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NEURAL PATHWAY IN THE RIGHT HEMISPHERE UNDERLIES VERBAL INSIGHT PROBLEM SOLVING

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Abstract—Verbal insight problem solving means to break mental sets, to select the novel semantic information and to form novel, task-related associations. Although previous studies have identified the brain regions associated with these key processes, the interaction among these regions during insight is still unclear. In the present study, we explored the functional connectivity between the key regions during solving Chinese 'chengyu' riddles by using event-related functional magnetic resonance imaging. Results showed that both insight and noninsight solutions activated the bilateral inferior frontal gyri, middle temporal gyri and hippocampi, and these regions constituted a frontal to temporal to hippocampal neural pathway. Compared with noninsight solution, insight solution had a stronger functional connectivity between the inferior frontal gyrus and middle temporal gyrus in the right hemisphere. Our study reveals the neural pathway of information processing during verbal insight problem solving, and supports the right-hemisphere advantage theory of insight.

Key words: insight, fMRI, functional connectivity, Chinese 'chengyu' riddle, right hemisphere.

INTRODUCTION

Since Köhler (1925) observed that chimpanzees could resolve problems suddenly rather than by an approach of trial and error, the processing of insight has attracted the attention of many researchers. Since unsuitable representations of problem would lead to the failure of effective problem solving in many situations, some cognitive psychologists proposed that the representation change such as constraint relaxation and chunk decomposition should be the crucial process of insight (Kaplan and Simon, 1990; Knoblich et al., 2001; Ormerod et al., 2002). Using some visual-representation-based problems such as the nine-dot problem and the Chinese chunk decomposition problem, researchers found that there were multiple sources of difficulty of particular insight problems, and that early perceptual processes could crucially affect thinking and problem solving (MacGregor et al., 2001; Kershaw and Ohlsson, 2004; Luo et al., 2006; Wu et al., 2013).

With the development of neuroimaging techniques, especially from 1990s onward, the investigations on the neural correlates of insight flourished (Dietrich and Kanso, 2010). However, since a number of homogenous mental events which can be repeatedly observed are required for the neuroimaging approach, the classic insightful paradigms such as nine-dot problem and six-matchstick problem are no longer suitable (Luo, 2004). Thus, a variety of verbal problems have been applied in the studies of insight, such as riddles, logogriphs and compound remote associates problems (Luo and Niki, 2003; Jung-Beeman et al., 2004; Qiu et al., 2010; Zhao et al., 2013). In these studies, researchers focused on two key components of insight processing, that is to break the mental sets and to form novel, task-related associations among the old nodes of concepts or cognitive skills (Luo and Niki, 2003; Bowden and Jung-Beeman, 2007).

Studies indicated that the frontal cortex played a key role in breaking mental sets. Therein, the anterior cingulate cortex was highlighted and proposed to monitor the cognitive conflicts resulting from mental sets (Luo et al., 2004; Mai et al., 2004; Qiu et al., 2008; Aziz-Zadeh et al., 2009). After detecting the cognitive conflicts, one should break its mental sets to solve the conflicts in insight. It was found that the lateral prefrontal cortex, including the inferior and middle frontal gyri, was activated in chunk decomposition of Chinese characters (Luo et al., 2006), set-shift problems (Goel and Vartanian, 2005) and insightful riddle solving

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Abbreviations: BOLD, blood oxygenation level dependent; EPI, echo planar imaging; fMRI, functional magnetic resonance imaging; LHIPP, left hippocampus; LIFG, left inferior frontal gyrus; LMTG, left middle temporal gyrus; ROI, region of interest; RIFG, right inferior frontal gyrus; RHIPP, right hippocampus; RTMD, right middle temporal gyrus; SPM, statistical parametric mapping.

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(Luo and Niki, 2003; Luo et al., 2004; Qiu et al., 2010). Due to its role in establishing and shifting the attentional sets (MacDonald et al., 2000; Luks et al., 2002), the lateral prefrontal cortex was thought to be associated with conflict resolution.

The breaking of mental sets would result in the retrieval of new information pieces. Then, the selection of novel information pieces and forming novel, task-related associations were the keys of insight problem solving (Bink and Marsh, 2000). According to the coarse semantic coding theory, the right-hemisphere engages in coarse semantic coding, weakly and diffusely activating alternative meanings and more distant associates (Faust and Chiarello, 1998; Beeman and Bowden, 2000; Bowden and Jung-Beeman, 2003). Therefore, some researchers highlighted the role of the right hemisphere (especially the right anterior superior temporal gyrus) in making connections across distantly related information during insight (Bowden and Jung-Beeman, 2003; Jung-Beeman et al., 2004). In fact, the right temporal cortex might be mainly in charge of processing novel semantic information (Faust and Mashal, 2007; Mashal et al., 2008; Pobric et al., 2008), while the hippocampus should be the key brain region in forming the novel associations (Luo and Niki, 2003; Zhao et al., 2013), due to its function in path reorientation (Redish, 2001), relational memory (Cohen et al., 1999; Luo and Niki, 2002) and response to novel stimuli (Knight, 1996; Johnson et al., 2008).

