

Function of Hippocampus in “Insight” of Problem Solving

Jing Luo¹ and Kazuhisa Niki^{2,3*}

¹Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing, China

²Neuroscience Research Institute, National Institute of Advanced Industrial Science and Technology (AIST), Tsukuba, Ibaraki, Japan

³Brainscience and Education, RISTEX, JST, Tokyo, Japan

ABSTRACT: Since the work of Wolfgang Köhler, the process of “insight” in problem solving has been the subject of considerable investigation. Yet, the neural correlates of “insight” remain unknown. Theoretically, “insight” means the reorientation of one’s thinking, including breaking of the unwarranted “fixation” and forming of novel, task-related associations among the old nodes of concepts or cognitive skills. Processes closely related to these aspects have been implicated in the hippocampus. In this research, the neural correlates of “insight” were investigated using Japanese riddles, by imaging the answer presentation and comprehension events, just after participants failed to resolve them. The results of event-related functional magnetic resonance imaging (fMRI) analysis demonstrated that the right hippocampus was critically highlighted and that a wide cerebral cortex was also involved in this “insight” event. To the best of our knowledge, this work is the first neuroimaging study to have investigated the neural correlates of “insight” in problem solving. *Hippocampus* 2003;13:316–323. © 2003 Wiley-Liss, Inc.

KEY WORDS: insight; hippocampus; event-related fMRI

INTRODUCTION

In 1917, Wolfgang Köhler observed that chimpanzees could resolve problems suddenly. The sudden onset, smoothness, and continuous emergence of this type of problem-solving behavior were proposed as evidence that (1) contrary to suggestions of learning theorists of that day, problem solving was not necessarily a trial-and-error process; and (2) constructs such as “insight” were necessary for an adequate account (Köhler, 1925; Epstein et al., 1984). Köhler’s observations have been the subject of investigation ever since (e.g., Weisberg and Alba, 1981; Epstein et al., 1984). However, the neural corre-

lates of “insight” remain unknown. As a high-level cognitive process, “insight” means to break the unwarranted “fixation” and to form novel, task-related associations among the old nodes of concepts or cognitive skills. Both aspects (facets) can be closely related to the function of hippocampus.

First, “insight” occurs when one breaks the unwarranted mental “fixation.” For example, in the nine-dot problem, in which subjects are to connect the nine dots (in a 3×3 matrix-like arrangement) with four connected straight lines, without lifting the pencil from the paper, subjects are assumed to be fixed on the unwarranted assumption that the lines must conform to the shape of the square (Scheerer, 1963). Only when subjects break this unsuitable assumption, can they attain the “insightful” resolution of the problem. Breaking of the unwarranted mental “fixation” can activate hippocampus through a reorientation-like process (Redish, 2001); it also necessitates the “self-reflection” (i.e., to realize one’s way of thinking, or to take idiothetic/self-movement information as reference), which is known to be involved in “path integration” and proved to be hippocampus dependent (e.g., Whishaw et al., 2001; see also Whishaw et al., 1997, for review).

Second, “insight” occurs when novel, task-related associations are formed on the old nodes of concepts or cognitive skills. In the case of chimpanzees’ “insightful” resolution to push the crate and climb on it to reach the banana, pushing objects toward targets and climbing on objects to reach other objects were basic distinct skills that were acquired previously. “Insight” occurred when the chimpanzees combined these two skills in the specific problem-solving situation (e.g., Epstein et al., 1984). The formation of novel, task-related associations can activate hippocampus, because the hippocampus is generally known for its role in forming of associations (for animal neuroscience research, see Eichenbaum et al., 1994; Wallenstein et al., 1998; for neuroimaging studies, see Cohen et al., 1999; for network model of hippocampus functions, see McClelland et al., 1995; Rolls, 1996).

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*Correspondence to: Kazuhisa Niki, Neuroscience Research Institute, National Institute of Advanced Industrial Science and Technology, Central building 2nd, 1-1-1 Umezono, Tsukuba, Ibaraki, 305-8568 Japan.

