation in this study. None of them had a history of neurological or psychiatric mental problems. The study was approved by the Institutional Human Participants Review Board of Beijing Normal University Imaging Center for Brain Research, and written consent was obtained from all the participants.

2.2. Design and materials

Three different conditions were used to investigate the neural basis for the generation of inventive conceptions: BFFAT, NBFFAT, and baseline tasks. In both functional feature association tasks, a trial consisted of a clue and a problem. The clue served to guide or direct to the solution of a problem. The

format of main tasks was “

A	→	B
C	→	?

”. Items “A”, “B”, “C”

and “?” represented living things or non-living things. “C → ?” was a problem in a trial, “A → B” was a clue to the problem. There were 80 stimulus trials of functional feature association tasks, half BFFAT and half NBFFAT (Table 1). Twenty items of

baseline tasks consisting of 8 asterisks “

*	*	*	*
*	*	*	*

” were

dispersed among stimulus trials of functional feature association tasks. The presentation of experimental trials was conducted in an event-related design.

The present study consisted of two phases: participants did experimental tasks in the scanner and then they did a questionnaire outside the scanner. At prescanning, participants had practices of these tasks. In the scanner, stimuli of two types of functional feature association tasks were presented in random order, and each stimulus trial lasted 6 s. The participants were instructed to think of an existent or non-existent thing corresponding to the question mark in a problem according to a clue of the task as soon as possible. During experiment, participants had to indicate whether they were

successful by pressing one of two buttons on a keypad, or press any button for baseline trials. With intention of controlling neural activations of the brain associated with motor action, nine of participants responded with the right index finger and others responded with the left index finger. After scanning, the participants completed a questionnaire with paper and pen. The “questions” were the same stimulus displays as during scanning. The participants were only requested to recall their answers for these tasks during the scanning process, and write statements to describe what they were.

2.3. Magnetic resonance imaging (MRI) acquisition

MRI scans were performed on a 3 T Siemens MAGNETOM Trio at Beijing Normal University. Participants laid supinely with their heads cozily fixed by belt and foam pads to reduce head movement. Earplugs were used to dampen scanner noise. Visual stimuli were presented through a projector onto a screen in the bore of the scanner. Participants viewed the stimuli through a mirror mounted to the head coil. Behavioral responses of participants were recorded by pressing buttons. High-resolution T1-weighted images were acquired for each participant to provide anatomical reference ($1 \times 1 \times 1 \text{ mm}^3$). Functional MRI (fMRI) data were collected using a T2* weighted gradient-echo echo planar imaging (EPI) sequence. In each volume, thirty-two slices (4-mm-thick) were acquired axially, interleaved slice mode to cover the whole brain. Data were recorded in a single session, and a total of 300 volumes were acquired with a repetition time (TR) of 2000 msec, an echo time (TE) of 30 msec, a flip angle of 90° , field of view (FOV) of $200 \times 200 \text{ mm}$, acquisition matrix of 64×64 , and spatial resolution of $3 \times 3 \times 4 \text{ mm}^3$.

2.4. Data analyses

Statistical Parametric Mapping (SPM2) (Friston et al., 1995) was employed for preprocessing and statistical analyses of imaging data with Matlab 6.5 (Mathworks). Slice timing correction was done before spatial processing due to acquisition of imaging data with interleaved slice mode. The functional image volumes were spatially realigned to reference volume, and then normalized to the standard brain template from the Montreal Neurological Institute (Evans et al., 1993) using non-linear basis functions (Ashburner and Friston, 1999). The images were spatially smoothed by an 8-mm full-width half-maximum (FWHM) isotropic Gaussian kernel (Worsley and Friston, 1995). Low-frequency drift in the BOLD signal was removed by a high-pass filter set at 128 s of cosine functions.

Individual analysis of imaging data was performed using the general linear model. The BOLD signal was modeled as a canonical hemodynamic response function. The contrasts of interest were examined after estimation of condition effects at each voxel. Our comparisons included BFFAT relative to baseline, NBFFAT relative to baseline, and BFFAT relative to NBFFAT. Each contrast produced a statistical parametric map of the t statistic (finally converted into Z values). The resulting activations were computed by a voxelwise intensity threshold of $p < .05$ using a correction of multiple comparisons via the false discovery rate (FDR) (Benjamini and Hochberg, 1995; Genovese et al., 2002), and a cluster size of a minimum of

Table 1 – Examples of stimuli used in experimental tasks.

BFFAT	NBFFAT
蛋壳 → 拱形屋顶	剪草机 → 草坪
树根 → ?	起子 → ?
(An eggshell → an arched roof)	(A mower → A lawn)
(A tree's root → ?)	(An opener → ?)
企鹅 → 滑雪板	犁 → 田地
跳蚤 → ?	斧头 → ?
(A penguin → A ski)	(A plow → A field)
(A flea → ?)	(An axe → ?)

twenty contiguous voxels. Contrasts of individual participants were entered to a second-level random effects model (Worsley et al., 1992) for group analysis. Activations that were within clusters of twenty or more contiguous voxels and above the FDR-corrected statistical threshold of $p < .05$ were considered significant. Brain regions were estimated from Talairach and Tournoux (Talairach and Tournoux, 1988) following adjustments for differences between MNI and Talairach coordinates.

3. Results

3.1. Behavioral data

During scanning participants were requested to do experimental tasks. The reaction time and completion rate were

recorded automatically. Statistical analyses of behavioral data indicated that the mean reaction time of successful solutions in BFFAT was significantly longer than that in NBFFAT, $t(17) = 21, p < .001$ (Fig. 1A). The difference in completion rates between BFFAT and NBFFAT was significant, $t(17) = 8, p < .001$ (Fig. 1B).

To examine what participants generated in their mind during scanning, we used a questionnaire to request them to use words to portray objects or devices generated in their mind after scanning without delay. According to the consensual assessment technique (Amabile, 1982), experts in the domain in question were asked to evaluate the originality and usefulness of these devices or objects participants generated. An expert evaluated (a) novelty of the objects generated in their mind in relation to existing devices and products in terms of a 5-point rating scale ranging from 1 (very unoriginal)