Obviously, verbal insight problem solving activates a distributed neural network including the anterior cingulate cortex, lateral prefrontal cortex, right temporal areas and hippocampus. Although previous studies have identified the roles of these brain regions, the information integrations among them are still unclear. The electroencephalograph study showed that good performance in the divergent thinking task was related to increased functional connectivity of central–parietal areas of both hemispheres and greater ipsilateral connections between the cortex regions of the right hemisphere in the beta2 band (Razoumnikova, 2000). And the study using diffusion tensor imaging reported significant positive relationships between individual creativity as measured by the divergent thinking test and fractional anisotropy in the white matter in or adjacent to the bilateral prefrontal cortices, the body of the corpus callosum, the bilateral basal ganglia, the bilateral temporal-parietal junction and the right inferior parietal lobule (Takeuchi et al., 2010). These studies indicated the importance of the information integration of different brain regions in creativity.

In verbal insight problem solving, the forming of novel associations is dependent on the selection of novel semantic information. Since the lateral prefrontal cortex, temporal areas and hippocampus are respectively associated with conflict resolution, semantic processing and relational memory, it is speculated that the functional connectivity between the lateral prefrontal cortex and temporal areas might reflect the information selection process in insight and that between right temporal areas and hippocampus might underlie the forming of novel association. The current work aims to reveal the functional connectivity among the key brain regions which underlies the cognitive processing in insight.

Additionally, according to the coarse semantic coding theory, the right temporal cortex should play a crucial role in verbal insight problem solving, and this is supported by several studies (Bowden and Jung-Beeman, 2003; Jung-Beeman et al., 2004; Zhang et al., 2011; Zhou et al., 2011). However, there are also some studies revealing bilateral activation patterns associated with insight events (Luo and Niki, 2003; Aziz-Zadeh et al., 2009; Zhao et al., 2013). There might be several reasons why the latter studies do not find the right hemisphere advantage. First, verbal insight problems cannot be solved by the conventional semantic information processing, and then the process of retrieving the novel semantic information is the key of insight solving. However, some of the latter studies adopted the paradigm of providing triggers to catalyze the insight processes. This would simplify the retrieval of the novel meanings and distant associates, and then weaken the activation of the right temporal cortex. Second, since insight solution comes to mind suddenly, the right temporal cortex should show greater activation at the time just prior to the solution (Jung-Beeman et al., 2004). However, most of the latter studies focused on the activation throughout the solving period, not exactly catching the key period of the activation in right temporal cortex. It is noticed that all these findings, no matter supporting the right hemisphere theory or not, are from the location analysis of brain functions. Thus, as one of the two patterns of brain functional organization (Tononi et al., 1994), the functional integration analysis may provide something new for the discussions on hemisphere difference in insight.

EXPERIMENTAL PROCEDURES

Participants

As paid volunteers, 20 undergraduates or graduates (13 women, 7 men), aged 21–35 years (mean age, 23.6 years) from the Central China Normal University, participated in the experiment, and gave their informed consent according to the requirements of Institutional Review Board of the Central China Normal University. All participants were healthy, right-handed, and had normal or corrected to normal vision. Two participants were excluded from analysis due to their experiencing of less than 15% normal associations during the experiment. Another participant was excluded due to the excessive head motion during functional magnetic resonance imaging (fMRI) scanning.

Stimuli and task

In the present study, we adopted the Chinese 'chengyu' (in Chinese pinyin) riddles to explore the underlying neural mechanism of insight. A Chinese 'chengyu' riddle may be a phrase, or a saying, and its answer is a four-character ‘chengyu’ which is a type of traditional Chinese idiomatic expressions. As each ‘chengyu’ only has one meaning, the meanings of its four component characters are constrained by the chunk of the ‘chengyu’. This prevents the successful riddle solving because the riddles aim at an unconstrained meaning of the key character rather than the meaning of the ‘chengyu’ as a whole. To solve the riddle, the chunk of ‘chengyu’ must be decomposed, and extensive meanings of individual characters must be explored and retrieved. For example, the answer of the riddle ‘shan zhan er duo mou’ (善战而多谋, means adept at fighting and planning) is the chengyu ‘jing da xi suan’ (精打细算, means being very careful in reckoning). The key character in this riddle is ‘da’ (打, one of its meanings is to hit), corresponding to ‘zhan’ (战, with the meaning to fight). However, inside the ‘chengyu’, the ‘da’ (打) is bound with ‘suan’ (算). And the meaning of their combination ‘da suan’ (打算) is to plan or to reckon. Obviously, the successful riddle solving relied on the successful constraint relaxation to the key character or the successful chunk decomposition. This is theoretically similar with the visual chunk decomposition of Chinese characters (Luo et al., 2006). Once extensive meanings of key character were retrieved, a number of temporary connections between the riddle and the ‘chengyu’ would be formed, and then the riddle would be solved by the selection process of task-related connections. Since there is a process of representation change when the participants tried to associate the riddle with the original answer, it is considered as the answer with novel association.