E-mail: k.niki@aist.go.jp

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Other terms, such as “conjunctive representation” and “pattern completion,” which have been associated with the function of hippocampus, can also be related to forming of novel associations in “insight” (for involvement of hippocampus in conjunctive representation, see Nadel et al., 1985; O’Keefe and Nadel, 1978; Anagnostaras et al., 1999; Fanselow et al., 1993; Maren et al., 1997; for involvement of hippocampus in pattern completion, see Marr, 1971; McNaughton and Morris, 1987; O’Reilly and McClelland, 1994; Rudy and O’Reilly, 1999).

Other problem-solving processes are different from the “insight.” For example, to engage in syllogistic reasoning, subjects need not reorientate their thinking and break the unwarranted mental “fixation.” Subjects can resolve syllogistic reasoning task by following a single logic rule. Although the Wisconsin Card Sorting Task involves the process of set shifting, subjects usually alter their rules of classification among few well-known dimensions repeatedly (i.e., among color, shape, and number of stimuli) and need not form novel associations (e.g., Berman et al., 1995; Nagahama et al., 1996, 2001; Goldberg et al., 1998; Konishi et al., 1998, 1999; Rogers et al., 2000; Monchi et al., 2001).

In the present research, interesting Japanese riddles were presented to the participants (e.g., “The thing that can move heavy logs, but cannot move a small nail”). If they failed to resolve the riddles, they were presented with the correct answers (e.g., “river”). Participants reported they had a feeling of “insight” when they saw the answers. The process of answer presentation and comprehension was imaged by functional magnetic resonance imaging (fMRI). In this way, we were able to detect the neural correlates of “insight,” which we proposed activates the hippocampus. Two approaches were adopted to enhance the efficiency of our investigation. For the first place, the materials were “participant-specific.” By pre-scan interviewing, we selected a suitable list of riddles as experimental materials for each participant, to make sure that (1) the question was very well understood, and (2) the answer was still unknown. Thus, we could anticipate that a robust “insight” effect occurred in the presentation and comprehension of the correct answer. Second, the analysis was “event-specific.” Using event-related fMRI, we recorded the neural correlates of “insight” events, at the time point when participants obtained the “insightful” resolutions to the riddles.

MATERIALS AND METHODS

Data Acquisition

All scanning was performed on a 3.0-tesla (T) MRI Scanner (GE 3T Signa) equipped with EPI capability. In this study, 18 axial slices (5.3 mm thick, interleaved) were prescribed to cover the whole brain. A T2*-weighted gradient echo EPI was employed. The imaging parameters were TR = 2 s, TE = 33 ms, FA = 70°, FOV = 20 × 20 cm (64 × 64 mesh); 3.0 T had sufficient field strength to avoid localization biases toward draining veins. To reduce the susceptibility noise artifact (especially the EPI distortion) in the lower part of the brain, including the anteromedial

temporal lobes, we adopted a wider bandwidth (130 kHz) and set the participant’s chin down. To avoid head movement, participants wore a neck brace and were asked not to talk or move during scanning. Motion correction was also performed in a standard realigning process in SPM99.