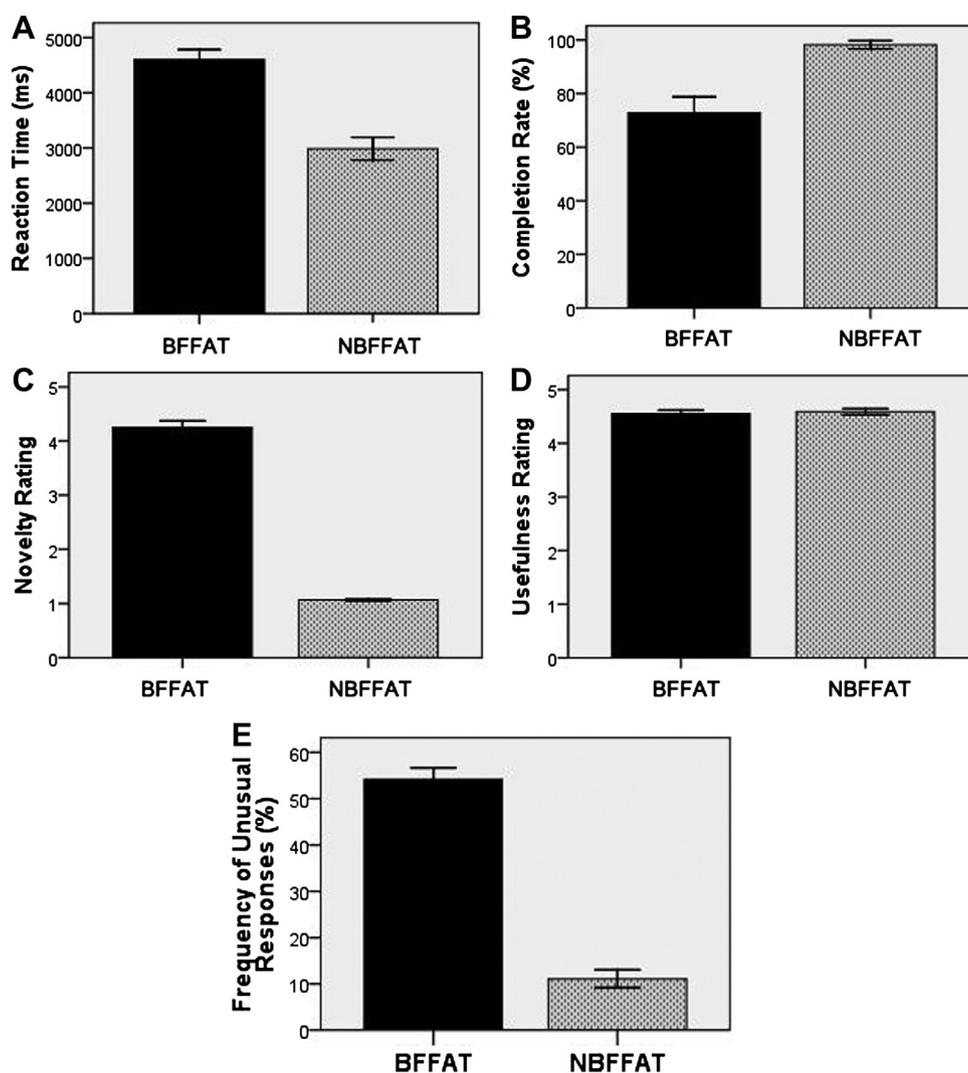


Fig. 1 – Behavioral performance. (A) Reaction time, (B) completion rate, (C) novelty rating, (D) usefulness rating, and (E) frequency of unusual responses. Reaction time and completion rate were collected in the scanning session. Reaction time is mean time of participants' responses in problem solving. Completion rate is percentage of solutions to problems. Novelty and usefulness rating were based on questionnaires in which the participants were requested to recall their answers without delay after scanning. The novelty is evaluated with a 5-point rating scale ranging from 1 (very unoriginal) to 5 (very original), and usefulness ranging from 1 (very useless) to 5 (very useful). Unusual response is reported by less than or equal to 5% responses in the same stimulus trial across all the participants. Error bars indicate standard error measurement.

to 5 (very original), and (b) usefulness in terms of the same rating scale ranging from 1 (very useless) to 5 (very useful). The difference in novelty rating between biological functional feature association trials and non-biological functional feature association trials was significant, $t(17) = 52, p < .001$ (Fig. 1C). The difference in usefulness rating between biological functional feature association trials and non-biological functional feature association trials was not significant, $t(17) = 1, p > .25$ (Fig. 1D). The questionnaire showed that BFFAT evoked generation of novel and useful objects or devices, and NBFFAT caused retrieval of ordinary and useful objects or devices. In order to reveal further the novelty of solutions, we did statistical analysis using an objective measurement of novelty responses by taking the frequency of unusual responses in the same stimulus trial across all the participants. Five college students who were not participants and were blind to the experimental hypothesis identified unusual responses. Any responses that were reported by less than or equal to 5% responses were considered to be unusual. Statistical analyses indicated that the mean frequency of unusual responses in BFFAT was significantly higher than that in NBFFAT, $t(4) = 27, p < .001$ (Fig. 1E).

3.2. Neuroimaging data

The inventive process involving different cognitive components recruits multiple neural regions of the brain. We are interested in segregating specific components of the neural network underlying the generation of inventive conceptions. Therefore, a series of statistical analyses were performed for functional MRI data of successful solutions in functional feature association tasks. The first comparison included experimental tasks versus baseline. One comparison between BFFAT versus baseline revealed that the cognitive operation of BFFAT involved significant activations in left superior frontal gyrus (Brodmann area – BA 6: $x = -5, y = 9, z = 65$), left inferior frontal gyrus (BA 9: $x = -41, y = 4, z = 32$), left inferior frontal gyrus (BA 47: $x = -41, y = 17, z = -6$), right precentral gyrus (BA 6: $x = 41, y = -8, z = 63$), left lingual gyrus and cuneus (BA 18: $x = -26, y = -99, z = -2$), right lingual gyrus (BA 17: $x = 17, y = -90, z = 0$), right inferior temporal gyrus (BA 20: $x = 32, y = -5, z = -37$), and right fusiform gyrus (BA 20: $x = 38, y = -12, z = -24$). The other comparison of NBFFAT versus baseline revealed that cognitive operation of NBFFAT involved significant activations in left inferior frontal gyrus (BA 9: $x = -44, y = 7, z = 32$), left superior frontal gyrus (BA 6: $x = -5, y = 6, z = 66$), right middle frontal gyrus (BA 46: $x = 56, y = 33, z = 25$), and right lingual gyrus and cuneus (BA 17: $x = 11, y = -96, z = 0$) (Table 2).

According to the principle of cognitive subtraction, by comparing the activity of the brain in BFFAT that utilizes a particular cognitive component with the activity of the brain in the control tasks, it is possible to infer which regions are specialized for the particular cognitive component. Thus we performed direct comparison of BFFAT versus NBFFAT to identify key neural components of the generation of inventive conceptions. The results of this comparison revealed that the cognitive operation of BFFAT was associated with significant activations in left inferior frontal gyrus (BA 47: $x = -29, y = 28, z = -9$) and left lingual gyrus (BA 18: $x = -11, y = -78, z = 3$)

Table 2 – Coordinates of activation peaks.