In the current work, a control with normal association was produced in a pretest. A group of subjects were asked to report the four-character ‘chengyu’ that came to mind first when they saw the riddle in the pretest. Mostly, they could not find the novel answer and gave some different answers. The ‘chengyu’ with the highest frequency was chosen as the control. Thus, there are two answers, one of which is novel, and the other is normal. For example, the novel answer to the riddle ‘shan zhan er duo mou’ (善战而多谋, means adept at fighting and planning) is the ‘chengyu’ of ‘jing da xi suan’ (精打细算, means being very careful in reckoning), while its normal answer is ‘zu zhi duo mou’ (足智多谋, means being able and adept at planning).

In order to determine the difference between the answers with novel and normal associations, we had another group of subjects (totally 32) to rate their understanding of the Reasonability (matching with the answers to riddles) and Novelty on a scale of 1–5 for each of the 120 riddles. In the end, 84 riddles whose answers (both novel and normal ones) were evaluated as reasonable (mean scores > 3.5) were selected as the test riddles. Results showed that there was a significant difference in novelty [paired t-test, t (83) = 16.84, $p < 0.001$] between the answers with novel (mean score = 3.6) and normal association (mean score = 2.6).

To familiarize the participants with the procedure and pace of this task, participants were trained with another set of 10 similar materials before they were put into the scanner. In the formal experiment, 84 test riddles were presented one by one with an event-related design. There was not any repetition of stimuli in the test. The Chinese characters, appearing in both the riddles and answers, had a font size of 28 (Song Ti font). The experimental paradigm was illustrated in Fig. 1. The trial began with an 8-s black plus, a sign for rest, and a star sign for 1 s, followed by a warning of the presentation of riddle. After the riddle was displayed for 4 s, the novel association answer, normal association answer and two answers with no associations were presented. Participants were asked to select a novel and reasonable answer among these options within a limited 8-s period. Then was a 1-s blank followed by the next trial. The spatial positions were balanced among the different answers.

Since it is difficult to solve the riddle on participants’ own initiative, the paradigm of providing a trigger to catalyze insight processes was adopted by some studies (Luo and Niki, 2003; Luo et al., 2004; Mai et al., 2004). This paradigm is helpful in investigating the processes of breaking mental sets and forming novel associations, but of little effect in exploring how participants retrieve the extensive information to solve problems. Therefore, the present study introduced the answer selection paradigm described above to investigate the information selection in insight. Participants were asked to select the novel and reasonable answer from four options, in which the novelty was more emphasized. According to the selections of participants, the trials are classified into insight and noninsight solutions, respectively. Since the normal answer points to the conventional thinking, it is easy to understand and should be found first. However, the normal answer is of less novelty, and then participants might actively look for the novel one from the others. If participants ultimately could not find the association between the novel answer and the riddle, they might select the normal one, in which case the problem solving is a simple process in the conventional thinking, and it is considered as noninsight-based solution. Once participants found the association between the novel answer and the riddle, they would select it as asked. In this case, there is a competition between the novel and normal answer, and the selection of novel answer just reflects the breaking of conventional thinking. Additionally, because of including a process of representation change, the selection of novel answer is indeed an insight-based solution.

Indeed, although the answer selection makes participants more active than solution recognition, it is different from the actual problem solving on participants’ own. The adoption of the answer selection paradigm is an inevitable compromise.

fMRI acquirement

During MRI scanning, whole brain T2*-weighted echo planar imaging, based on blood oxygenation level-dependent contrast (EPI-BOLD) fMRI data, was

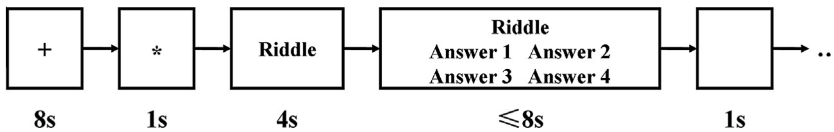

Fig. 1. The flow map of the formal experiment.

acquired with a Siemens Trio 3.0-T MR-scanner using a standard head coil at the MRI Center of the Wuhan Union Hospital. 32 interleaved slices, covering the entire brain, were acquired using a gradient-echo echo-planar pulse sequence. The slice thickness was 3.75 mm and the voxel size was 3×3 mm (TR = 2 s, TE = 30 ms, FA = 78°, FOV = 192×192 mm, Matrix size = 64×64). Head motion was restricted with plastic braces and foam padding. The whole scanning sequence was divided into two runs, each consisting of 42 trials.

fMRI data analysis

Preprocessing. The statistical parametric mapping (SPM5, http://www.fil.ion.ucl.ac.uk/spm/) was used for image preprocessing and voxel-based statistical analysis. Scans were first slice-time corrected, realigned, normalized (using the functional EPI template provided in SPM5), and smoothed (a Gaussian kernel with a full width at the full width at half maximum – FWHM of 8 mm). The resultant images had cubic voxels of $3 \times 3 \times 3$ mm.