Experimental Paradigm

A total of 300 Japanese riddles were obtained from the Internet. We selected the top 45 riddles that were evaluated as highly interesting and reasonable (matching with the solutions to riddles) by a group of subjects who did not participate in the formal fMRI experiment. The selected riddles had the solutions that were not definitely associated, but incredibly fitted with the questions; this fitted the concept of “insight” well (see for discussion, Weisberg and Alba, 1981). For example, to the question “The thing that can move heavy logs, but cannot move a small nail,” the answer is “river.” Participants were familiar with this type of riddle from their childhood and were willing to do this task. The length of each question was controlled to be within 16 characters of Japanese Kanji or Hiragana, and each answer to be within seven characters. The words that appeared in the questions and the answers were high-frequency words. In the pre-scan interviewing, participants were provided with the initial list of 45 riddles, and asked to resolve them. For each riddle, participants were asked to indicate one of three possible responses: (1) I can understand this question very well and know the answer (they were also required to write down the answer in this situation); (2) I can understand this question very well and feel it is interesting, but I do not know the answer; or (3) I cannot understand this question and do not know the answer. For each riddle, participants were given a maximum of 3 min. This pre-scan test would stop if participants had provided more than 16 items of “2”-type answers. About 55 min after the pre-scan interviewing, the formal scanning started. In the fMRI scanning, the 16 riddles judged to be “2” type in the pre-scan interviewing were presented in a randomized order relative to the order in pre-scan interviewing. Thus, the riddles in the fMRI scanning were “participant-specific.” To each participant, each riddle was well understood, but the solution was unknown. Each riddle was presented for 6 s, and participants were asked to indicate whether they knew the solution to it, because it was possible that they resolved the riddle when seeing it again in scanning session. Participants pressed the left key of the button box, which was attached to their right leg, with their right index finger if they resolved the riddle. Pressing of right key by the left middle finger indicated not knowing the solution. After 8 s of unfilled delay, the solution to the riddle was uncovered for 2 s, followed by an 8.2-s ITI delay. Participants were required to press the left or right key to indicate whether they understood the meaning of the answer (left key: yes, I can understand; right key: no, I cannot understand). The task is illustrated in Figure 1. Only those trials in which the questions were judged as “I do not know the answer” and the answers were judged as “I can understand the meaning” were selected into critical analysis. To familiarize the participants with the procedure and pace of this task, participants were trained with another set of similar materials in the same procedure before the formal experiment.

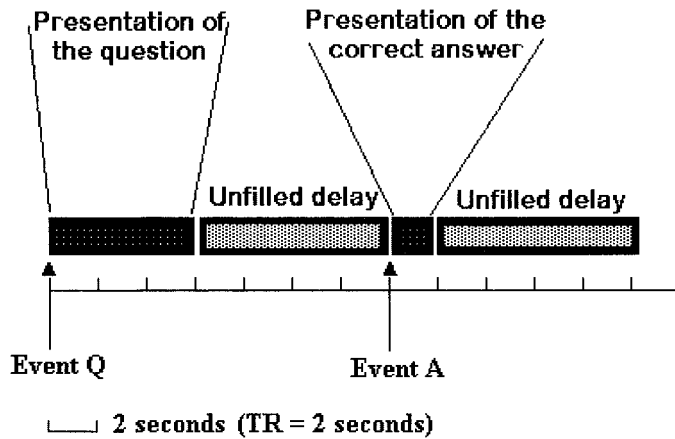


FIGURE 1. Illustration of the cognitive task.

Participants

Seven healthy, right-handed volunteers (4 female, 3 male), aged 20–22, recruited from the undergraduates of University of Tsukuba, participated in this experiment. They were interviewed 1 or 2 days before attending the fMRI experiment and were given informed consent that followed the MRI Ethics Committee of the Neuroscience Research Institute, AIST. Participants were excluded if they had any medical, neurological, or psychiatric illness, or if they did not feel well while in the MRI machine.

Data Analysis

Images were pre-processed (timeslice adjusted, realigned, normalized, and smoothed) by SPM99. Image data regarding the seven subjects were then estimated to establish a fixed-effects model by the Event-Related Analysis module of SPM99. Three types of events were defined in the analysis: (1) presentation of the question to which participants indicated they did not know the answer (Event Q); (2) presentation of the answer to which participants indicated they could understand the meaning of the answer (Event A, this event was time-locked at the beginning of answer presentation); and (3) presentation of the answer to which participants indicated they could not understand the meaning of the answer (Event AD). In all seven participants, there was no riddle question to which participants indicated they solved it. We did not consider the results of Event AD, because of insufficient number of trials. Only Events Q and A, which provided enough events (more than 12 for each participant), were considered. The threshold was set at $P < 0.05$ (corrected for multiple comparisons) and ten or more contiguous voxels.

RESULTS

In response to 90% of the riddles, participants indicated “I do not know the solution” to the questions, and “I understand the meaning” to the solutions of riddles. The averaged reaction time

for the judgment of question (resolving/not resolving) was 5.60 s (SD = 2.34) and for judgment of answer (understanding/not understanding), 1.44 s (SD = 1.02).