Regions activated	BA	x	y	z	Z-score
NBFFAT–baseline					
<i>Frontal lobe</i>					
Left inferior frontal gyrus	9	-44	7	32	6.27
Left superior frontal gyrus	6	-5	6	66	5.70
Right middle frontal gyrus	46	56	33	25	3.55
<i>Occipital lobe</i>					
Right lingual gyrus & cuneus	17	11	-96	0	7.07
<i>Subcortical regions</i>					
Left cerebellum		-17	-39	-35	2.97
Right lentiform nucleus		14	-3	-2	3.80
Right lentiform nucleus		20	6	13	2.29
BFFAT–baseline					
<i>Frontal lobe</i>					
Left superior frontal gyrus	6	-5	9	65	5.92
Left inferior frontal gyrus	9	-41	4	32	5.79
Left inferior frontal gyrus	47	-41	17	-6	2.89
Right precentral gyrus	6	41	-8	63	5.77
<i>Occipital lobe</i>					
Left lingual gyrus & cuneus	18	-26	-99	-2	7.11
Right lingual gyrus	17	17	-90	0	7.29
<i>Temporal lobe</i>					
Right inferior temporal gyrus	20	32	-5	-37	3.03
Right fusiform gyrus	20	38	-12	-24	2.93
<i>Subcortical regions</i>					
Left lateral geniculum body		-23	-26	-3	3.96
Right lateral ventricle		14	-4	25	3.85
Right lentiform nucleus		14	-3	-4	3.34
NBFFAT–BFFAT					
<i>Frontal lobe</i>					
Left middle frontal gyrus	11	-26	42	-14	2.95
<i>Occipital lobe</i>					
Left middle occipital gyrus	19	-32	-89	21	3.68
Left cuneus	18	-14	-98	13	3.53
Right cuneus	7	8	-65	33	5.48
<i>Temporal lobe</i>					
Right inferior parietal lobule	40	41	-49	52	5.71
<i>Subcortical regions</i>					
Left cerebellum		-44	-63	-39	3.29
Left thalamus		-11	-28	12	2.60
Right caudate body		5	14	7	2.80
BFFAT–NBFFAT					
<i>Frontal lobe</i>					
Left inferior frontal gyrus	47	-29	28	-9	4.20
<i>Occipital lobe</i>					
Left lingual gyrus	18	-11	-78	3	5.42

x, y, and z represent position in Talairach coordinate space.

(Fig. 2A and B). However, the other comparison between NBFFAT versus BFFAT revealed that the cognitive operation of NBFFAT was associated with significant activation in left middle frontal gyrus (BA 11: $x = -26, y = 42, z = -14$), left middle occipital gyrus (BA 19: $x = -32, y = -89, z = 21$), left cuneus (BA 18: $x = -14, y = -98, z = 13$), right cuneus (BA 7: $x = 8, y = -65, z = 33$), and right inferior parietal lobule (BA 40: $x = 41, y = -49, z = 52$).

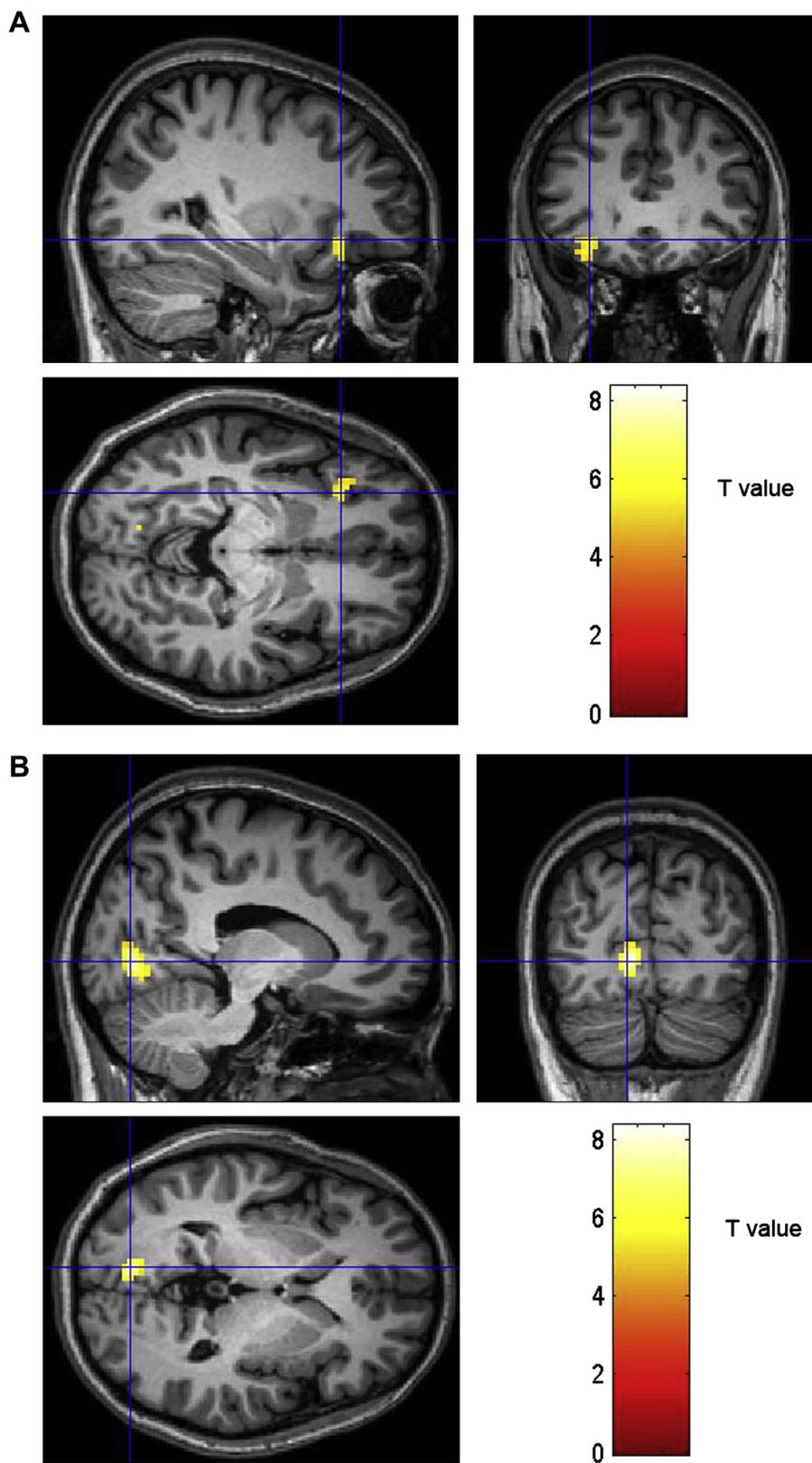


Fig. 2 – Significant activations elicited by BFFAT. Regions showing significant activations were associated with performance in BFFAT versus NBFFAT. (A) Activations at BA 47 in left inferior frontal gyrus. These are sagittal, coronal and axial sections. (B) Activations at BA 18 in left lingual gyrus. These are sagittal, coronal and axial sections. The significance thresholds are $p < .05$ FDR-corrected with an extent threshold of 20 contiguous voxels. Functional maps shown at sagittal, coronal and axial sections are overlaid on the T1-weighted images.