Mapping brain activation. Two types of events, the insight solution and the noninsight solution, were defined according to participants' selections to the answers. Since the participants could not solve the riddle by themselves in the initial 4 s of riddle presentation (Zhu et al., 2009), the event was defined as the answer selection process for each type which began at the onset of the answers' presentation and ended in the participants' pressing. Then, the time vector of the event was convoluted by the classic haemodynamic response function. Finally, by the general linear model, the activated brain regions associated with the insight solution and the noninsight solution, as well as the differences between the two conditions, were obtained for each participant, and then combined in a random effect analysis to identify differences consistent across all participants. For insight vs. rest and noninsight vs. rest, the thresholds were set at $p < 0.001$ (False Discovery Rate control for multiple comparisons) and 30 or more contiguous voxels, while for insight vs. noninsight solution, the threshold was set at $p < 0.05$ (False Discovery Rate control for multiple comparisons) and 30 or more contiguous voxels.

Functional connectivity. In the current work, we were interested in the functional connectivity among several brain regions including bilateral inferior/middle frontal gyri, middle/superior temporal gyri and hippocampi. Using the Automated Anatomical Labeling (Tzourio-Mazoyer et al., 2002), the activated voxels in these regions were obtained. The region of interest (ROI) was defined as a cube of $9 \times 9 \times 9$ mm centered at the activation peak in each brain region, and its BOLD time series was defined as the mean of all the voxels in the cube. If there were more than one peak in a region, the most central one located in the activation cluster was selected. Then, the time series associated with insight and noninsight solution was respectively segregated from the whole. Since the BOLD signal delayed for six seconds according to the haemodynamic response function by SPM, and the reaction time was about 4 s (see in Results), the time series of each condition was defined from 0 to 10 s after the presentation of optional answers. For each condition, the functional connectivity was evaluated by computing the temporal partial correlation between all pair-wise combinations of ROIs controlling the effects of the others (Friston et al., 1993). Finally, the correlation coefficients were compared across conditions after the Fisher transformation.

RESULTS

On average, in 61.7% of trials participants selected the answers with novel associations (average reaction time was 3.70 s with a standard deviation of 0.78 s), and in 26.3% of trials they selected the answers with normal associations (average reaction time was 4.06 s with a standard deviation of 0.94 s). The larger trial percentage of insight solutions might result from the instruction before the experiment that asked participants to select a novel and reasonable answer.

Our fMRI results demonstrated that both of the insight and noninsight solution induced extensive changes of brain activity in the bilateral inferior frontal gyri, middle temporal gyri and hippocampi (see in Fig. 2 and Table 1). Compared with noninsight solution, insight solution activated more in bilateral middle temporal gyri and hippocampi. The activation of the bilateral inferior frontal gyri showed no significant differences between two conditions.

As mentioned in Experimental procedures, the peaks of ROIs for insight solution were located at $(-60, -42, 0)$ in left middle temporal gyrus (LMTG), $(-48, 9, 24)$ in left inferior frontal gyrus (LIFG), $(-24, -27, -9)$ in left hippocampus (LHIPP), $(21, -33, -3)$ in right hippocampus (RHIPP), $(45, -63, -3)$ in right middle temporal gyrus (RTMD) and $(48, 15, 24)$ in right inferior frontal gyrus (RIFG). And the peaks of ROIs for noninsight solution were located at $(-57, -45, 9)$ in LMTG, $(-42, 9, 27)$ in LIFG, $(-21, -27, -9)$ in LHIPP, $(21, -30, -3)$ in RHIPP, $(42, -63, 9)$ in RTMD and $(51, 18, 30)$ in RIFG.