To extract and define the neural networks underlying the “insight” event, Event A was analyzed against the implicit baseline following the standard procedure of SPM99’s event-related fMRI analysis. The result showed widely distributed activities in frontal, temporal, parietal, and occipital (Table 1). Critically, a right hippocampal activity was highlighted in Event A (Fig. 2). The event-related plots (of the best-fitting canonical hemodynamic response function), which were taken from the voxel that has the maximal value in the contrasts, exhibited positive signal changes (percentage). Further analysis showed that Event A minus Q also exhibited right hippocampal activity in the same location observed in Event A (Fig. 2). Neither the reverse contrast (Event Q minus A) nor the Event Q showed superthreshold activation in the hippocampal and other MTL areas. In the present study, we concentrated only on the activation located in MTL area. The complete list of activations for each condition and contrast can be obtained by contacting the authors.

DISCUSSION

In this research, participants first saw the questions of the riddles they failed to resolve in the pre-scan test; they then obtained “insight” when the correct answers were revealed to them. Right hippocampal activation was observed in the event of answer presentation and comprehension (Event A relative to baseline) and in the contrast of “answer presentation minus question presentation” (Event A minus Q). In the training session outside the MRI machine, participants exhibited “insight”-like responses (“Aha,” “En,” or “Oh”) when they saw the correct answer. The significant activation of hippocampus in the event of answer presentation and comprehension implied that hippocampus was involved in the neural network subserving the “insight” process of problem solving. We consider some possible functions of hippocampus in “insight.”

Formation of Novel Associations

The solutions to the riddles are everyday concepts that have been acquired during childhood and strengthened throughout a lifetime of use. Therefore, it is unlikely that the hippocampus activation observed in answer presentation and comprehension was caused by the stimulus novelty that was known to activate the hippocampus (Tulving et al., 1994, 1996; Knight, 1996; Grunwald et al., 1998). Rather, it was the formation of novel associations among the old “nodes” of concepts that activated the hippocampus. The riddles were composed in such a way that the usual things (e.g., “river”) were described in unusual ways (e.g., “The thing that can move heavy logs, but cannot move a small nail”). Although the explicit memory retrieval made a clear reference to previous learning episodes, most of the research on word recognition failed to challenge the hippocampus. Subjects could recognize a learned word simply

TABLE 1.

Activations Shown in Event A

Area	T	Z	Talairach coordinates			
			x	y	z	
Bilateral superior frontal gyrus	6.21	6.19	-20	39	44	L BA 8
	6.16	6.14	-28	59	17	L BA 10
	6.12	6.1	-22	63	12	L BA 10
	4.95	4.93	-20	53	10	L BA 10
	4.84	4.83	22	56	32	R BA 9
	7.17	7.13	6	43	49	R BA 8
Bilateral middle frontal gyrus	7.26	7.22	-34	33	39	L BA 9
	6.4	6.37	-44	44	16	L BA 46
	5.45	5.43	48	31	35	R BA 9
	5.26	5.25	34	29	41	R BA 8
	5.1	5.09	26	37	42	R BA 8
	6.54	6.51	-4	60	1	L BA 10
	5.83	5.81	-2	63	10	L BA 10
	5.03	5.01	-4	50	-14	L BA 11
	5.83	5.81	4	-20	67	R BA 6
Left anterior cingulate cortex	4.69	4.68	0	15	-2	BA 25
Right precentral gyrus	6.48	6.45	34	-23	53	BA 4
	6.45	6.42	32	-16	39	BA 4
Bilateral inferior frontal gyrus	8.88	(Inf)	50	41	5	R BA 46
	6.68	6.65	-50	41	7	L BA 46
Right cingulate gyrus	6.35	6.32	2	-14	36	BA 24
	5.99	5.96	4	-23	40	BA 31
	5.85	5.83	6	0	30	BA 24
Bilateral superior temporal gyrus	4.8	4.79	-53	-16	1	L BA 21
	5.16	5.14	67	-21	3	R BA 22
	5.07	5.05	53	-15	6	R BA 22
	4.46	4.45	61	-12	1	R BA 21
	4.96	4.95	42	-27	11	R BA 41
Right hippocampus	5.76	5.74	36	-16	-14	
Right subgyral	7.43	7.39	24	-38	53	R BA 40
Left caudate	4.93	4.92	-20	-38	15	
Left inferior temporal gyrus	6.17	6.14	-53	-55	-12	L BA 20
	5.12	5.1	-57	-45	-10	L BA 20
Left inferior parietal lobule	7.74	7.69	-48	-56	45	BA 40
Left superior parietal lobule	7.58	7.53	-36	-55	58	BA 7
Right precuneus (BA 7)	7.05	7.01	4	-64	47	BA 7
Bilateral occipital lobe	7.54	7.49	6	-76	2	R lingual gyrus, BA 18
	4.66	4.65	-8	-70	-8	L lingual gyrus, BA 18
	4.85	4.84	-26	-51	-13	L fusiform gyrus, BA 37