Different reaction time is often considered as a cue to measure the difficulty of an experimental task. We performed a covariance analysis and entered reaction time as a covariate of no interest to reveal activations of regions irrespective of task difficulty. While reaction time was co-varied out, the comparison between BFFAT and NBFFAT showed significant activations at left inferior frontal gyrus (BA 47: $x = -29$, $y = 28$, $z = -9$) and left lingual gyrus (BA 18: $x = -11$, $y = -78$, $z = 3$). This further revealed that activations of the two regions BAs 47 and 18 were task specific, not evoked by task difficulty (Stephan et al., 2003).

4. Discussion

The present study employed functional feature association tasks and event-related functional MRI technique to identify neural architecture of the brain specialized for the generation of inventive conceptions. A key comparison of BFFAT relative to NBFFAT revealed significant activations at BA 47 in the left inferior frontal gyrus and at BA 18 in the left lingual gyrus. These results suggest that the left inferior frontal gyrus (BA 47) and the left lingual gyrus (BA 18) are key components of the neural network underlying the generation of novelty-based representations in the inventive process.

BFFAT involve at least word recognition, semantic retrieval, associative search, relatedness formation, and imagery recall. These cognitive components are carried out by activation of widely distributed areas of the brain. This is consistent with the comparison of BFFAT relative to baseline (Table 2). Moreover, it is noteworthy that neural activity patterns in BFFAT relative to baseline were different from the neural patterns in NBFFAT relative to baseline, albeit there were a few common activations. It showed that BFFAT are distinct from NBFFAT. This was in agreement with the behavioral responses of the participants in performing BFFAT and NBFFAT (Fig. 1A–E). The behavioral difference in novelty responses, reaction time, completion rates further reflects distinct mental operations engaged in the biological and non-biological association tasks. That is, BFFAT mainly involves the formation of novel semantic relatedness, but NBFFAT involves the retrieval of familiar semantic relatedness. Therefore, solving biological association tasks requires more processing time and gets less completion rate than solving non-biological association tasks.

The difference in cognitive mechanisms between the biological and non-biological association tasks is further supported by questionnaire records. For example, when a NBFFAT “A mower → A lawn An opener → ?” was presented, participants reported the answer: a bottle of wine. In the case when reading a clue “A mower → A lawn”, semantic information of “A mower” and “A lawn” were retrieved from long-term memory following word recognition. Then associative search for “a mower and a lawn” proceeded and it was realized that a mower can be applied to a lawn. According to this clue, when reading the problem “An opener → ?”, participants retrieved semantic information of “An opener”, then finished the associative search: an opener can be applied to a bottle of wine. In contrast, when a BFFAT “An eggshell → An arched roof A tree’s root → ?” was presented, participants reported

the answer such as a new design of the foundation of a building consisting of multiple crossed piles for anti-earthquake, which is embedded firmly and deeply in the ground and on which the building is built. Similar to NBFFAT, when reading a clue “An eggshell → An arched roof”, semantic information related to “An eggshell” and “An arched roof” were retrieved from long-term memory following word recognition. Then associative search for “an eggshell and an arched roof” proceeded. Because there was a lack of direct associative knowledge of an eggshell and an arched roof in long-term memory, participants had to form new relatedness that the mechanics of an eggshell can be applied to the design and construction of the roof of a building. According to this clue, when reading the problem “A tree’s root → ?” and retrieved semantic information of “A tree’s root”, then associative search proceeded, but there was a lack of direct relevant associative knowledge in memory. At that time participants had to form new relatedness: the mechanics of a tree’s root can be applied to a new design of the foundation of a building consisting of multiple crossed piles for resistance to earthquake. Also, a visual imagery of the substructure of multiple crossed piles might appear in their mind. Different from NBFFAT, BFFAT necessitate participants to form novel semantic relatedness in addition to word recognition, semantic retrieval, associative search, and imagery recall.

This role of the left inferior prefrontal cortex in the generation of ideas has been suggested by considerable neuropsychological evidence and neuroimaging data (Bechtereva et al., 2004; Gazzaniga, 2000; Janowsky et al., 1989; Perret, 1974), although there are reports about the right regions of the brain. Patients with the left frontal pathology were significantly worse than those with the right frontal lesions on the generation of semantic fluency (Laine and Niemi, 1988), and patients with the left prefrontal lesions were most impaired in the generation of verbal fluency (Stuss et al., 1998). Moreover, a patient with the left orbitofrontal lesion generated words much less than an age-matched control did (Luria, 1966). Fluency tasks are a measure of divergent production that requires participants to avoid previous responses and initiate new things relating to a specific cue (Guilford, 1967). These patient studies have consistently supported the left ventral prefrontal cortex mediating divergent processing. Recent functional MRI studies have suggested that inferior frontal gyrus was recruited for the creative process (Ellamil et al., 2011; Fink et al., 2009; Greake and Hansen, 2005; Mashal et al., 2007). The creative process is characterized by the production of new ideas and the assessment of their usefulness. An functional MRI with a compatible drawing tablet system was employed to identify the neural activity of a twofold processing in the creative process (Ellamil et al., 2011). The experimental task was to design book cover illustrations according to book descriptions from documentary summaries about public issues. In the experiment, after viewing a book description, participants drew or wrote down their ideas (creative generation) and drew or wrote down their evaluations of the ideas (creative evaluation). Their results showed that wide spread regions in frontal, parietal and temporal cortex were dedicated to creative generation, while executive and default network regions were engaged in creative evaluation. Interestingly, the left inferior frontal gyrus in the frontal

cortex was recruited for the generation of ideas. Similarly, in another functional MRI study (Fink et al., 2009), experimental tasks were, for example, unusual uses test for generating original uses of everyday objects, and the name invention task for generating as original names as possible to given abbreviations. In comparison with fixation, either unusual uses test or name invention task elicited consistently strong activation in the left inferior frontal gyrus. This revealed further that the left inferior frontal gyrus was dedicated to the appearance of a new semantic representation in divergent thinking. Chavez-Eakle et al. (2007) used a single photon emission computerized tomography to study a series of divergent thinking tasks (e.g., just suppose, unusual uses). Their research results showed greater activity of region cerebral blood flow in the left BA 47 in highly creative individuals compared to normal controls. Moreover, the greater activity in the left inferior frontal gyrus (BA 47) among regions of the brain was strongly correlated with cognitive components of fluency and flexibility. In brief, previous studies have implicated that involvement of the left inferior frontal cortex (BA 47) is associated with the generation of ideas in divergent thinking and novelty response.

