



A meta- analysis of neuroimaging studies on divergent thinking using activation likelihood estimation

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A meta-analysis of neuroimaging studies on divergent thinking using activation likelihood estimation

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Running Head: Divergent thinking

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Abstract

In this study, an activation likelihood estimation (ALE) meta-analysis was used to conduct a quantitative investigation of neuroimaging studies on divergent thinking. Based on the ALE results, the functional magnetic resonance imaging (fMRI) studies showed that distributed brain regions were more active under divergent thinking tasks (DTTs) than those under control tasks, but a large portion of the brain regions were deactivated. The ALE results indicated that the brain networks of the creative idea generation in DTTs may be composed of the lateral prefrontal cortex, posterior parietal cortex [such as the inferior parietal lobule (BA 40) and precuneus (BA 7)], anterior cingulate cortex (BA 32), and several regions in the temporal cortex [such as the left middle temporal gyrus (BA 39) and left fusiform gyrus (BA 37)]. The left dorsolateral prefrontal cortex (BA 47) was related to selecting the loosely and remotely associated concepts and organizing them into creative ideas, whereas the anterior cingulate cortex (BA 32) was related to observing and forming distant semantic associations in performing DTTs. The posterior parietal cortex may be involved in the semantic information related to the retrieval and buffering of the formed creative ideas, and several regions in the temporal cortex may be related to the stored long-term memory. In addition, the ALE results of the structural studies showed that divergent thinking was related to the dopaminergic system (e.g., left caudate and claustrum). Based on the ALE results, both fMRI and structural MRI studies could uncover the neural basis of divergent thinking from different aspects (e.g., specific cognitive processing and stable individual difference of cognitive capability).

Key words: creativity, divergent thinking, activation likelihood estimation; MRI studies

1 Introduction

Creativity is the foundation of human civilizations, and all progress and innovation depend on the ability of humans to create new things. Thus, finding the mechanism of creativity in various fields, such as psychology, education, economics, and industry, is important (Fink et al., 2013). Previous studies suggested that creative people are characterized by their ability to generate ideas by fluency (produce large quantities of ideas), flexibility (produce different ideas), and originality (produce novel outputs) (Guilford, 1950; Fink et al., 2009). Motivated by Guilford's definition of creative people, experimental investigations on creativity are mainly facilitated by divergent thinking tasks (DTTs). DTTs comprise an important domain in elucidating the neural mechanisms of creative thinking. With the recent development of neuroimaging techniques, DTTs have been widely used in investigating the neural basis of creative thinking.

1.1 Experimental tasks in neuroimaging studies on divergent thinking

Several DTTs, such as alternative uses test (AUT) (Guilford, 1967), creative story or sentence generation tasks (Howard-Jones et al., 2005; Shah et al., 2011), creative metaphors (Mashal et al., 2007; Benedek et al., 2014b), match problems and remote associates test (Dietrich and Kanso, 2010), and Torrance test of creative thinking (Dietrich and Kanso, 2010; Fink et al., 2010), are widely used to investigate the neural basis of creativity (Dietrich and Kanso, 2010). The match problems (Goel and Vartanian, 2005) and remote associates test (Jung-Beeman et al., 2004; Kounios et al., 2004; Subramaniam et al., 2009) are employed to investigate the neural basis of insight problem solving and mainly present one effective solution. Divergent thinking is often regarded as the ability to generate multiple original solutions to an open-ended problem (Guilford, 1967). In completing DTTs, subjects should simultaneously attend to numerous things (defocused attention) and form distant and unusual associations between different semantic concepts (Fink et al., 2009), or expand the concept of an object to generate novel and original ideas (Abraham et al., 2013). In the present study, the DTTs mainly refer to semantic divergent tasks, such as AUT, creative story generation, and novel metaphor task.

1.1.1 AUT

AUT is a widely used prototypical example of divergent thinking and well-validated measure of creativity (Kühn et al., 2013; Fink et al., 2010; Jung et al., 2010b). In classic AUT, subjects are instructed to generate alternative uses of conventional everyday objects, such as bricks or newspapers. Fluency, flexibility, and originality are investigated using AUT. To investigate the neural basis of divergent thinking, the uses of the objects test are considered control tasks (CTs), in which the subjects are asked to list as many common uses of a given object as possible (Kühn et al., 2013). In addition, other studies used the object characteristics task (OCT) as CTs, in which the subjects are asked to name typical attributes of conventional objects (Fink et al., 2009, 2010).

1.1.2 Sentence or story generation task

In creative sentence or story generation task, the subjects are asked to generate a story or sentence based on a set of words (Howard-Jones, 2005; Bechtereva et al., 2004; Bekhtereva et al., 2000). **Similar to AUT**, to generate a creative sentence or story, semantic divergence is required to obtain contextual elements that are associated with a set of words, and find additional relationships or select combinations that contribute to the objective (Howard-Jones, 2005).

1.1.3 Novel metaphor task

A metaphor is a figure of speech that describes a subject by asserting that it is, at some point of comparison, similar to an unrelated object. Benedek et al. (2014b) suggested that “metaphor comprehension involves forming an abstract connection between two concepts in semantic memory” and the connection is formed by extracting and relating similar properties of different concepts (Glucksberg, 2001, 2003). For example, the metaphor “the close friends were a bag of toffees” involves the identification of the conceptual category “something that is sweet” extraction of related properties of close friends and toffee, and simultaneous inhibition of their unrelated properties. Therefore, semantic divergence, such as verbal fluency, is believed to be required for metaphor comprehension, as suggested by Beaty and Silvia (2013).

Based on the aforementioned discussion, AUT, creative story generation, and novel metaphor tasks are possibly open-ended problems that require several common cognitive

processes, such as semantic processing, defocused attention, as well as distant and unusual associations (e.g., Fink et al., 2009; 2010; 2011; Howard-Jones et al., 2005; Abraham et al., 2012; Kleibeuker et al., 2013). Therefore, discovering the brain basis of divergent thinking by integrating the functional magnetic resonance imaging (fMRI) results from these DTTs could be important and effective.

1.2 Neural basis of divergent thinking

1.2.2 fMRI studies on divergent thinking

Prefrontal cortex is critical for creativity using DTTs (Mashal et al., 2007; Abraham et al., 2012; Kleibeuker et al., 2014). Several studies have determined that the dorsolateral prefrontal cortex (DLPFC) and the ventrolateral prefrontal cortex (VLPFC) are involved in the comprehension of novel metaphors and generation of creative uses of common objects (Mashal et al., 2007; Abraham et al., 2012). However, using AUT as experimental tasks, Kleibeuker et al. (2014) found that DLPFC (BA 6 or/and BA 9) is involved in generating creative ideas, whereas VLPFC is not. By comparing AU (completing AUT) and OC (completing OCT), Fink et al. (2009, 2010) discovered that the prefrontal cortex is not associated with generating creative uses (Fink et al., 2009). However, the comparison of AU and fixation revealed that the left inferior frontal gyrus is involved in the creative idea generation in DTTs. In addition, several studies have indicated that the anterior cingulate cortex (ACC) is involved in completing DTTs (Abraham et al., 2012; Fink et al., 2009; Howard-Jones et al., 2005; Kleibeuker et al., 2013).