BA, Brodmann area; L, left; R, right. Coordinates (x,y,z) are the locations containing the peak voxel within the area of a given activation. The anatomical regions were the approximate Talairach locations according to their coordinates (x,y,z). The threshold was set at $P < 0.05$ (corrected for multiple comparisons) and 10 or more contiguous voxels. T- and Z-scores of the activations were also shown.

based on its perceptual familiarity or smoothness of processing (e.g., Jacoby and Whitehouse, 1989; Rajaram, 1993). When a word was recognized, accompanied by rich recollective experiences (i.e., it was bound with rich novel episodic associations, as it was in a “R-response”) (Tulving, 1985), the hippocampus would be highlighted (Eldridge et al., 2000). These findings are consistent with the general view of the role of the hippocampus in the formation of associations (Eichenbaum et al., 1994; Wallenstein et al., 1998; Cohen et al., 1999; McClelland et al., 1995; Rolls, 1996) and with observations that the hippocampus participates in “conjunctive representation” and “pattern completion” (Nadel et al., 1985; O’Keefe and Nadel, 1978; Anagnostaras et al., 1999; Fanselow et

al., 1993; Maren et al., 1997; Marr, 1971; McNaughton and Morris, 1987; O’Reilly and McClelland, 1994; Rudy and O’Reilly, 1999).

Breaking of the Unwarranted Mental “Fixation”

Another possibility was that hippocampus mediated the process of breaking of the mental “fixation” in “insight.” The riddles always contain some misleading descriptions, for example, in the riddle “The thing that can move heavy logs, but cannot move a small nail,” the words “move” and “heavy logs” usually mislead the participants to think about something like a crane. When uncov-