The formation of original ideas depends on not only generating these ideas in divergent thinking but also selecting the most novel idea from activated semantic network. Abstract semantic associations are represented in the left ventral prefrontal cortex of the brain (Dapretto and Bookheimer, 1999; Demb et al., 1995; Devlin et al., 2003; Fiez, 1997; Fletcher et al., 2000; Gabrieli et al., 1998; Goldberg et al., 2007; Kapur et al., 1994; Poldrack et al., 1999; Thompson-Schill et al., 1997). Moreover, the left inferior frontal gyrus is emphasized to play an important role in semantic selection by selecting one concept and inhibiting competing activated concepts (Jung-Beeman, 2005; Kan and Thompson-Schill, 2004; Thompson-Schill et al., 1997; Zhang et al., 2004). Several functional MRI studies of verbal four-term analogy have revealed that the prefrontal cortex is a central in analogical reasoning in that the left inferior frontal gyrus engages in semantic search and selection (Bunge et al., 2005; Green et al., 2010), the left rostrolateral prefrontal cortex serves abstract relation integration (Green et al., 2006), and the right rostrolateral prefrontal cortex controls visuo-spatial relation integration (Krawczyk et al., 2010). For example, Bunge et al. (2005) used functional MRI to examine neural correlates of analogy and semantic tasks. A direct comparison of tasks revealed that the left inferior prefrontal cortex and the left frontopolar cortex were more active in analogy than in semantic trials. Neural activity in the left inferior prefrontal cortex was believed to involve with associative strength of semantic retrieval between a pair of words, while the left frontopolar cortex involved with mapping across multiple retrieved relations in analogical tasks. This is in accord with some literature on non-analogy tasks about mechanisms of selective semantic associations in the left inferior frontal gyrus (Bokde et al., 2001; Kan and Thompson-Schill, 2004; Yang et al., 2009; Zhang et al., 2004). Green et al. (2010) further found that neural activity in the left frontopolar cortex and the left inferior prefrontal cortex co-varied parametrically with increasing semantic distance between items in analogical reasoning. It means that the left inferior prefrontal cortex is recruited for selecting more

semantically distant demand. As noted by Heilman et al. (2003), the creative process involves with selectively activating remote conceptual networks and inhibiting similar semantic information circuits. On the whole, previous studies suggest that the left inferior frontal gyrus is recruited for the generation of semantic relatedness and selection of semantic relatedness. These existing studies are consistent with our research suggestion of the left BA 47 functions responsible for novelty-based representations engaged in forming novel semantic relatedness between biological features and artificial devices in biological functional feature tasks, and selecting a more original conception among possible alternatives.

Recent relevant studies are in congruence with our findings. Kowatari et al. (2009) have investigated artistic creativity. In their experiment while the pictures of a pen were presented, participants were asked to think of a new design for the pen. The originality of a designed pen was evaluated by comparison of the pen participants drawn relative to an example. The participants were from students in the department of art and design who had received at least 2 years of artistic training (expert subjects) or students of other disciplines without artistic training (novice subjects). The researchers found that creativity of expert participants was correlated with the degree of dominance of the right prefrontal cortex over that of the left one, although contrasts between the pen design task and the counting number task in either expert subjects or novice subjects did not show significant differences. They argued that art training suppressed the activity in the left prefrontal cortex and the bilateral parietal cortex in turn fed positive signals to the right prefrontal cortex. Thus, the right prefrontal cortex activity overrode the left prefrontal cortex one, also activity in the bilateral parietal cortex decreased. Unlike experts, a negative correlation between activity in the bilateral parietal cortex and creativity was observed in novice participants, because visual-spatial process in the parietal cortex was interfering with the creative process leading to new designs. Different from Kowatari et al. research, our task is based on the biological functional features to generate different devices that are both novel and useful, which involves remote semantic relatedness rather than designing a pen in artistic dimension. Thus, activation appeared in the left prefrontal cortex is associated with the formation and selection of novel semantic relatedness during the generation of inventive conceptions. In the case of artistic creativity, new design for a pen is mainly based on processing of visual and spatial information on the shape, color and esthetic senses of a pen, such information inevitably entails the right hemisphere over the left hemisphere of the brain, except the argument of training suppression made by Kowatari et al.

The present study is somewhat similar to a study of metaphor processing by Rapp et al. (2004). In their experiment, metaphoric sentence (e.g., the lovers words are harp sounds) and literal sentence were presented and participants were requested to read these sentences silently and judged whether words in a sentence had a positive or negative connotation. Processing of metaphors relative to literal sentences in their study showed activation in the left inferior frontal gyrus (BAs 45 and 47) and the left temporal gyrus (BAs 20 and 37). In reality, our study differs from the study of

metaphor processing in several aspects. Rapp et al. used a semantic decision task to examine metaphor comprehension. Metaphors are about comprehension of abstract ideas (e.g., the truth) in our lives expressed by figurative language. This expression serves to facilitate the understanding of the tenor (the subject), described by the vehicle (the object) (Richards, 1936). Whereas our study used the BFFAT to investigate the inventive process. Our task was to apply optimization of biological functional features to design of artificial devices. In addition, Rapp et al. presented a sentence and participants had to understand the subject via the object in different categories. But we used four items in a trial (two items as a cue and the other two items as a problem), and participants had to generate an inventive conception. These factors may explain the differences in results between Rapp et al. and our study. For example, the left BAs 45, 20 and 37 of the brain were recruited to comprehension of figurative language, rather than the generation of inventive conceptions. However, metaphor processing involves semantic inference in understanding of figurative sense, this processing possibly brought about activation in the left inferior frontal gyrus (BAs 45 and 47).

Recent patient study has investigated correlations between lesion locations and original responses using creative tasks (Shamay-Tsoory et al., 2011). In Torrance test of creative thinking (Torrance, 1974) participants were presented with 30 identical circles on a page, and were requested to draw as many different drawings of meaningful objects as possible, each of which must include at least one circle. In alternative uses task, participants were presented with a list of six common objects and were asked to list as many alternate uses as possible for each objects. Shamay-Tsoory et al. found that lesions in the right medial prefrontal cortex were associated with impaired originality, and lesions in the left parietal and temporal cortex were associated with somewhat elevated levels of originality. The data have supported the role of the right prefrontal cortex in creativity of geometric or object stimuli. Concerning that lesions in the left parietal cortex are associated with somewhat elevated levels of originality, as the authors argued, cognitive processes mediated by the left parietal and temporal cortex interferes with creative cognition. For this reason, lesions in the regions may bring about elevated levels of originality. This result is consistent with our findings on the role of the left prefrontal cortex in generation of inventive conceptions. That is, the generation and selection of semantic relatedness are associated with the left inferior frontal gyrus. Because the left parietal cortex, particularly the left temporoparietal region and the left inferior parietal lobe, are extremely important for language production (Metter et al., 1990; Stoerckel et al., 2009), it competes or interferes with the formation of novel semantic relatedness in the left inferior frontal gyrus. Therefore, damage to the left PC may be conducive to the generation of inventive conceptions.