The functional connectivity analysis showed that the ROIs were significantly connected with the ipsilateral

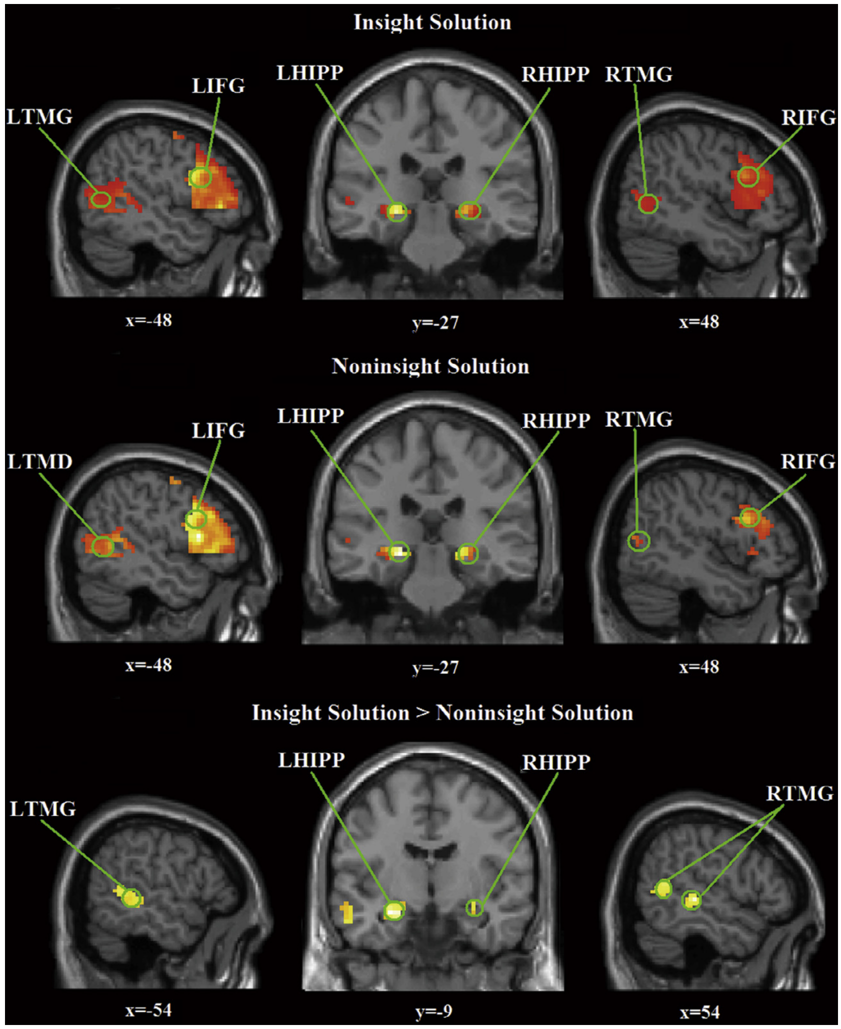

Fig. 2. Brain areas activated for insight solution and noninsight solution as well as the difference between the two conditions in the six regions of interest. For insight vs. rest and noninsight vs. rest, the thresholds were set at $p < 0.001$ (False Discovery Rate control for multiple comparisons) and 30 or more contiguous voxels, while for insight vs. nonisight solution, the threshold was set at $p < 0.05$ (False Discovery Rate control for multiple comparisons) and 30 or more contiguous voxels.

regions and the homologous regions in the other hemisphere. In each hemisphere, there was a neural pathway from the inferior frontal gyrus to middle temporal gyrus to hippocampus for both insight and noninsight solution. The functional connectivity between the RIFG and RTMD was stronger for insight than noninsight solution, while that between the LMTG and RHIPP was stronger for noninsight than insight solution ($p < 0.05$, paired t-test).

DISCUSSION

Information selection in verbal insight problem solving

As a type of traditional Chinese idiomatic expressions, the 'chengyu' could be regarded as a chunk. Then, the meanings of four component characters enhanced by the 'chengyu' should be their normal meanings, and their other meanings could be considered as novel ones. Although the left hemisphere is dominant in language processing, it is the right temporal cortex that processes the novel meaning of idioms (Faust and Mashal, 2007; Mashal et al., 2008; Pobric et al., 2008). In the current work, the greater activation in right temporal gyrus for insight than noninsight solution indicated more retrieval of novel semantic information.

However, the novel semantic information is generally weak in retrieval (Giora, 1997). This conflict might be resolved by the lateral prefrontal cortex due to its role in establishing and shifting the attentional sets (MacDonald et al., 2000; Luks et al., 2002). Although there was no significant difference of activation strength in bilateral prefrontal cortices at the given threshold between insight and noninsight solution, the RIFG was stronger functionally connected to the RTMD for insight than noninsight solution. The frontal–temporal neural pathway might reflect the selection of novel semantic information in verbal insight problem solving.