Apart from the numerous studies that have emphasized the prominent role of the prefrontal cortex in divergent thinking, several studies have determined that a few regions of the parietal cortex, such as the left inferior parietal lobule (IPL) (Abraham et al., 2012; Benedek et al., 2014a; Fink et al., 2010), left supramarginal gyrus (SMG), and right angular gyrus (Fink et al., 2010), are involved in completing DTTs. In addition, activities in several regions of the temporal and occipital cortices, such as the left middle temporal gyrus (MTG) (Bechtereva et al., 2004; Mashal et al., 2007; Fink et al., 2009) and left fusiform gyrus (FG) (Fink et al., 2011; Abraham et al., 2012), are observed when participants perform DTTs.

1.2.2 Structural MRI studies on divergent thinking

Kanai and Rees (2011) suggested that “in the neuroscience of human behavior and

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cognition, inter-individual differences are often treated as a source of ‘noise’ and therefore discarded through averaging data from a group of participants.” Creative individuals have been argued to possess several innate traits different from those of lower/non-creative individuals, such as defocused attention (Mendelsohn, 1976) and flat associative hierarchies (Mednick, 1962). Moreover, structural differences may reveal a few innate traits or abilities of creative individuals (Fink et al., 2013). Inter-individual variability in divergent thinking has been recently predicted from the structures of gray (Jung et al., 2010b; Fink et al., 2013; Kühn et al., 2013) and white matter (Jung et al., 2010a; Takeuchi et al., 2010b) using structural MRI. Previous studies on brain structure determined that many regions in the posterior brain, such as the right cuneus (Jung et al., 2010; Fink et al., 2013) and inferior parietal gyrus (IPG, BA 19) (Jung et al., 2010), are associated with divergent thinking. Therefore, we speculated that these brain regions observed in the structural MRI studies on divergent thinking may be related to several innate traits of creative individuals.

1.3 Hypotheses of the present study

Although previous reviews (Arden et al. 2010; Dietrich and Kanso, 2010) have summarized the brain activity patterns related to creativity, an integrated understanding of the information is difficult to obtain because of the diverse tasks employed in creativity studies. Activation likelihood estimation (ALE) is a foci-based meta-analysis technique and can estimate the likelihood of brain activations across multiple studies (Eickhoff et al., 2009; Laird et al., 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002). Thus, a significant convergence between activation foci from different experiments (contrast between experiment condition) may be observed using ALE (Herz et al., 2013; Krall et al., 2014).

Based on previous studies, we hypothesized that the brain networks of creative idea generation in DTTs may be composed of the lateral prefrontal cortices (LPFC), such as DLPFC and VLPFC (Mashal et al., 2007; Abraham et al., 2012; Kleibeuker et al., 2014), ACC (e.g., Abraham et al., 2012; Fink et al., 2009; Howard-Jones et al., 2005; Kleibeuker et al., 2013), the posterior parietal regions (e.g., Fink et al., 2009; 2010; 2011), and the temporal and the occipital cortex (e.g., Bechtereva et al., 2004; Mashal et al., 2007; Fink et al., 2009).

First, numerous studies have demonstrated the involvement of semantic knowledge in generating creative ideas on divergent thinking (Fink et al., 2009; Howard-Jones et al., 2005).

Distributed networks in the brain represent semantic knowledge (Broadbent, 1879; Lissauer and Jackson, 1988). Previous studies (Demonet et al., 1992; Martin and Chao, 2001) also indicated that the semantic brain regions are distributed in the ventral and lateral temporal cortices (VTC and LTC, respectively), and the activation of these regions is affected by object categories (Martin and Chao, 2001). Binder (2009) concluded that seven brain regions are associated with semantic processes, which refers to the cognitive act of accessing stored semantic knowledge about the world. These regions include the posterior IPL, LTC, VTC, dorsomedial prefrontal cortex (DMPFC), inferior frontal gyrus (IFG), ventromedial prefrontal cortex (VMPFC), and posterior cingulate gyrus (CG). Thus, several brain regions that are associated with semantic processing, such as the left IPL, left IFG, left VTC, and LTC, could be observed in the present ALE study.

Second, as Fink had explained, creative idea generation requires more internal cognitive demands, and the inhibition of irrelevant cognitive processes ensures that creative idea generation is not disturbed by irrelevant information (e.g., Fink et al., 2009; 2010; 2011). Therefore, several brain regions associated with cognitive control and attentional networks, such as ACC (Botvinick et al., 2004; Kerns et al., 2004; Weissman et al., 2003), right DLPFC (Fox et al., 2006; Dietrich, 2004), and right posterior parietal regions (Posner & Petersen, 1989; Cabeza & Nyberg, 2000; Fink et al. 2009; 2010; 2011), could be observed in the present ALE study.

Third, based on previous structural studies (Fink et al., 2013; Jung et al., 2009; Takeuchi et al., 2010a), we speculated that a few innate traits of creative individuals may be observed through ALE analysis of the structural studies in the divergent thinking.

2 Method

2.1 Selection of the studies

We searched the PNAS, PLOS, MITPress, SAGE, Oxford Press Wiley, Elsevier Science, and Springer databases using the following keywords: creative, creativity, insight, innovation, drawing, music, art, divergent thinking, problem solving, fMRI, MRI, positron emission tomography (PET), neural correlations, and imaging.

A total of 34 published fMRI and PET studies on the neural basis of creativity were

selected based on the following requirements: all the subjects in the study, which used MRI techniques, were healthy adults; the coordinates in each of the studies were in the standard Montreal Neurological Institute or Talairach space; and all the reported activation coordinates were based on the entire brain and obtained by comparing experimental tasks (i.e., DTTs) with CTs.

Based on the definition of divergent thinking (Guilford, 1950; Fink et al., 2009) and previous studies (Dietrich and Kanso, 2010; Howard-Jones et al., 2005; Mashal et al., 2007; Fink et al., 2010), 17 published studies (10 fMRI and 7 structural studies; Table 1) were selected for the meta-analysis of divergent thinking. Moreover, seven studies (Table 1), which included the results of DTTs > CTs and CTs > DTTs, were selected from the 11 fMRI studies for the meta-analysis to obtain the brain images of deactivation under DTTs than CTs.

INSERT TABLE 1 ABOUT HERE

2.2 ALE technique

ALE is a common method to integrate neuroimaging results across studies (Turkeltaub et al., 2002; Laird et al., 2005). In ALE, the significantly reported coordinates, namely, the active foci, were treated not as single points but as centers for 3D Gaussian probability distributions that reveal the spatial uncertainty associated with neuroimaging results (Turkeltaub et al., 2002; Spaniol et al., 2009). Thereafter, the probability distributions of each experiment were combined into a modeled activation (MA) map using the recently proposed approach that prevents undue summation between foci (Turkeltaub et al., 2012). The ALE scores were then calculated by considering the voxel-wise union based on these individual MA maps. The likelihood of activation for each standard-space voxel was calculated under a null distribution of spatial independence (Fitzgerald et al., 2008; Sabatinelli et al., 2011). For statistical inference, the ALE results were assessed against a null distribution of random spatial association between experiments, which was conducted using a recently proposed analytical method (Eickhoff et al. 2012).