In addition, our results also showed activation in the left lingual gyrus, which may involve relevant visual imagery in processing of semantic relatedness. This is consonant with prior relevant studies (Behrmann et al., 1994). Visual imagery is an important component of conscious experience (Paivio, 1969). It can be seeing by “mind’s eyes” (Kosslyn, 1994;

Marks, 1973), hearing by “mind’s ears” (Halpern, 1988; Pitt and Crowder, 1992) and touching by “mind’s hands” (Yoo et al., 2003). As reported in behavioral studies, there is the generation of new visual imagery in the creative process (Anderson and Helstrup, 1993; Finke, 1990; Lebouillier and Marks, 2003). Much neuroimaging data show significant activations in occipital cortex while visual imagery is generated (Kosslyn et al., 1993; Kosslyn and Ochsner, 1994; Miyashita, 1995), and there is a dominance of the left hemisphere (Charlot et al., 1992; Farah et al., 1985; Goldenberg et al., 1989; Kosslyn et al., 1993; Stangalino et al., 1995; Tippet, 1992). Some studies further reveal that the left BA 18 is involved in spatial property processing (Hubel and Livingstone, 1987; Shelton and Gabrieli, 2002; Slotnick and Schacter, 2006), vivid visual imagery (Olivetti Belardinelli et al., 2009), and motion imagery (Malouin et al., 2003). Interestingly, a recent study (Jung et al., 2010) used structural MRI to examine cortical thickness of the brain related to the creative process in young participants. These tasks (e.g., the design fluency task) made participants generate novel drawings, and were correlated with decreased cortical thickness at the left BA 18. As many researchers claimed (Durstun and Casey, 2006), Jung et al. proposed that such thinning is involved in a more focused function. They concluded that the left BA 18 in lingual gyrus is responsible for novel patterns or designs in these tasks. In agreement with their findings, our study suggested that the left BA 18 in lingual gyrus of the occipital cortex involves relevant imagery processing in the generation of inventive conceptions.

Invention is one of the most important activities in human civilization. Neural mechanisms of the inventive process have been perplexed us for a long time. The present study using BFFAT and functional MRI technique investigated the neural basis of the formation of inventive conceptions. Our results suggested that two neural architectures of the brain are the seat for the generation of inventive conceptions in the inventive process: the left BA 47 in inferior frontal gyrus and the left BA 18 in lingual gyrus. The findings of the present study advance our understanding of neural mechanisms of the inventive process.

Competing interest

The authors have declared that no competing interests exist.

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REFERENCES

- Amabile TM. Social psychology of creativity: A consensual assessment technique. *Journal of Personality and Social Psychology*, 43: 997–1013, 1982.
- Anderson RE and Helstrup T. Visual discovery in mind and on paper. *Memory and Cognition*, 21(3): 283–293, 1993.
- Arden R, Chavez RS, Grazioplene R, and Jung RE. Neuroimaging creativity: A psychometric view. *Behavioural Brain Research*, 214: 143–156, 2010.
- Argentina M, Skotheim J, and Mahadevan L. Settling and swimming of flexible fluid-lubricated foils. *Physical Review Letters*, 99: 224503, 2007.
- Ashburner J and Friston KJ. Nonlinear spatial normalization using basis functions. *Human Brain Mapping*, 7(4): 254–266, 1999.
- Baer J. The case for domain specificity in creativity. *Creativity Research Journal*, 11: 173–177, 1998.
- Bar-Cohen Y. *Biomimetics: Biological Inspired Technologies*. Taylor & Francis, 2005.
- Barthlott W and Neinhuis C. Purity of the sacred lotus, or escape from contamination in biological surfaces. *Planta*, 202(1): 1–8, 1997.
- Bechtereva NP, Korotkov AD, Pakhomov SV, Roudas MS, Starchenko MG, and Medvedev SV. PET study of brain maintenance of verbal creative activity. *International Journal of Psychophysiology*, 53: 11–20, 2004.
- Beeman MJ and Bowden EM. The right hemisphere maintains solution-related activation for yet-to-be-solved problems. *Memory and Cognition*, 28: 1231–1241, 2000.
- Behrmann M, Moscovitch M, and Winocur G. Intact visual imagery and impaired visual perception in a patient with visual agnosia. *Journal of Experimental Psychology: Human Perception and Performance*, 20: 1068–1087, 1994.
- Bengtsson SL, Csikszentmihalyi M, and Ullen F. Cortical regions involved in the generation of musical structures during improvisation in pianists. *Journal of Cognitive Neuroscience*, 19: 830–842, 2007.
- Benjamini Y and Hochberg Y. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57: 289–300, 1995.
- Berkowitz A and Ansari D. Generation of novel motor sequences: The neural correlates of musical improvisation. *NeuroImage*, 41: 535–543, 2008.
- Bokde AL, Tagamets MA, Friedman RB, and Horwitz B. Functional interactions of the inferior frontal cortex during the processing of words and word-like stimuli. *Neuron*, 30: 609–617, 2001.
- Britannica encyclopedia *Invention*. Encyclopedia Britannica Online, <http://www.britannica.com/EBchecked/topic/292272/invention>; October 2012.
- Bunge SA, Wendelken C, Badre D, and Wagner AD. Analogical reasoning and prefrontal cortex: Evidence for separable retrieval and integration mechanisms. *Cerebral Cortex*, 15: 239–249, 2005.
- Chanute O. *Progress in Flying Machines*. New York: Dover, 1997.
- Charlot V, Tzourio N, Zilbovicius M, Mazoye B, and Denis M. Different mental imagery abilities result in different regional cerebral blood flow activation patterns during cognitive tasks. *Neuropsychologia*, 30: 565–580, 1992.
- Chavez-Eakle RA, Graff-Guero A, Garcia-Reyna J, Vaugier V, and Cruz-Fuentes C. Cerebral blood flow associated with creative performance: A comparative study. *NeuroImage*, 38: 519–528, 2007.
- Dapretto M and Bookheimer SY. Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, 24: 427–432, 1999.
- Darwin C. *On the Origin of Species*. London: Murray, 1859.
- Demb JB, Desmond JE, Wagner AD, Vaidya CJ, Glover GH, and Gabrieli JDE. Semantic encoding and retrieval in the left inferior prefrontal cortex: A functional MRI study of task difficulty and process specificity. *Journal of Neuroscience*, 15: 5870–5878, 1995.
- Devlin JT, Matthews PM, and Rushworth MF. Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience*, 15(1): 71–84, 2003.
- Dickinson MH. Bionics: Biological insight into mechanical design. *The Proceedings of the National Academy of Sciences USA*, 96(2): 14208–14209, 1999.
- Dietrich A and Kanso R. A review of EEG, ERP, and neuroimaging studies of creativity and insight. *Psychological Bulletin*, 136: 822–848, 2010.
- Durston S and Casey BJ. What have we learned about cognitive development from neuroimaging? *Neuropsychologia*, 44: 2149–2157, 2006.
- Dyer MG, Flowers M, and Hodges J. Edison: An engineering design invention system operating naively. *Artificial Intelligence in Engineering*, 1(1): 36–44, 1986.
- Ellamil M, Dobson C, Beeman M, and Christoff K. Evaluative and generative modes of thought during the creative process. *NeuroImage*, 59: 1783–1794, 2011.
- Estes Z and Ward T. The emergence of novel attributes in concept modification. *Creativity Research Journal*, 14: 149–156, 2002.
- Evans AC, Collins DL, Mills SR, Brown ED, Kelly RL, and Peters TM. *Proceeding IEEE-Nuclear Science Symposium and Medical Imaging Conference*, 1813–1817, 1993.
- Fagerberg J. Innovation: A guide to the literature. In Fagerberg J, Mowery DC, and Nelson RR (Eds), *The Oxford Handbook of Innovation*. Oxford University Press, 2004: 1–26.
- Farah MJ, Gazzaniga MS, Holtzman JD, and Kosslyn SM. A left hemisphere basis for visual mental imagery? *Neuropsychologia*, 23(1): 115–118, 1985.
- Fiez AF. Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping*, 5: 79–83, 1997.
- Fink A, Grabner RH, Benedek M, Reishofer G, Hauswirth V, Fally M, et al. The creative brain: Investigation of brain activity during creative problem solving by means of EEG and fMRI. *Human Brain Mapping*, 30: 734–748, 2009.
- Finke RA. *Creative Imagery: Discoveries and Inventions in Visualization*. Hillsdale, NJ: Erlbaum, 1990.
- Fletcher PC, Shallice T, and Dolan RJ. “Sculpting the response space” – an account of left prefrontal activation at encoding. *NeuroImage*, 12: 404–417, 2000.
- Friston K, Holmes A, Worsley K, Polin JB, Frith C, and Frackowiak T. *Human Brain Mapping*, 2: 189–210, 1995.
- Gabrieli JD, Poldrack RA, and Desmond JE. The role of left prefrontal cortex in language and memory. *Proceedings of the National Academy of Sciences of the United States of America*, 95(3): 906–913, 1998.
- Gazzaniga MS. Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain*, 123: 1293–1326, 2000.
- Genovese CR, Laza NA, and Nichols T. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage*, 15: 870–878, 2002.
- Gibson C, Folley BS, and Park S. Enhanced divergent thinking and creativity in musicians: A behavioural and near-infrared spectroscopy study. *Brain and Cognition*, 69: 162–169, 2009.
- Goel V and Vartanian O. Dissociating the roles of right ventral lateral and dorsal lateral prefrontal cortex in generation and maintenance of hypotheses in set-shift problems. *Cerebral Cortex*, 15: 1170–1177, 2005.