Forming novel association in verbal insight problem solving

Previous studies indicated the hippocampus was involved in the relational memory and its activation strength was

Table 1. Brain areas activated for insight solution and noninsight solution as well as the difference between the two conditions in the six regions of interest

Area	BA	Voxels	x	y	z	T	Z
Insight solution							
Left inferior frontal gyrus	47	1051	−33	30	3	20.66	7.21
	44		−48	9	24	15.59	6.59
Left hippocampus	20	147	−24	−27	−9	18.13	6.93
	20		−33	−18	−9	9.47	5.42
Right hippocampus	27	123	21	−33	−3	14.28	6.40
	20		24	−27	−9	11.19	5.83
Right inferior frontal gyrus	47	731	36	27	3	10.51	5.68
	48		48	15	24	9.56	5.45
Left middle temporal gyrus	21	524	−60	−42	0	10.10	5.58
	22		−54	−45	9	9.94	5.54
Right middle temporal gyrus	37	113	45	−69	9	7.21	4.74
	37		45	−63	−3	6.72	4.57
Noninsight solution							
Left hippocampus	20	82	−21	−27	−9	13.80	6.32
Left inferior frontal gyrus	48	914	−48	15	12	13.55	6.28
	44		−42	9	27	13.19	6.21
Right hippocampus	27	65	21	−30	−3	11.41	5.87
Right inferior frontal gyrus	47	348	36	27	3	10.82	5.75
	48		51	18	30	8.42	5.13
Left middle temporal gyrus	21	392	−57	−45	9	9.41	5.41
	21		−60	−33	3	7.58	4.87
Right middle temporal gyrus	37	32	48	−72	12	5.82	4.20
	37		42	−63	9	5.45	4.04
Insight solution > noninsight solution							
Left hippocampus	20	48	−27	−9	−18	6.87	4.63
Right middle temporal gyrus	21	205	54	−30	0	6.41	4.45
	21		54	−54	12	5.39	4.01
Left middle temporal gyrus	22	126	−57	−36	3	5.09	3.87
	22		−54	−48	6	5.00	3.82
Left middle temporal gyrus	21	34	−54	−6	−24	4.96	3.81
Right hippocampus	20	6	30	−9	−12	4.74	3.69

BA, Brodmann area. Coordinates (x, y, z) were the MNI (Montreal Neurological Institute) coordinates. For insight vs. rest and noninsight vs. rest, the thresholds were set at $p < 0.001$ (False Discovery Rate control for multiple comparisons) and 30 or more contiguous voxels, while for insight vs. nonisight solution, the threshold was set at $p < 0.05$ (False Discovery Rate control for multiple comparisons) and 30 or more contiguous voxels. T- and Z-scores of the activations were also shown. Note that the six voxels in RHIPP were included in a larger cluster with 116 contiguous voxels mostly located in right amygdala. At a looser threshold ($p < 0.005$ uncorrected), there were 84 contiguous voxels more activated in RHIPP for insight than noninsight solution.

associated with the novelty degree of stimuli (Luo and Niki, 2002, 2005; Johnson et al., 2008). Therefore, it was proposed as the key brain region of forming novel association (Luo and Niki, 2003; Zhao et al., 2013). In the present study, the bilateral hippocampi were involved in both insight and noninsight solution, but more activated for insight solution. These might reflect that the associations between the riddle and the selected answer were formed in both insight and noninsight solution, but the novel associations only existed in insight solution.

In insight 'chengyu' riddle solving, the forming of novel associations was dependent on the retrieval of the novel meaning of the key character. Our results showed that the RHIPP was functionally connected with the RTMD in insight solution, Fig. 3 but the strength was not larger than that in noninsight solution. However, the functional connectivity between the RHIPP and LMTG was stronger in noninsight than insight solution. This might reflect that the retrieval of normal semantic information resulted in the normal associations in noninsight solution.

Right-hemisphere theory in verbal insight problem solving

Since the key of creative problem solving is the selection of novel information (Bink and Marsh, 2000), and the right temporal cortex engages in relatively coarse and novel semantic processing (Beeman and Bowden, 2000; Mashal et al., 2008), it is proposed that there is a right-hemisphere advantage in insight problem solving (Bowden and Jung-Beeman, 2003). In particular, the right superior temporal gyrus is found in several studies and it is considered to facilitate the formation of remote associations (Jung-Beeman et al., 2004; Kounios et al., 2008; Zhang et al., 2011). However, the present study showed the bilateral middle temporal gyri involved in insight solution, even at the time just prior to the solution (Zhao et al., 2013). The paradigm adopted by the present study might be the reason why the advantage of right hemisphere was not found. Although the answer selection paradigm made participants more active than solution recognition, it still simplified the retrieval of the novel meanings and distant associates,