INSERT TABLE 2, TABLE 3 and TABLE 4 ABOUT HERE

2.3 ALE analysis of the neuroimaging studies

Meta-analysis was performed using the revised version (Eickhoff et al., 2009, 2012) of

the ALE approach using GingerALE 2.1 software (<http://brainmap.org/>). In the ALE analysis of single datasets, COIs of fMRI studies on DTTs > CTs (17 contrast and 85 foci; Table 2) and CTs > DTTs (7 contrast and **30** foci; Table 3), as well as on structural studies (15 contrast and 67 foci; Table 4), were input separately. To obtain the optimal brain patterns of divergent thinking, the threshold of the results was set to a false discovery rate-corrected $p < 0.05$ **with a minimum volume of 100 mm³**. The results were viewed using Mango software (<http://ric.uthscsa.edu/mango/>) and overlaid to a standard space using the Talairach file (Colin1.1.nii) (www.brainmap.org/ale). In the conjunction analysis, we compared the ALE results of functional studies and the ALE results of structural studies. Krall et al. (2014) argued that “the usage of peak coordinates might lead to mis- or over-interpretation of the results in ALE analysis.” Thus, in the present study, we reported the peak coordinates of the significant cluster and demonstrated the brain regions nearest the peak coordinates within ± 5 mm.

3 Results

Seventeen MRI publications of divergent thinking (10 for fMRI studies; 7 for structural MRI studies) with an average sample size of 27.27 ± 10.06 (153 females; 147 males) for fMRI studies and 88.57 ± 88.26 (301 females and 313 male) for structural MRI studies were included in the present ALE analysis. The ages of the subjects in the selected publications mainly ranged from 18 to 30.

As shown in Table 2, although the generated ideas were evaluated based on originality, appropriateness, novelty, creativity, or not evaluated, the instruction of each study almost required subjects to generate as many creative (original) ideas as possible. Thus, we thought that these brain functional patterns associated with DTs might be effective for ALE analysis by comparing the divergent thinking condition to the control condition.

3.1 ALE results of active regions in DTTs

Table 4 and Figure 1 show the ALE results of fMRI studies on divergent thinking. Six clusters in the left hemisphere were more active under DTTs than those under CTs. The peak ALE values of the first cluster were located in IPL (BA 40) [the cluster coordinates are from $(-62, -38, 28)$ to $(-48, -28, 38)$] and the main brain regions in the cluster included IPL (BA

40) and SMG (BA 40). The peak ALE values of the second cluster were located in the amygdala [the cluster coordinates are from (-30, -18, -18) to (-20, -8, -8)], and the main brain regions in the cluster included the hippocampus, amygdala, lateral globus pallidus, and parahippocampal (BA 28). The peak ALE values of the third cluster were located in the left FG (BA 37) [the cluster coordinates are from (-52, -64, -16) to (-42, -54, -2)], and the main brain regions in the cluster included FG (BA 37), the middle occipital gyrus (BA 19, BA 20 and BA 37), and the inferior temporal gyrus (BA 19 and BA 37). The peak ALE values of the fourth cluster were located in the middle frontal gyrus (MFG, BA 46) [the cluster coordinates are from (-48, 28, 12) to (-42, 36, 24)], and the main brain regions in the cluster included MFG (BA 46) and the inferior frontal gyrus (BA 46). The peak ALE values of the fifth cluster were located in the precentral gyrus (BA 6) [the cluster coordinates are from (-52, 0, 20) to (-44, 14, 26)], and the main brain regions in the cluster included MFG (BA 9) and the IFG (BA 9 and BA 44). The peak ALE values of the sixth cluster were located in the MTG (BA 39) [the cluster coordinates are from (-46, -74, 18) to (-44, -66, 24)], and the main brain regions in the cluster included MTG (BA 39).

Three other clusters were located in the right hemisphere. The peak ALE values of the first cluster were located in the cingulate gyrus (BA 32) [the cluster coordinates are from (-4, 18, 26) to (10, 26, 36)], and the main brain regions in the cluster included CG (BA 32 and BA 24). The second peak ALE values were observed in MFG (BA 46) [the cluster coordinates are from (46, 18, 20) to (50, 24, 26)], and the main brain regions in the cluster included MFG (BA 46) and IFG (BA 45). The peak ALE values of the three cluster were observed in ACC (BA 32) [the cluster coordinates are from (10, 32, 18) to (16, 38, 22)], and the main brain regions in the cluster included ACC (BA 32) and the medial frontal gyrus (BA 9).

INSERT TABLE 5 AND FIGURE 1 ABOUT HERE

3.2 ALE results of deactivated regions under DTTs

Table 4 and Figure 2 show the ALE results of fMRI studies on divergent thinking. Two clusters in the right hemisphere were more deactivated under DTTs than those under CTs. The peak ALE values of the first cluster were located in the precuneus (BA 19) [the cluster coordinates are from (26, -66, 40) to (34, -58, 46)], and the main brain regions in the cluster included the superior parietal lobule (SPL, BA 7), precuneus (BA 19), and inferior parietal

lobule (IPL, BA 39). The peak ALE values of the second cluster were located in IPL (BA 40) [the cluster coordinates are from (44, -56, 36) to (52, -52, 44)], and the main brain regions in the cluster included IPL (BA 40).

3.3 ALE results of structural studies on divergent thinking

Table 5 and Figure 2 show the ALE results of DTTs. Three clusters were located in the left hemisphere. The peak ALE values of the first cluster were located in the insula of the prefrontal cortex (BA 13) [the cluster coordinates are from (-46, 6, -8) to (-36, 14, 2)], and the main brain regions in the cluster included the insula (BA 13), inferior frontal gyrus (BA 47), and superior temporal gyrus (BA 38 and BA 22)]. The peak ALE values of the second cluster were located in the caudate tail [the cluster coordinates are from (-30, -38, 6) to (-22, -28, 14)], and the main brain regions in the cluster included the caudate tail and pulvinar. The peak ALE values of the third cluster were located in the claustrum [the cluster coordinates are from (-26, 22, 4) to (-18, 28, 10)], and the main brain regions in the cluster included the claustrum and caudate head.

Four other clusters were located in the right hemisphere. The peak ALE values of the first cluster were located in the cuneus (BA 18) [the cluster coordinates are from (2, -78, 14) to (16, -68, 24)], and the main brain regions in the cluster included the cuneus (BA 17 and BA 18) and the precuneus (BA 31). The peak ALE values of the second cluster were located in the middle temporal gyrus (MTG, BA 39) [the cluster coordinates are from (42, -58, 20) to (46, -50, 28)], and the main brain regions in the cluster included MTG (BA 39) and STG (BA 39). The peak ALE values of the second cluster were located in CG (BA 24) [the cluster coordinates are from (6, -6, 36) to (16, -2, 40)], and the main brain regions in the cluster included CG (BA 24). The peak ALE values of the fourth cluster were located in the middle temporal gyrus and middle occipital gyrus (MOG, BA 19) [the cluster coordinates are from (36, -66, 8) to (40, -62, 14)], and the main brain regions in the cluster included MOG (BA 19) and MTG (BA 39 and BA 37).

INSERT TABLE 6 AND FIGURE 2 ABOUT HERE

Furthermore, the results of the conjunction analysis indicated that no common region existed between the ALE results of DTTs > CTs and the results of the structural studies.

4 Discussion

In this study, an ALE meta-analysis was conducted to investigate the integrated brain patterns of divergent thinking. Based on our criteria, 17 studies (10 fMRI studies and 7 structural studies) on divergent thinking were selected. The ALE results of the fMRI studies showed that the bilateral DLPFC (BA 46), the right ACC (BA 32), the posterior parietal cortex (BA 7 and BA 40), and the left FG (BA 37) and MTG (BA 39) were involved in the creative idea generation. In addition, the ALE results of the structural studies indicated that several key brain regions associated with individual differences on divergent thinking, such as the right cuneus (BA 18), right MFG (BA 39), right SPG (BA 39), right MOG (BA 19), left caudate tail, and left claustrum, were mainly located in the right hemisphere. The implications of these key regions in divergent thinking are discussed in the following section.