- Goldberg RF, Perfetti CA, Fiez JA, and Schneider W. Selective retrieval of abstract semantic knowledge in left prefrontal cortex. *The Journal of Neuroscience*, 27(14): 3790–3798, 2007.
- Goldenberg G, Podreka I, Steiner M, Willmes K, Suess E, and Deecke L. Regional cerebral blood flow patterns in visual imagery. *Neuropsychologia*, 27: 641–664, 1989.
- Greake JG and Hansen PC. Neural correlates of intelligence as revealed by fMRI of fluid analogies. *NeuroImage*, 26: 555–564, 2005.
- Green AE, Fugelsang JA, Kraemer DJM, Shamosh NA, and Dunbar KN. Frontopolar cortex mediates abstract integration in analogy. *Brain Research*, 1096: 125–137, 2006.
- Green AE, Kraemer DJM, Fugelsang JA, Gray JR, and Dunbar KN. Connecting long distance: Semantic distance in analogical reasoning modulates frontopolar cortex activity. *Cerebral Cortex*, 20: 70–76, 2010.
- Guilford JP. *The Nature of Human Intelligence*. New York: McGraw-Hill, 1967.
- Halpern AR. Mental scanning in auditory imagery for songs. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 14: 193–202, 1988.
- Hampton JA. Emergent attributes in combined concepts. In Ward TB, Smith SM, and Vaid J (Eds), *Creative Thought: An Investigation of Conceptual Structures and Processes*. Washington DC: American Psychological Association, 1997: 83–110.
- Heilman KM, Nadeau SE, and Beversdorf DO. Creative innovation: Possible brain mechanisms. *Neurocase*, 9: 369–379, 2003.
- Henderson SJ. Inventors: The ordinary genius next door. In Sternberg RJ, Grigorenko EL, and Singer JL (Eds), *Creativity from Potential to Realization*. Washington DC: American Psychological Association, 2004: 103–125.
- Howard-Jones P, Blakemore S, Samuel E, Rummery I, and Claxton G. Semantic divergence and creative story generation: An fMRI investigation. *Cognitive Brain Research*, 25: 240–250, 2005.
- Hubel DH and Livingstone MS. Segregation of form, color and stereopsis in primate area 18. *Journal of Neuroscience*, 7: 3378–3415, 1987.
- Janowsky JS, Shimamura AP, Kritchevsky M, and Squire LR. Cognitive impairment following frontal lobe damage and its relevance to human amnesia. *Behavioral Neuroscience*, 103: 548–560, 1989.
- Jung RE, Segall JM, Bockholt HJ, Flores RA, Smith SM, Chavez RS, et al. Neuroanatomy of creativity. *Human Brain Mapping*, 31: 398–409, 2010.
- Jung-Beeman M. Bilateral brain processes for comprehending natural language. *Trends in Cognitive Sciences*, 9: 512–518, 2005.
- Jung-Beeman M, Bowden M, Haberman J, Frymiare J, Aramber-Liu S, Greenblatt R, et al. Neural activity when people solve problems with insight. *PLoS Biology*, 2: 500–510, 2004.
- Kan IP and Thompson-Schill SL. Selection from perceptual and conceptual representations. *Cognitive, Affective, & Behavioral Neuroscience*, 4: 466–482, 2004.
- Kapur S, Rose R, Liddle PF, Zipursky RB, Brown GM, Stuss D, et al. The role of the left prefrontal cortex in verbal processing: Semantic processing or willed action? *NeuroReport*, 5: 2193–2196, 1994.
- King RD, Rowland J, Oliver SG, Young M, Aubrey W, Byrne E, et al. The automation of science. *Science*, 324(5923): 85–89, 2009.
- Koestler A. *The Act of Creation*. New York: Dell, 1964.
- Kosslyn SM. *Image and Brain: The Resolution of the Imagery Debate*. Cambridge, MA: MIT Press, 1994.
- Kosslyn SM, Alpert NM, Thompson WL, Maljkovic V, Weise S, Chabris CE, et al. Visual mental imagery activates topographically organized visual cortex: PET investigations. *Journal of Cognitive Neuroscience*, 5: 263–287, 1993.
- Kosslyn SM and Ochsner K. In search of occipital activation during visual mental imagery. *Trends in Neurosciences*, 17: 290–292, 1994.
- Kowatari Y, Lee SH, Yamamura H, Nagamori Y, Levy P, Yamane S, et al. Neural networks involved in artistic creativity. *Human Brain Mapping*, 30: 1678–1690, 2009.
- Krawczyk DC, McClelland MM, Donovan CM, Tillman GD, and Maguire MJ. An fMRI investigation of cognitive stages in reasoning by analogy. *Brain Research*, 1342: 63–73, 2010.
- Laine M and Niemi J. Word fluency production strategies of neurological patients: Semantic and letter-based clustering. *Journal of Clinical and Experimental Neuropsychology*, 10: 28, 1988.
- Leboultier N and Marks DF. Mental imagery and creativity: A meta-analytic review study. *British Journal of Psychology*, 94: 29–44, 2003.
- Limb C and Braun A. Neural substrates of spontaneous musical performance: An fMRI study of jazz improvisation. *PLoS ONE* 3: e1679. <http://dx.doi.org/10.1371/journal.pone.0001679>, 2008.
- Luria AR. *Higher Cortical Functions in Man*. New York: Basic Books, 1966.
- Malouin F, Richards CL, Jackson PL, Dumas F, and Doyon J. Brain activations during motor imagery of locomotor-related tasks: A PET study. *Human Brain Mapping*, 19: 47–62, 2003.
- Marks DF. Visual imagery differences in the recall of pictures. *British Journal of Psychology*, 64: 17–24, 1973.
- Mashal N, Faust M, Hendler T, and Jung-Beeman M. An fMRI investigation of the neural correlates underlying the processing of novel metaphoric expressions. *Brain and Language*, 100: 115–126, 2007.
- Mednick SA. The associative basis of the creative process. *Psychological Review*, 69(3): 220–232, 1962.
- Metter EJ, Hanson WR, Jackson CA, Kempler D, van Lancker D, Massiotto JC, et al. Temporoparietal cortex in aphasia: Evidence from positron emission tomography. *Archives of Neurology*, 47(11): 1235, 1990.
- Miyashita Y. How the brain creates imagery: Projection to primary visual cortex. *Science*, 268: 1719–1720, 1995.
- Mobley MI, Doares LM, and Mumford MD. Process analytic models of creative capacities: Evidence for the combination and reorganization process. *Creativity Research Journal*, 5: 125–155, 1992.
- Olivetti Belardinelli M, Palmiero M, Sestieri C, Nardo D, Di Matteo R, Londei A, et al. An fMRI investigation on image generation in different sensory modalities: The influence of vividness. *Acta Psychologica*, 132: 190–200, 2009.
- Paivio A. Mental imagery in associative learning and memory. *Psychological Review*, 76: 241–263, 1969.
- Perret E. The left frontal lobe of man and the suppression of habitual responses in verbal categorical behavior. *Neuropsychologia*, 12: 323–330, 1974.
- Pitt MA and Crowder RG. The role of spectral and dynamic cues in imagery for musical timbre. *Journal of Experimental Psychology: Human Perception and Performance*, 18(3): 728–738, 1992.
- Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, and Gabrieli JD. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage*, 10(1): 15–35, 1999.
- Rapp AM, Leube DT, Erb M, Grodd W, and Kircher TTJ. Correlates of metaphor processing. *Cognitive Brain Research*, 20: 395–402, 2004.
- Razumnikova OM. Creativity related cortex activity in the remote associates task. *Brain Research Bulletin*, 73: 96–102, 2007.
- Richards IA. *The Philosophy of Rhetoric*. Oxford: Oxford University Press, 1936.
- Royce J. The psychology of invention. *The Psychological Review*, 2: 113–144, 1898.
- Shamay-Tsoory SG, Adler N, Aharon-Peretz J, Perry D, and Mayseless N. The origins of originality: The neural bases of creative thinking and originality. *Neuropsychologia*, 49: 178–185, 2011.