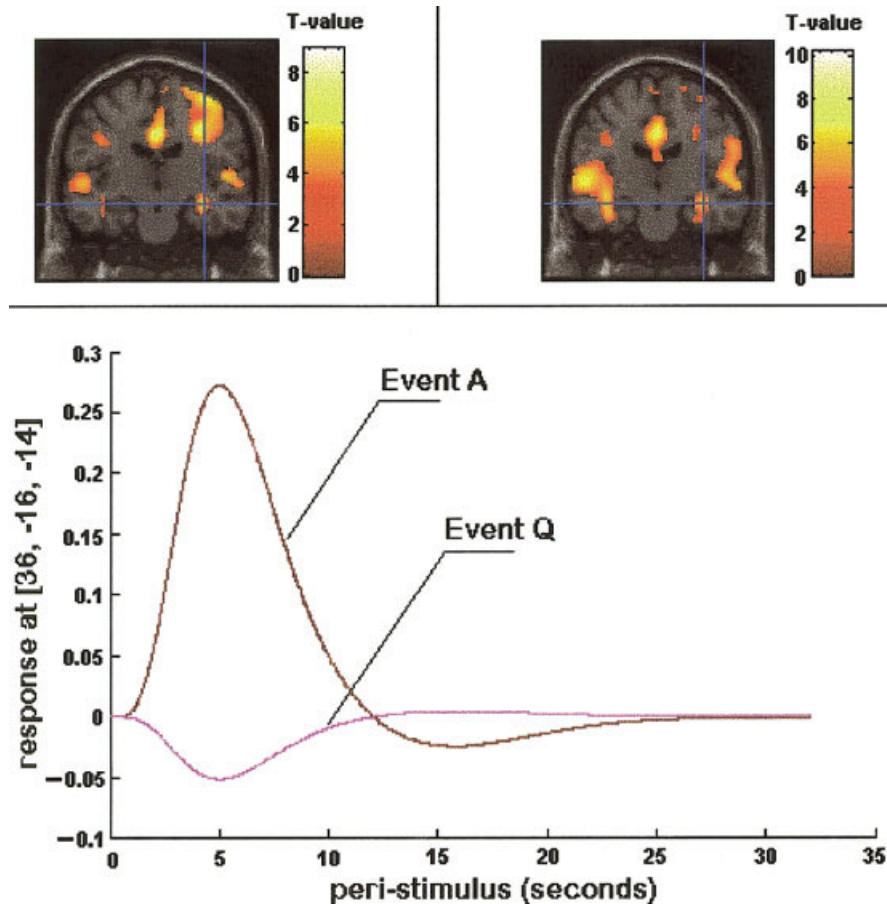


FIGURE 2. Hippocampal activation revealed in Event A (relative to baseline) (top left) and in the contrast of “Event A minus Event Q” (top right). The event-related plots (bottom) were averaged signal change (percentage) of the best-fitting canonical hemodynamic response function from the voxel in the maxima of the activations

(marked by the blue cross in the coronal sections and located at the position of $x = 36$, $y = -16$, $z = -14$ of Talairach space). The coronal sections are shown in the threshold of $P < 0.001$ (uncorrected for multiple comparisons). The results are shown for seven subjects, normalized and imposed on a universal brain.

ered with the correct answer, participants realized the incorrectness of their previous assumption and got rid of that mental “fixation.” To realize one’s own way of thinking and to get rid of the unsuitable “fixation” (i.e., to compare one’s own thinking with the correct answer, to realize what one’s original thinking was and where it was misled and stuck), these processes could be mediated by hippocampus in a similar way as in path integration and reorientation (e.g., Whishaw et al., 1997; Redish, 2001). Previous research has associated problem solving with the function of frontal lobe (e.g., Delis et al., 1992; Koechlin et al., 1999; Crozier et al., 1999; Duncan and Owen, 2000) and that of temporal lobe (e.g., Prabhakaran et al., 2001; Goel et al., 2000; Hodges et al., 1999). However, no hippocampal activation was detected in those tasks (e.g., syllogistic reasoning task, see Goel et al., 2000). One possibility is that there is no process of realizing and breaking the mental “fixation” in these tasks.

Things Behind “Forming of Novel Associations” and “Breaking of Mental Fixation”

Both the process of forming novel associations and the process of realizing and breaking the “fixation” could challenge hippocam-

pus. However, we still cannot differentiate between them. In “insight,” it might be true that the “realizing and breaking of fixation” could occur only when the “forming of novel associations” occurred, but the reverse situation might also be true; they were two aspects (facets) of “insight,” rather than two separate subprocesses of “insight.” In fact, the difference between these two possibilities is quite basic—that of the role of the hippocampus in the cognitive map and in declarative memory. To form novel associations roughly corresponds with the declarative memory point of view, while to break the mental “fixation” corresponds with the navigation point of view.

Some frameworks were advocated to bridge the role of the hippocampus in the cognitive map and declarative memory. For example, to account for both functions, Redish (2001) regarded the major role of the hippocampus as correcting the accumulation errors that occur within idiothetic navigation systems, recalling a context, and bridging a contextual gap. The most robust evidence in support of this point of view came from research on reorientation in an animal that is lost. It is reasonable to adopt the general proposal that the role of the hippocampus in “insight” as “reorientation of one’s thinking,” with the “re” in “reorientation” implying

both abandonment of something old (i.e., to break the old mental “fixations”) and the creation of something new (i.e., to form novel associations).¹