4.1 Function of the brain regions in divergent thinking

4.1.1 Function of the frontal cortex in divergent thinking

Our meta-analysis results showed that the bilateral DLPFC (BA 46), including MFG (BA 46) and IFG (BA 46), was more active under DTTs than that under CTs. Previous studies indicated that DLPFC is mainly related to the manipulation or observation of active information within working memory (Petrides, 1994; Owen et al., 1999; Carpenter et al., 2000). In particular, Blumenfeld and Ranganath (2006, 2007) found that DLPFC is possibly involved in organization, such as the comparison or transformation of relationships among items that are active in the working memory (Wagner et al., 2001; Blumenfeld and Ranganath, 2006; Crone et al., 2006; Mohr et al., 2006) or chunking (organizing separate pieces of information into fewer units) (Miller et al., 1960; Bor et al., 2003; 2004). Moreover, the lateral prefrontal cortex (DLPFC and VLPFC) had been suggested to have played important roles in the creative idea generation in DTTs, such as in semantic processing (Abraham et al., 2012; Fink et al., 2009), selective attention (Fink et al., 2009; Dietrich, 2004), cognitive flexibility (particularly switching between semantic categories or sub-categories) (Hirshorn and Thompson-Schill, 2006; Kleibecker et al., 2013), sustained attention (Shah et al., 2011; Dietrich, 2004), and combining existing stored information (Dietrich, 2004; Kleibecker et al., 2013). Moreover, the lateral prefrontal cortex, such as the inferior frontal gyrus (IFG), was

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3 sensitive to the influence of semantic distance or associative strength between concepts, such
4 as weaker associative strength leading to a stronger BOLD response in these areas (Bunge,
5 Wendelken, Badre, & Wagner, 2005; Green, Kraemer, Fugelsang, Gray, & Dunbar, 2010;
6 Abraham et al., 2012). Benedek et al. (2014) further suggested that the “IFG involved in
7 retrieving and selecting relevant remote associations, integration of loosely related semantic
8 concepts, and eventually verbal elaboration of ideas.” Therefore, DLPFC (BA 46) may be
9 involved in novel idea organization, such as organizing loosely or remotely related semantic
10 concepts into creative ideas in working memory and retrieving and selecting relevant remote
11 associations.
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20 In addition, the right ACC (BA 32) was strongly activated under DTTs than that under
21 CTs. The right ACC is related to numerous cognitive processes, such as monitoring conflict
22 (Botvinick et al., 2004; Kerns et al., 2004; Weissman et al., 2003), generating creative ideas
23 (Howard-Jones et al., 2005), and evaluating (Ellamil et al., 2011). Based on conflict
24 monitoring theory (Botvinick et al., 2004; Kerns et al., 2004; Weissman et al., 2003), ACC is
25 also related to the observation of competing responses, such as multiple associations or
26 strategies involved in solving problems (Subramaniam et al., 2009). Previous studies likewise
27 indicated that ACC is involved in suppressing irrelevant thoughts (Wyland et al., 2003;
28 Anderson et al., 2004) and the semantic processing of distant associations (Howard-Jones et
29 al., 2005; Seger et al., 2000). Thus, our findings suggested that the right ACC (BA 32) may be
30 involved in monitoring and forming distant semantic associations by suppressing irrelevant
31 thoughts when performing DTTs.
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43 ***4.1.2 Function of posterior parietal brain areas in divergent thinking***

44 The ALE results showed that the left IPL (BA 40), including SMG (BA 40), was more
45 active under DTTs than that under CTs. To a certain extent, many studies indicated that the
46 left parietal regions in BA 40 play important roles in generating creative ideas (Bechtereva et
47 al., 2004; Abraham et al., 2012; Fink et al., 2010). In a recent study, Benedek et al. (2014)
48 suggested that the left IPL (BA 40) may be involved in episodic memory retrieval when
49 generating new ideas. Other studies also indicated that IPL (BA 40) is related to the verbal
50 generation of creative ideas (Pavlova and Romanenko, 1988; Bechtereva et al., 2004). Binder
51 et al. (2009) suggested that the posterior IPL is an important region for semantic processing.
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Moreover, the phonological loop store is related to the left posterior parietal cortices (BA 40), whereas the articulatory rehearsal process is related to the Broca's area (BA 6/44) (Paulesu et al., 1993; Jonides et al., 1996; Baddeley, 2003). Therefore, we speculated that the stronger activation of the posterior parietal cortices (IPL, BA 40) may be related to the buffering of the relevant semantic information during divergent thinking.

In addition, the clusters exhibited peak values in the right precuneus (BA 19), including the right SPL (BA 7), and the right IPL (BA 40) demonstrated greater deactivation under DTTs than that under CTs. Posner and Petersen (1989) and Cabeza and Nyberg (2000) demonstrated the involvement of the right posterior parietal regions in attention. Cabeza et al. (2008) reported that the right posterior parietal regions are composed of the dorsal parietal cortex (DPC), including the intraparietal sulcus and SPL, and the ventral parietal cortex (VPC), including the supramarginal and angular gyri (also known as IPL). They argued that the DPC activity is related to preparatory top-down attention (allocation of attentional resources to memory retrieval based on current goals), whereas the VPC activity reveals the capture of bottom-up attention by the target (attention captured by the bottom-up information that enters a working memory either from the senses or from long-term memory) (Cabeza et al., 2008, 2011). Therefore, as suggested by previous studies (Fink et al., 2009; 2010; 2011), the creative idea generation requires more internal processing demands, and the deactivation of the right SPL (BA 7) and IPL (BA 40) may be related to the inhibition of irrelevant cognitive processes (such as retrieval of prevalent, typical, or directly stimulus-related information) under DTTs relative to CTs.

4.1.3 Function of the posterior temporal cortex in divergent thinking

Our results indicated that the posterior temporal cortex [left MTG (BA 37) and left FG (BA 37)] was related to divergent thinking. Objective concepts are suggested to be possibly represented by distributed networks in the brain (Broadbent, 1879; Lissauer and Jackson, 1988), and storage and retrieval partially depend on VTC and LTC (Gorno-Tempini et al., 2004; Thompson-Schill et al., 2005). Moreover, Martin and Chao (2001) indicated that object naming and identifying are related to distributed brain regions, such as the left MTG and left FG. In addition, Knight and D'Esposito (2003) found that DLPFC is related to the maintenance operation or top-down process that influences the individual external or internal

milieu maintained by other posterior areas. In particular, the posterior cortical regions, such as the middle temporal cortex, are influenced by top-down feedback information from the prefrontal cortex (Badre et al., 2005; Gold et al., 2006). Therefore, the posterior temporal cortex [left MTG (BA 39) and left FG (BA 37)] and left DLPFC (BA 46) may be related to the generation of new ideas. We suggested that the posterior temporal cortex may be correlated with the activation of semantic items related to novel ideas, whereas the left DLPC (BA 46) may be involved in organizing these items into novel ideas.