- Shelton AL and Gabrieli JDE. Neural correlates of encoding space from route and survey perspectives. *The Journal of Neuroscience*, 22(7): 2711–2717, 2002.
- Sieborger F, Ferstl E, and von Gramon Y. Making sense of nonsense: An fMRI study of task induced inference processes during discourse comprehension. *Brain Research*, 1166: 77–91, 2007.
- Simon HA. Discovery, invention, and development: Human creative thinking. *Proceedings of the National Academy of Sciences of the United States of America*, 80: 4569–4571, 1983.
- Slotnick SD and Schacter DL. The nature of memory related activity in early visual areas. *Neuropsychologia*, 44: 2874–2886, 2006.
- Stangalino C, Semenza C, and Mondini S. Generating visual mental images: Deficit after brain damage. *Neuropsychologia*, 33: 1473–1483, 1995.
- Sternberg R. The domain generality versus domain specificity debate: How should it be posed? In Kaufman JC and Baer J (Eds), *Creativity Across Domains: Faces of the Muse*. Hillsdale, NJ: Erlbaum, 2005: 299–306.
- Stephan KE, Marshall JC, Freiton KJ, Rewe JB, Retzl A, Silles K, et al. Lateralized cognitive processes and lateralized task control in the human brain. *Science*, 301(5631): 384–386, 2003.
- Stoeckel C, Gough PM, Watkins KE, and Devlin JT. Supramarginal gyrus involvement in visual word recognition. *Cortex*, 45(9): 1091–1096, 2009.
- Stuss DT, Alexander MP, Hamer L, Palumbo C, Dempster R, Binns M, et al. The effects of focal anterior and posterior brain lesions on verbal fluency. *Journal of the International Neuropsychological Society*, 4: 265–278, 1998.
- Talairach J and Tournoux P. *Co-planar Stereotaxic Atlas of the Human Brain*. New York: Thieme Medical Publishers, 1988.
- The World Book Encyclopedia. World Book Inc., 1990: 356–366.
- Thompson-Schill SL, D'Esposito M, Aguirre GK, and Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences of the United States of America*, 94: 14792–14797, 1997.
- Tippet LJ. The generation of mental images: A review of neuropsychological research and theory. *Psychological Bulletin*, 112: 415–432, 1992.
- Torrance EP. *Guiding Creative Talent*. Englewood Cliffs, NJ: Prentice-Hall, 1962.
- Torrance EP. *Torrance Tests of Creative Thinking: Norms-technical Manual*. Lexington, MA: Ginn, 1974.
- Vogel S. *Cats' Paws and Catapults: Mechanical Worlds of Nature and People*. New York: Norton, 1998.
- Ward TB, Smith SM, and Finke RA. Creative cognition. In Sternberg RJ (Ed), *Handbook of Creativity*. Cambridge University Press, 1999: 189–212.
- Wiener N. *Invention: The Care and Feeding of Ideas*. MA: MIT Press, 1993.
- Worsley KJ, Evans AC, Marrett S, and Neelin PA. Three-dimensional statistical analysis for CBF activation studies in human brain. *Journal of Cerebral Blood Flow and Metabolism*, 12: 900–912, 1992.
- Worsley KJ and Friston KJ. Analysis of functional MRI time-series revisited again. *NeuroImage*, 2: 173–181, 1995.
- Yang FG, Edens J, Simpson C, and Krawczyk DC. Differences in task demands influence the hemispheric lateralization and neural correlates of metaphor. *Brain and Language*, 111: 114–124, 2009.
- Yoo SS, Freeman DK, McCarthy JJ, and Jolesz FA. Neural substrates of tactile imagery: A functional MRI study. *NeuroReport*, 14(4): 581–585, 2003.
- Zhang JX, Feng CM, Fox PT, Gao JH, and Tan LH. Is left inferior frontal gyrus a general mechanism for selection? *NeuroImage*, 23: 596–603, 2004.