The framework proposed by Redish also included a subsystem of “reference frame” that is goal or task dependent (Redish, 2001; Redish and Touretzky, 1997) this is consistent with the observation made by Eichenbaum and colleagues that the “goal approach” cells in the hippocampus fired during orientation movement with respect to specific targets of attention, i.e., to the goals, rather than to the specific location itself (Eichenbaum et al., 1997; see also Hampson et al., 1993). This can be a critical mechanism in orientation. In parallel, by using semantically related or unrelated word pairs and semantic judgment task (on the relationship of these word pairs), we found the hippocampus to be more responsive to the process of “forming of task-related associations” than to “forming of novel associations” (Luo and Niki, 2002). Moreover, the same types of word pairs (relationships) could activate the hippocampus more when they were task-related than when they were not; in addition, the right hippocampal location we observed in “forming task-related associations” overlapped with the one we observed in “insight” (J. Luo and K. Niki, unpublished observations) (Fig. 3). The role of the hippocampus in forming task-related associations implied that the goal or task could impose the “top-down” regulations on forming associations. It is possible that taking the old “nodes” of concepts out of their original context (i.e., to break the “fixation”) and binding them into the new context (i.e., to form the novel associations) was motivated or regulated by the requirements of the tasks or goals.

After reviewing recent neuroimaging research on the hippocampus, Maguire (2001) concluded that right hippocampus subserves navigation, whereas the left hippocampus is more responsive to memories for events that occur in a specific time and place. The involvement of the right hippocampus in the process of “insight” implied that a navigation-like process might also occur in problem solving. Reorientation of one’s thinking could be subserved by a similar hippocampal function to that of reorientation in navigation.

“Insight” and Memory

It is natural to know that the “insightful” experiences can be very well kept in memory. Experimental animals consistently exhibited the specific problem-solving behavior once they gained “insight” (e.g., Epstein et al., 1984). Human subjects remembered the content for which they got an “aha” experience better than the content for which they failed to get the “aha” effect (e.g., Auble et al., 1979; Wills et al., 2000). Our research also showed that the forming of task-related associations (word pairs) was not only associated with more hippocampal activation, but was also better remembered, relative to the same type, but task-unrelated associations (J. Luo and K. Niki, unpublished observations). From an evolutionary perspective, the property of responding to the “insightful” experi-

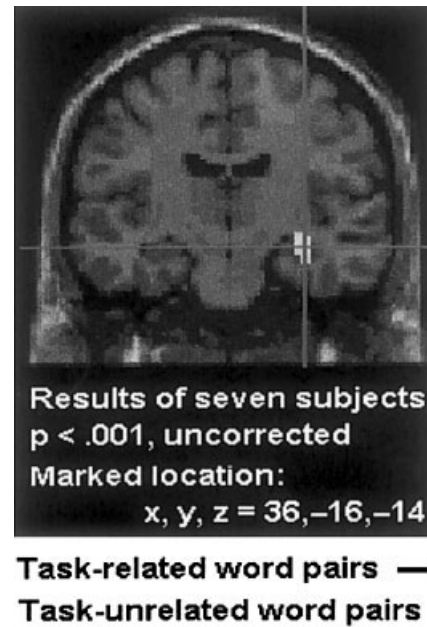


FIGURE 3. Right hippocampal activation exhibited in forming of task-related associations. This picture is taken from our recent research (J. Luo and K. Niki, unpublished observations). In this research, the requirements of semantic judgment were changed across different task blocks, so that the same types of items could be “task-related” or “task-unrelated.” This picture shows the hippocampal activation associated with the processing of task-related items (word pairs) relative to the semantically unrelated word pairs. The location of the peak activation is marked by the blue cross. This is the result of event-related analysis of seven undergraduate participants (scanned by 3T CE Signa and estimated by the fixed-effect model of SPM99). The activation shown in the picture has a T-value of 3.77 ($P < 0.001$, uncorrected).

ences and of fixing them into long-term memory can greatly enhance the possibility of an animal’s survival (Luo and Niki, 2002). This property of the hippocampus enables the organism to preserve the information that keeps great survival values in mind for future usage.

It was not plausible that the hippocampus alone could achieve “insight.” In fact, broad cerebral cortex activities, including frontal, temporal, parietal, and occipital lobes, were observed to be associated with the “insight” events. Although the focus of this study is the role subserved by the hippocampus, other areas, such as the frontal lobe, are also likely to be important. The advantage of whole brain scanning is that we retained information pertaining to other regions that may be relevant to future studies. Stricter experimental designs and more specific analysis methods (e.g., see Niki et al., 2001) are also needed to dissociate the various functional areas that contribute to this interesting process.

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