4.1.4 Brain networks of divergent thinking based on ALE analyses of fMRI studies

As the parieto-frontal integration theory (Jung and Haier, 2007) suggested, the brain network of the intelligence mainly includes the DLPFC (BAs 6, 9, 10, 45, 46, 47), IPL (BA 40 and BA 39), SPL (BA 7), and ACC (BA 32), as well as the regions within the temporal (BAs 21, 37) and occipital (BAs 18, 19) lobes. Based on our ALE results, we determined that the creative idea generation (DT) may have a few brain regions similar to intelligence, such as LPFC (BA 46), posterior parietal regions [IPL (BA 40) and SPL (BA 7)], ACC (BA 32), and posterior temporal cortex [MTG (BA 37) and FG (BA 37)]. Thus, we speculated that the brain networks of creative idea generation in DTTs may be also composed of these regions. Thereafter, we will discuss the brain networks associated with creativity based on the specific functions of each brain regions.

First, the left IFG (46), left IPL (40), left MTG (BA 37), and left FG (BA 37) were associated with the semantic system (e.g., Binder et al., 2009; Gorno-Tempini et al., 2004; Thompson-Schill et al., 2005), which may be involved in creative idea generation. In particular, IFG (BA 46) was related to retrieving and selecting relevant remote association (e.g., Bunge, Wendelken, Badre, & Wagner, 2005; Green, Kraemer, Fugelsang, Gray, & Dunbar, 2010; Abraham et al., 2012; Benedek et al., 2014); SPL (BA 40) may be involved in the buffering of the relevant semantic information in the working memory; and the left MTG (BA 37) and the left FG (BA 37) may be associated with the activated long-term memory related to the creative idea generation. In addition, the left MFG (BA 46) may be related to organizing loosely or remotely related semantic concepts into creative ideas (e.g., Wagner et al., 2001; Blumenfeld and Ranganath, 2006; Crone et al., 2006; Mohr et al., 2006). ACC (BA 32) is involved in monitoring and forming distant semantic associations by suppressing

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3 irrelevant thoughts (e.g., Wyland et al., 2003; Anderson et al., 2004; Howard-Jones et al.,
4 2005; Seger et al., 2000). We speculated that the semantic system may play an important role
5 in creative idea generation, including activating long-term memory (left MTG), retrieving and
6 selecting relevant remote association (IFG), organizing loosely or remotely related semantic
7 concepts into creative ideas (left MFG), buffering of relevant semantic information (left SPL),
8 and monitoring and forming distant semantic associations by suppressing irrelevant thoughts
9 (right ACC).

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Second, as Fink had explained, creative idea generation requires more internal cognitive demands, and the inhibition of irrelevant cognitive processes ensures that the creative idea generation is not disturbed by irrelevant information (e.g., Fink et al., 2009; 2010; 2011). Therefore, we speculated that the deactivation of the right posterior parietal regions [IPL (BA 40) and SPL (BA 7)] may be associated with the inhibition of the irrelevant cognitive processes. Moreover, the posterior parietal regions (DPC and VPC) have direct anatomical connections with the prefrontal cortex, particularly DLPFC (Cavada & Goldman-Rakic; 1989; Lewis & Essen, 2000; Petrides & Pandya, 1999). MFG specifically contains intermixed neuronal populations connected with both DPC and VPC (Fox et al., 2006a), and the activation of the right DPC and VPC is related to the spontaneous activity in the right MFG. Dietrich (2004) also argued that the right DLPFC is involved in the sustained attention, which is required by the processes involved in creative idea generation. Hence, our results indicated that the right frontal-parieto brain network (e.g., right MFG and DLPFC-right IPL and SPL) may be highly important for divergent thinking. In particular, we speculated that the right MFG (BA 46) may be related to focusing an individual's attention to the processes involved in creative idea generation, while interacting with the posterior parietal regions involved in the inhibition of the irrelevant cognitive processes.

4.2 Structural studies on divergent thinking

Creative individuals had been argued to possess several innate traits different from the lower/non-creative individuals, such as defocused attention (Mendelsohn, 1976) and flat associative hierarchies (Mednick, 1962). Moreover, DTTs are the widely used creative tests in the difference of creative individuals. We speculated that the structural studies of individual difference in divergent thinking may uncover several brain mechanisms of creativity.

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3 First, as our ALE results indicated, numerous brain regions in TOP, such as the right
4 cuneus (BA 18), right MTG (BA 39), and right MOG (BA 19), were related to the individuals'
5 differences in divergent thinking. Fink et al. (2013) showed that the gray matter density of the
6 right cuneus (BA 18) is positively related to BIS fluency, as well as the flexibility and
7 originality of AUT. Jung et al. (2010b) also demonstrated that the cortical thickness of the
8 right cuneus (BA 18) and angular (BA 39) is negatively correlated with divergent thinking.
9 The lower cortical thickness makes information flow more efficiently among the brain areas
10 (Jung et al., 2010b), and higher gray matter density results in less energy use when the area is
11 employed for specific cognitive tasks (Haier et al., 2004). In 2004, Dietrich argued that TOP
12 may be devoted primarily to perception and long-term memory. In addition, the visual cortices,
13 the lingual gyrus, and the cuneus may be involved in the processing of the verbal stimuli in
14 the performance of a word association task during visual mental imagery (Kosslyn et al., 2001;
15 Andreasen and Ramchandran; 2012). Therefore, we speculated that the individual difference
16 of TOP may reveal that higher creative individuals have several innate traits in long-term
17 memory, perception, and mental imagery.
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31 In addition, as shown in Table 2, the left caudate tail and left claustrum (the basal ganglia)
32 were related to divergent thinking. The basal ganglia have been suggested to contain a high
33 density of dopamine receptors, which are believed to be related to working memory (McNab
34 and Klingberg, 2007; Goldman-Rakic, 1994). By disinhibiting the thalamocortical loops, the
35 basal ganglia regulate the selective gating mechanism (Gruber et al., 2006). Weinberger and
36 Laruelle (2001) showed that a significant elevation in dopamine D2 receptors in the striatum
37 is associated with schizophrenia. Moreover, previous studies suggested that schizophrenia is
38 related to certain aspects of creativity, such as the lack of constraints and inhibition in their
39 thinking, which resulted from hyperactive neurotransmitter dopamine signal transduction
40 (Eysenck, 1993; Bleuler, 1978; Davis et al., 1990). Takeuchi et al. (2010) also suggested that
41 "the increased regional gray matter volume in striatum (information filtering system) may be
42 one of the common neural correlates of creativity and schizophrenia." Thus, in the present
43 study, the significant relationship between divergent thinking and basal ganglia, such as the
44 left caudate tail and left claustrum, may be related to the dopaminergic system, which may be
45 associated with an inferior and irrelevant information filtering system (acquiring high scores
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3 in DTTs) that conversely facilitated the generation of creative ideas (Eysenck, 1993; Bleuler,
4 1978; Davis et al., 1990). Thus, the innate trait of creative people may ensure them to attend
5 to more things (objects and ideas) at the same time (defocused attention).
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8 9 **4.3 Differences between fMRI and structural studies**

10 Results showed that fMRI and structural studies had no common regions, which may
11 suggest that these studies uncovered different aspects of divergent thinking. The results of
12 fMRI studies may reveal a few cognitive processes, such as semantic processing (e.g., Bunge,
13 Wendelken, Badre, & Wagner, 2005; Green, Kraemer, Fugelsang, Gray, & Dunbar, 2010;
14 Abraham et al., 2012), working memory (e.g., Fink et al., 2009), and cognitive control
15 (Howard-Jones et al., 2005; Subramaniam et al., 2009). The structural studies of gray and
16 white matter using structural MRI may reveal several inter-individual variability in divergent
17 thinking, such as information flowing among brain areas more efficiently (Jung et al., 2010)
18 and creative ability (Fink et al., 2013). In addition, Kanai and Rees (2011) suggested that “in
19 the neuroscience of human behavior and cognition, inter-individual differences are often
20 treated as a source of ‘noise’ and therefore discarded through averaging data from a group of
21 participants.” This perspective may remind us that inter-individual variability should be
22 considered and multimodal MRI techniques should be used to investigate the comprehensive
23 brain networks of divergent thinking in future studies in the future MRI studies.
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37 **5 Limitation and future directions**