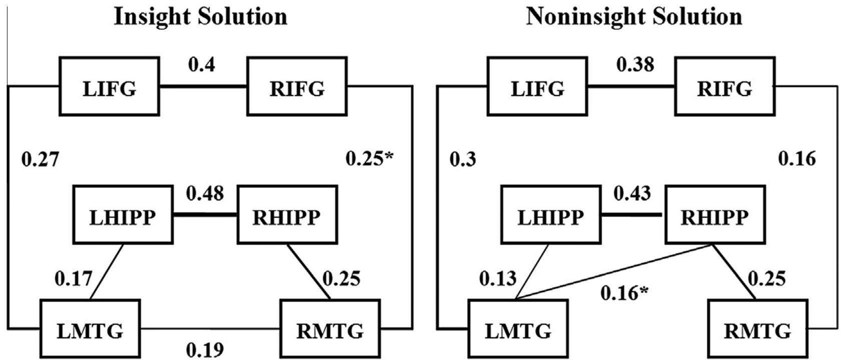

Fig. 3. The functional connectivity among the ROIs for insight and noninsight solution. A line between two regions indicates that the region-to-region correlation is statistically significant, and the thickness of the line reflects the strength of functional connectivity. The star means significant difference between two conditions ($p < 0.05$, paired t-test).

and then weakened the activation of the right temporal cortex.

However, the brain activity contains two aspects: the activation of local regions and the interaction among them. Most previous debates about the right-hemisphere advantage in insight were only based on the results of the activation in local regions. In the present study, the functional connectivity among the key brain regions in insight and noninsight solution was evaluated. Results showed that there was a neural pathway from the inferior frontal gyrus to middle temporal gyrus to hippocampus for insight solution in the both hemispheres, but insight solution had greater ipsilateral frontal–temporal connectivity in the right hemisphere than noninsight solution. This implied that verbal insight problem solving needed the participations of both the left and right hemispheres, in which the right hemisphere might be more important compared with common verbal problem solving.

CONCLUSION

Our results demonstrated that verbal insight problem solving activated broad brain regions including the lateral prefrontal cortex, middle temporal gyrus and hippocampus in both hemispheres. There regions constituted a frontal–temporal–hippocampal neural pathway, especially in right hemisphere, which might reflect the selection of novel semantic information and the forming of novel associations. Compared with noninsight solution, insight solution showed greater ipsilateral frontal–temporal connectivity in the right hemisphere. Our result supported the right-hemisphere advantage theory of insight in a new angle of view.

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REFERENCES

Aziz-Zadeh L, Kaplan JT, Iacoboni M (2009) “Aha!”: the neural correlates of verbal insight solutions. Hum Brain Mapp 30:908–916.

Beeman MJ, Bowden EM (2000) The right hemisphere maintains solution-related activation for yet-to-be-solved problems. Mem Cogn 28:1231–1241.

Bink ML, Marsh RL (2000) Cognitive regularities in creative activity. Rev Gen Psychol 4:57–78.

Bowden EM, Jung-Beeman M (2003) Aha! Insight experience correlates with solution activation in the right hemisphere. Psychon Bull Rev 10:730–737.

Bowden EM, Jung-Beeman M (2007) Methods for investigating the neural components of insight. Methods 42:87–99.

Cohen NJ, Ryan J, Hunt C, Romine L, Wszalek T, Nash C (1999) Hippocampal system and declarative (relational) memory: summarizing the data from functional neuroimaging studies. Hippocampus 9:83–98.

Dietrich A, Kanso R (2010) A review of EEG, ERP, and neuroimaging studies of creativity and insight. Psychol Bull 136:822–848.

Faust M, Chiarello C (1998) Sentence context and lexical ambiguity resolution by the two hemispheres. Neuropsychologia 36:827–835.

Faust M, Mashal N (2007) The role of the right cerebral hemisphere in processing novel metaphoric expressions taken from poetry: a divided visual field study. Neuropsychologia 45:860–870.

Friston KJ, Frith CD, Liddle PF, Frackowiak RS (1993) Functional connectivity: the principal-component analysis of large (PET) data sets. J Cereb Blood Flow Metab 13:5–14.

Giora R (1997) Understanding figurative and literal language: the graded salience hypothesis. Cogn Linguist 7:183–206.

Goel V, Vartanian O (2005) Dissociating the roles of right ventral lateral and dorsal lateral prefrontal cortex in generation and maintenance of hypotheses in set-shift problems. Cereb Cortex 15:1170–1177.

Johnson JD, Muftuler LT, Rugg MD (2008) Multiple repetitions reveal functionally and anatomically distinct patterns of hippocampal activity during continuous recognition memory. Hippocampus 18:975–980.

Jung-Beeman M, Bowden EM, Haberman J, Frymiare JL, Arambel-Liu S, Greenblatt R, Reber PJ, Kounios J (2004) Neural activity when people solve verbal problems with insight. PLoS Biol 2:E97.

Kaplan CA, Simon HA (1990) In search of insight. Cogn Psychol 22:374–419.

Kershaw TC, Ohlsson S (2004) Multiple causes of difficulty in insight: the case of the nine-dot problem. J Exp Psychol Learn Mem Cogn 30:3–13.

Knight R (1996) Contribution of human hippocampal region to novelty detection. Nature 383:256–259.