38 In this study, an ALE meta-analysis was conducted to quantitatively investigate
39 neuroimaging studies on divergent thinking. The ALE results of the fMRI studies showed that
40 the brain patterns of the creative idea generation in DTTs were composed of the lateral
41 prefrontal cortex (such as MFG, IFG, and ACC), posterior parietal cortex, and TOP. To a
42 certain extent, these brain regions may be separated into two brain networks, namely,
43 semantic (such as left IFG, left MFG, left IPL, and left MTG) and cognitive control systems
44 (right ACC, right MFG, and right IPL). Basing on our ALE results of the structural studies,
45 we determined that numerous brain regions may be related to a few innate traits of the
46 creative idea generation in DTTs, such as the brain regions in the occipital cortex and the
47 temporal cortex [cuneus (BA 18), right MTG (BA 39), and right MOG (BA 19)], as well as
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the brain regions in the dopamine system (left caudate tail and left claustrum). However, several limitations should be considered when interpreting our ALE results. First, the available number of publications included in these meta-analyses is relatively small. Although these selected publications presented similar cognitive processes (such as semantic divergent thinking), the experiment paradigms (e.g., the duration of the creative idea generation, the type of the CTs), image acquisition techniques (such as 3-T MRI and 1.5-T MR), and the image analysis methods (such as the threshold of results: corrected or not, minimum cluster size) were not completely heterogeneous. Second, as the authors only presented results that they were interested in reporting (such as DTTs > CTs), several original data sets based on the meta-analyses are not yet available. Thus, we could not determine whether the results are affected by unpublished data. Third, complex cognitive processes could be related to divergent thinking, such as working memory, cognitive control, semantic processing, and attention. However, our results could not conclusively uncover the integration of these cognitive processes on divergent thinking. Therefore, detailed experiments, advanced paradigms, and different MRI modalities should be used in future studies to determine the neural basis of divergent thinking.

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3 Table 1: Studies selected by the present meta-analysis

4 Table 2: COIs of fMRI studies selected in ALE meta-analysis of divergent thinking (DTTs > CTs)

5 Table 3: COIs of fMRI studies selected in ALE meta-analysis of divergent thinking (CTs > CTTs)

6 Table 4: COIs of structural studies selected in ALE meta-analysis of divergent thinking

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8 Table 5: Brain regions showing significant activation likelihood across fMRI studies of DTTs in ALE
9 meta-analysis (FDR-corrected $p < 0.05$ with 100 mm^3 cluster volume); ALE clusters were overlaid on the
10 standard space using the Talairach file (Colin1.1.nii).

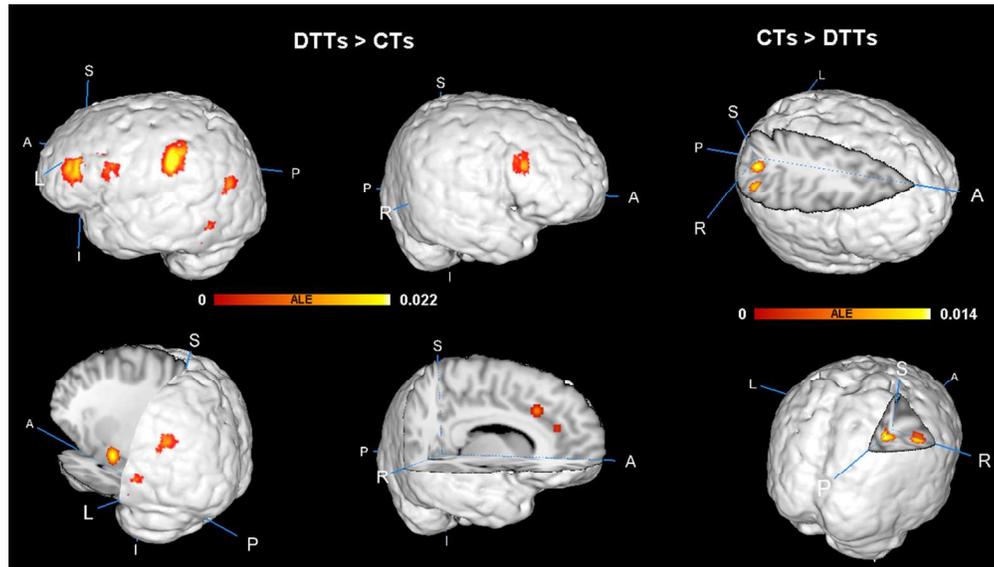
11 Table 6: Brain regions showing significant activation likelihood across structural studies of DTTs in ALE
12 meta-analysis (FDR-corrected $p < 0.05$ with 100 mm^3 cluster volume); ALE clusters were overlaid on the
13 standard space using the Talairach file (Colin1.1.nii).

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15 Figure 1: Brain regions showing significant activation likelihood across fMRI studies of DTTs vs CTs in
16 ALE meta-analysis (FDR-corrected $p < 0.05$ with 100 mm^3 cluster volume); ALE clusters were overlaid on
17 the standard space using the Talairach file (Colin1.1.nii).

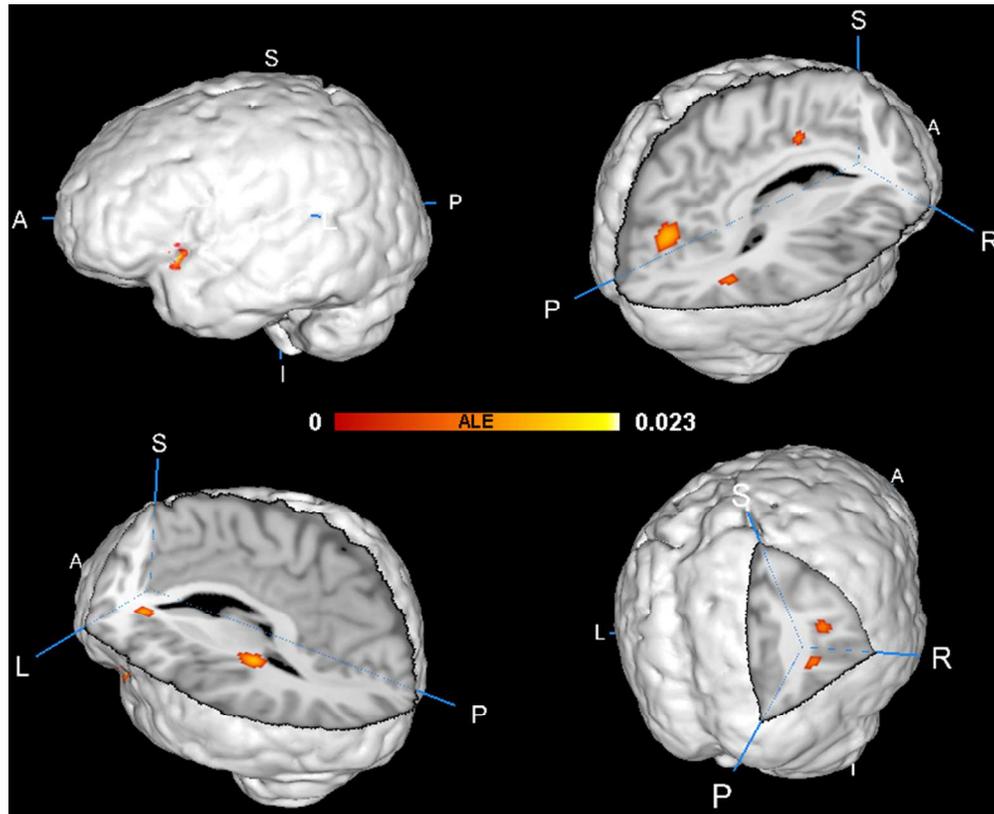
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19 Figure 2: Brain regions showing significant activation likelihood across structural studies of DTTs in ALE
20 meta-analysis (FDR-corrected $p < 0.05$ with 100 mm^3 cluster volume); ALE clusters were overlaid on the
21 standard space using the Talairach file (Colin1.1.nii).

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Brain regions showing significant activation likelihood across fMRI studies of DTTs vs CTs in ALE meta-analysis (FDR-corrected $p < 0.05$ with 100 mm³ cluster volume); ALE clusters were overlaid on the standard space using the Talairach file (Colin1.1.nii).
150x85mm (300 x 300 DPI)



Brain regions showing significant activation likelihood across structural studies of DTTs in ALE meta-analysis (FDR-corrected $p < 0.05$ with 100 mm³ cluster volume); ALE clusters were overlaid on the standard space using the Talairach file (Colin1.1.nii) 119x97mm (300 x 300 DPI)

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Table 1

The MRI studies (fMRI and structural MRI studies) selected in ALE meta- analysis of divergent thinking

fMRI Studies	Scanner	Type of MRI	Sample	F/M	Age	DTTs	CTs	Time of DTT
Abraham et al. (2012)	1.5-T MRI	fMRI	29	11/18	19–29	AUT	OLT	20 s
Benedek et al. (2014a)*	3.0-T MRI	fMRI	35	24/11	18–29	New ideas of AUT	Old ideas of AUT	60 s
Benedek et al. (2014b)	3.0-T MRI	fMRI	28	18/10	19–49	NPT	LCT	10 s
Fink et al (2009)*	3.0-T MRI	fMRI	21	11/10	20-32	AUT	OCTs	20 s
Fink et al (2010)*	3.0-T MRI	fMRI	31	18/13	19-29	AUT	OCTs	21 s
Fink et al (2011)*	3.0-T MRI	fMRI	24	14/10	21-30	AUT	AUT	12 s
Howard-Jones et al. (2005)*	1.5-T MRI	fMRI	8	7/1	19–28	CSG	UCSG	10 s
Kleibeuker et al (2014)*	3.0-T MRI	fMRI	adolescents:19	10/9	15–17	AUT	OCTs	15 s
	1.5-T MRI		adults:24	12/12	25–30			
Mashal et al (2007)	3.0-T MRI	fMRI	15	7/8	21–31	NMT	CMT	15 s
Shah et al. (2011)	1.5-T MRI	fMRI	28	14/14	24.0 ± 1.9	CWT	Copying	140 s
Structural studies								
Fink et al. (2013)	3.0-T MRI	Gray matter	71	44/27	24.5 ± 44.9	BIS; AUT		2-2.5 min for BIS; 2 min for AUT
Jung et al. (2010a)	3.0-T MRI	Gray matter	72	32/40	22.1±2.9	3 DTTs: Free condition of DFT; Four Line Condition of the DFT; AUT		5 min for DFT; 4 min for FLC; 1 min for AUT
Jung et al. (2010b)	3.0-T MRI	Whit matter	61	28/33	23.7± 4.2	3 DTTs: Verbal and Drawing Creativity Tasks; AUT; generation of captions		5 min for each task of the 3 DTTs
Kühn et al. (2013)	3.0-T MRI	Gray matter	21	16/5	21.3±1.85	AUT		2 min
Takeuchi et al. (2010a)	3.0-T MRI	Gray matter	55	13/42	21.7±1.44	S-A creativity test		5 min for each task
Takeuchi et al. (2010b)	3.0-T MRI	Whit matter	55	13/42	21.7±1.44	S-A creativity test		5 min for each task
Continuous of Table 1								
Zhu et al. (2013)	3.0-T MRI	Gray matter	285	155/130	F: 20.1 ± 1.2 M: 19.68 ± 1.01	Verbal TTCT		45 min

Abbreviation: F = female; M = male; DTTs = divergent thinking tasks; CTs = Control tasks

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AUTs = Alternate Uses tasks, in which subjects were asked to generate unusual/original uses of conventional everyday objects; **New ideas of AUT** = the generated ideas were newly created; **Old ideas of AUT** = the generated creative ideas were retrieved from memory; **OCTs** = Object Characteristics Tasks, in which participants had to think of typical characteristics of conventional everyday objects; **OLT** = Object Location Task, in which a word of an object was presented with an location (e.g. Objects -> Office) and the participants were asked to generated a different object in the location; **NPT** = Novel Production Task, in which a short phrases relating a noun to an adjective in parentheses were presented and participants were asked to produce a creative metaphor that conveys the meaning of the adjective; **LCT** = literal control task, in which a short phrases relating a noun to an adjective in parentheses were presented and participants were asked to produce a synonym that conveys the meaning of the adjective; **CSG** = Creative Story generation, in which a 3-words list was presented and the participants were asked to generate a creative story including these 3 words; **UCSG** = Uncreative Story generation, in which a 3-words list was presented and the participants were asked to generate a uncreative story including these 3 words; **NMT** = Novel Metaphors Tasks, in which the participants were asked to indicate whither the two words presented were related metaphorically; **CMT** = Conventional Metaphors Tasks; **DFT** = Design Fluency Test, **in the Free Condition of the DFT**, subjects were instructed to draw as many unique designs; **in For the Four Line condition of DFT**, they were constrained in drawing designs composed of certain types of lines; **Time of DTT** = the period of idea generation; **S-A creativity test** is similar to TTCT and has three problems: improve a product, find interesting and unusual uses for a certain object and list all the consequences should an improbable situation occur

The studies marked "*" including the contrasts of DTTs > CTs and CTs > DTTs

Table 2

The COIs of fMRI studies selected in ALE meta- analysis of divergent thinking (DTTs > CTs)