Knoblich G, Ohlsson S, Raney GE (2001) An eye movement study of insight problem solving. Mem Cogn 29:1000–1009.
Köhler W (1925) The mentality of apes. London: Routledge & Kegan Paul.
Kounios J, Fleck JI, Green DL, Payne L, Stevenson JL, Bowden EM, Jung-Beeman M (2008) The origins of insight in resting-state brain activity. Neuropsychologia 46:281–291.
Luks TL, Simpson GV, Feiwell RJ, Miller WL (2002) Evidence for anterior cingulate cortex involvement in monitoring preparatory attentional set. Neuroimage 17:792–802.
Luo J (2004) Neural correlates of insight. Acta Psychol Sin 36:219–234.
Luo J, Niki K (2002) Role of medial temporal lobe in extensive retrieval of task-related knowledge. Hippocampus 12:487–494.
Luo J, Niki K (2003) Function of hippocampus in ''insight'' of problem solving. Hippocampus 13:316–323.
Luo J, Niki K (2005) Does hippocampus associate discontiguous events? Evidence from event-related fMRI. Hippocampus 15:141–148.
Luo J, Niki K, Phillips S (2004) Neural correlates of the 'Aha! reaction'. Neuroreport 15:2013–2017.
Luo J, Niki K, Knoblich G (2006) Perceptual contributions to problem solving: chunk decomposition of Chinese characters. Brain Res Bull 70:430–443.
MacDonald 3rd AW, Cohen JD, Stenger VA, Carter CS (2000) Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 288:1835–1838.
MacGregor JN, Ormerod TC, Chronicle EP (2001) Information processing and insight: a process model of performance on the nine-dot and related problems. J Exp Psychol Learn Mem Cogn 27:176–201.
Mai XQ, Luo J, Wu JH, Luo YJ (2004) ''Aha!'' effects in a guessing riddle task: an event-related potential study. Hum Brain Mapp 22:261–270.
Mashal N, Faust M, Hendler T, Jung-Beeman M (2008) Hemispheric differences in processing the literal interpretation of idioms: converging evidence from behavioral and fMRI studies. Cortex 44:848–860.
Ormerod TC, MacGregor JN, Chronicle EP (2002) Dynamics and constraints in insight problem solving. J Exp Psychol Learn Mem Cogn 28:791–799.
Pobric G, Mashal N, Faust M, Lavidor M (2008) The role of the right cerebral hemisphere in processing novel metaphoric expressions: a transcranial magnetic stimulation study. J Cogn Neurosci 20:170–181.
Qiu J, Li H, Yang D, Luo Y, Li Y, Wu Z, Zhang Q (2008) The neural basis of insight problem solving: an event-related potential study. Brain Cogn 68:100–106.
Qiu J, Li H, Jou J, Liu J, Luo Y, Feng T, Wu Z, Zhang Q (2010) Neural correlates of the ''Aha'' experiences: evidence from an fMRI study of insight problem solving. Cortex 46:397–403.
Razoumnikova OM (2000) Functional organization of different brain areas during convergent and divergent thinking: an EEG investigation. Brain Res Cogn Brain Res 10:11–18.
Redish AD (2001) The hippocampal debate: are we asking the right questions? Behav Brain Res 127:81–98.
Takeuchi H, Taki Y, Sassa Y, Hashizume H, Sekiguchi A, Fukushima A, Kawashima R (2010) White matter structures associated with creativity: evidence from diffusion tensor imaging. Neuroimage 51:11–18.
Tononi G, Sporns O, Edelman GM (1994) A measure for brain complexity: relating functional segregation and integration in the nervous system. Proc Natl Acad Sci USA 91:5033–5037.
Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15:273–289.
Wu L, Knoblich G, Luo J (2013) The role of chunk tightness and chunk familiarity in problem solving: evidence from ERPs and fMRI. Hum Brain Mapp 34(5):1173–1186.
Zhang M, Tian F, Wu X, Liao S, Qiu J (2011) The neural correlates of insight in Chinese verbal problems: an event related-potential study. Brain Res Bull 84:210–214.
Zhao QB, Zhou ZJ, Xu HB, Chen S, Xu F, Fan WL, Han L (2013) Dynamic neural network of insight: a functional magnetic resonance imaging study on solving Chinese 'chengyu' riddles. PLoS one 8:e59351.
Zhou ZJ, Xu HB, Zhao QB, Zhao LL, Liao MJ (2011). The processing of novel semantic association in Chinese: Converging evidence from behavior and fMRI studies. In: The 4th international conference on image and signal processing (CISP 2011), Shanghai. Vol. 3, pp 1588–1592.
Zhu XC, Li RJ, Zhou ZJ (2009) The role of clues in Chinese idiom riddle solving. Acta Psychol Sin 41:397–405.

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