Studies	Conditions	COI	Foci	Response	Ideas evaluation
Abraham et al. (2012)	<i>Divergent condition</i>	DivH > DivL (inclusive mask: DivH > ConH)	15	Button Presses: idea generation and response periods were not separated	the generated ideas not evaluated
	DivH: completing AUT				
	DivL: completing Object-Location task				
	<i>Control condition</i>				
	ConH: completing 2-back working memory Task				
	ConL: completing 1-back working memory Task				
Benedek et al. (2014a)	OLD: generating idea retrieved from memory	NEW > OLD	1	Verbal Report: idea generation and response periods were not separated	the generated ideas evaluated according to both originality and appropriateness
	NEW: the newly created resulting idea				
Benedek et al. (2014b)	METAPHOR: completing a NPT	METAPHOR > LITERAL	7	Verbal Report: idea generation and response periods were separated	the generated ideas evaluated according to remoteness, novelty, and cleverness
	LITERAL: completing a LCT				
Fink et al. (2009)	AU: Completing AUT	AU > OC	1	Verbal Report: idea generation and response periods were not separated	the generated ideas evaluated according novelty and plausibility
	OC: Completing Object Characteristics Task				
Fink et al. (2010)	AU and OC same with Fink et al. (2009)	AU > OC	1	Verbal Report: idea generation and response periods were separated	the generated ideas not evaluated
	AUinc: reflecting on ideas or responses they gave during AUT	AU > AUinc	2		
	AUstim: creative idea generation stimulated by external ideas	AUinc > AU	1		
		AUstim > AU	3		
Fink et al. (2011)	Orig: generating an unusual/original us of an objects stimulated by original usages generated by other people	Orig > Contr	1	Verbal Report: idea generation and response periods were separated	the generated ideas evaluated according to originality
	Comm: generating an unusual/original us of an objects stimulated by common usages generated by other people	Orig > Comm	3		
	Contr: generating an unusual/original us of an objects stimulated by meaningless words				

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Howard-Jones et al. (2005)	Creative Condition (CC): generate creative stories using word list	CC > UC	4	Verbal Report: idea generation and response periods were separated	the generated ideas evaluated according to originality
	Uncreative Condition (UC): generate uncreative stories using word list	CC > UC with UC > RC	1		
	Related Condition (RC): the words in the word list being related each other				
	Unrelated Condition (UC): the words in the word list not being related each other				
Kleibecker et al (2014)	AU & OC	AU > OC	16	Verbal Report: idea generation and response periods were separated	the generated ideas evaluated according to creativity
Mashal et al. (2007)	NM: completing the NMT	NM > CM	3	Verbal Report: idea generation and response periods were separated	the generated ideas not evaluated
	CM: completing the NMT	NM > L	5		
	UR: unrelated word pairs	NM > UR	15		
Shah et al. (2011)	L: Literal expressions				
	creative writing & copying	creative writing > copying	6	Silently decided	

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Table 3

The COIs of fMRI studies selected in ALE meta- analysis of divergent thinking (CTs > CTTs)

Studies	Conditions	CTs > DTTs	Foci
Benedek et al. (2014a)	REST: fixation epochs	OLD & NEW < 0	2
	OLD: resulting idea retrieved from memory		
	NEW: the newly created resulting idea		
	SPEECH		
Fink et al. (2009)	AU: Completing AUT	OC > AU	1
	OC: Completing Object Characteristics Task		
Fink et al. (2010)	AU and OC same with Fink et al. (2009)	OC > AU	2
	AUinc: reflecting on ideas or responses they gave during		
	AUT		
	AUstim: creative idea generation stimulated by external ideas		
Fink et al. (2011)	Orig: object name presented with original answers of this object	Contr > Comm	2
	Comm: object name presented with common answers of this object	Contr > Orig	2
	Contr: object name presented with meaningless words		
Howard-Jones et al. (2005)	Creative Condition (CC): indication to generate creative stories	UC > CC	3
	Uncreative Condition (UC): indication to generate uncreative stories		
	Related Condition (RC): the words in the list related		
	Unrelated Condition (URC): the words in the list not related		
Kleibeuker et al (2014)	AU & OC	OC > AU	18

Table 4

The COIs of structural studies selected in ALE meta- analysis of divergent thinking

Studies	Conditions	COI	Foci
Fink et al. (2013)	BIS fluency/flexibility	BIS fluency/flexibility positive association with gray matter density	2
	AU originality	AU originality positive association with gray matter density	2
Jung et al. (2010a)	CCI: composite creativity index obtained by averaging the scores of four divergent thinking tasks	BIS \cap AU	1
	FA: fractional anisotropy	CCI correlated to FA	2
	AD: Axial Diffusivity	CCI correlated to RD	3
	RD: Radial Diffusivity	CCI correlated to AD	2
Jung et al. (2010b)	CCI: composite creativity index combined the scores of fluency, flexibility and uniqueness of AUT	negative correlation between cortical thickness and CCI	5
		positive correlation between cortical thickness and CCI	1
Kühn et al. (2013)	Average Creativity of AUT	Positive Correlation between Gray Matter Volume and Cognitive Flexibility	5
	Cognitive Flexibility of AUT	Positive Correlation between Gray Matter Volume and Average Uniqueness	5
	Average Uniqueness of AUT	Positive Correlation between Gray Matter Volume and Average Creativity	4
Takeuchi et al. (2010a)	S-A creativity test	positive correlations between rGMV and S-A creativity test score	6
	rGMV: regional gray matter volume		
Takeuchi et al. (2010b)	S-A creativity test	correlations between FA values and the scores from the S-A creativity test	25
	FA		
Zhu et al. (2013)	Verbal TTCT	rGMV correlated with verbal creativity test score	2
	rGMV: regional gray matter volume	rWMV correlated with verbal creativity test score	2
	rGWV: regional whit matter volume		

Table 5 The brain regions showing significant activation likelihood across fMRI studies of DTTs in ALE meta-analysis (FDR-corrected $p < 0.05$ with 100 mm^3 cluster volume); ALE clusters were overlaid to the standard space using the Talairach file (Colin1.1.nii).

Cluster	Volume (mm^3)	Extrema Value	x	y	z	Brain regions
DTTs > CC						
1	1064	0.022	-56	-32	34	Left Inferior Parietal Lobule (BA 40)
2	840	0.022	-24	-12	-12	Left Amygdala
3	688	0.012	6	22	32	Right Cingulate Cortex (BA 32)
4	640	0.016	-46	-56	-10	Left Fusiform Gyrus (BA 37)
5	640	0.016	-46	32	18	Left middle frontal gyrus (BA 46)
6	264	0.012	-48	2	26	Left Precentral Gyrus (BA 6)
7	248	0.010	48	22	22	Right middle frontal gyrus (BA 46)
8	184	0.010	48	22	22	Right Anterior Cingulate (BA 32)
9	168	0.010	-46	-68	20	Left Middle Temporal Gyrus (BA 39)
CTs > DTTs						
1	328	0.016	30	-62	42	Right Precuneus (BA 19)
2	296	0.015	46	-54	42	Right Inferior Parietal Lobule (BA 40)

Coordinates of the local maxima in Talairach space are given

Table 6

The brain regions showing significant activation likelihood across structural studies of DTTs in ALE meta-analysis (FDR-corrected $p < 0.05$ with 100 mm^3 cluster volume); ALE clusters were overlaid to the standard space using the Talairach file (Colin1.1.nii).

Cluster	Volume (mm^3)	ALE Value	x	y	z	Brain regions
1	792	0.018	6	-74	18	Right Cuneus (BA 18)
		0.010	14	-68	20	Right Cuneus (BA 18)
2	736	0.023	-42	10	-4	Left Insula (BA 13)
3	528	0.017	-26	-34	10	Left Caudate Tail
4	416	0.019	-22	26	8	Left Claustrum
5	176	0.011	44	-56	22	Right Middle Temporal Gyrus (BA 39)
		0.011	44	-52	26	Right Superior Temporal Gyrus (BA 39)
6	176	0.011	8	-4	38	Right Cingulate Gyrus (BA 24)
		0.011	14	-4	38	Right Cingulate Gyrus (BA 24)
7	136	0.011	38	-64	10	Right Middle Occipital Gyrus (BA 19)

Coordinates of the local maxima in Talairach space are given