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Sustained activity within the default mode network during an implicit memory task

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Abstract

Recent neuroimaging studies have shown that several brain regions -- namely, the posterior cingulate cortex (PCC), ventral medial prefrontal cortex (vmPFC), and the bilateral angular gyrus -- are more active during resting states than during cognitive tasks (i.e., default mode network). Although there is evidence showing that the default mode network is associated with unconscious state, it is unclear whether this network is associated with unconscious processing when normal human subjects perform tasks without awareness. We manipulated the level of conscious processing in normal subjects by asking them to perform an implicit and an explicit memory task, and analyzed signal changes in the default mode network for the stimuli versus baseline in both tasks. The fMRI analysis showed that the level of activation in regions within this network during the implicit task was not significantly different from that during the baseline, except in the left angular gyrus and the insula. There was strong deactivation for the explicit task when compared with the implicit task in the default mode regions, except in the left angular gyrus and the left middle temporal gyrus. These data suggest that the activity in the default network is sustained and less disrupted when an implicit memory task is performed, but is suspended when explicit retrieval is required. These results provide evidence that the default mode network is associated with unconscious processing when human subjects perform an implicit memory task.

Keywords

default mode network; unconscious processing; implicit memory

1. Introduction

In recent years, converging neuroimaging studies have shown that several brain regions consistently exhibit hemodynamic signal decreases during many cognitive tasks when compared with passive states, such as the resting state with eyes closed, visual fixation, or passive viewing of simple stimuli (Gusnard and Raichle, 2001; Mazoyer et al., 2001; Shulman

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et al., 1997). These brain regions include the posterior cingulate cortex (PCC)/precuneus, ventral and dorsal medial prefrontal cortex (vmPFC, dmPFC), bilateral inferior parietal lobule (IPL, i.e., angular gyrus and supramarginal gyrus, Brodmann area (BA) 39, 40), and middle temporal gyrus (MTG, BA 21, 22, 19). The deactivation in these brain regions varies little in their locations across a wide range of cognitive tasks (Mazoyer et al., 2001; Shulman et al., 1997). As the deactivation network is also thought to be more active during resting states, it is variably called the default mode network (Raichle et al., 2001), the conscious resting state (Binder et al., 1999; Mazoyer et al., 2001), or task-induced/independent deactivation (McKiernan et al., 2003).

One of the important issues is what functions this default mode network might subservise (Gusnard and Raichle, 2001; Mazoyer et al., 2001; Raichle and Mintun, 2006; Shulman et al., 1997). There are mainly three different approaches to investigate this issue. One is to find an abnormal population (e.g., coma or dementia) in which the default network is significantly different from normal subjects during resting states (e.g., Laureys et al., 1999; Lustig et al., 2004), and then infer that the default network is related to the functions that the abnormal population is impaired. The second is to find a task condition during which the activity in the default mode regions is sustained (e.g., Binder et al., 1999), or even increased (e.g., Gusnard et al., 2001), and then infer that the default network shares the similar cognitive process underlying the task. The third is to find relationship between the default mode regions and offline task performance (e.g., Wig et al., 2008), and then infer that the default network is related to the cognitive functions underlying the task.

Based on studies that adopted the approaches described above, the default mode network is regarded to be involved in different on-going information processing (Raichle and Mintun, 2006; Mazoyer et al., 2001), such as monitoring the internal mental and external environment, preparing for a potential threat (Gusnard and Raichle, 2001), representing self and body image (Gusnard and Raichle, 2001), and maintaining a coherent flow of mental activities. For example, Mason et al. (2007) found that mind-wandering is associated with activity in regions of the default network. In addition, individuals' reports of the tendency of their minds to wander are correlated with activity in this network. There are also remarkable overlaps between regions in the default network and brain regions involved in self-projection and social cognition (for reviews, see Buckner and Carroll, 2007; Schilbach et al., 2008). During the resting state, rather than being passively activated by sensory input, the default mode regions may continuously process information to remember the past (Christoff et al., 2004; Schilbach et al., 2008), to consider another person's perspective (Buckner and Carroll, 2007), to generate associations between object features (e.g., PCC and mPFC, Bar, 2007; Bar and Aminoff, 2003), and to construct future plans (e.g., Hassabis et al., 2007). For example, the parietal cortex and the mPFC are involved in processing self-referential and socially relevant information (e.g., Buckner and Carroll, 2007; Lou et al., 2004; Mitchell et al., 2005). The autistic patients, who have deficits in emotion and social interactions, show less deactivation in the mPFC (Kennedy et al., 2006). These data thereby help to integrate different functions as forms of self-projection, and provide a social context in which events become personally meaningful (Buckner and Carroll, 2007; Schilbach et al., 2008).

Among these candidate functions, one interesting issue is to what extent these functions depend on conscious processing. Previous studies have suggested that the default mode network is associated with conscious awareness (e.g., Binder et al., 1999; Fiset et al., 1999; Laureys et al., 1999, 2005). This hypothesis has gained support mainly from studies on abnormal conscious states. For example, activity in the medial/lateral parietal cortices and the PCC is reduced during situations when consciousness is absent, such as sleep, deep anesthesia, a vegetative state, propofol-induced loss of consciousness, and epileptic patients in general seizures (Blumenfeld et al., 2004; Fiset et al., 1999; Laureys et al., 1999, 2005). On the other

hand, activity in the default mode network is still detectable even during anesthesia and other unconscious states (Pinsk and Kastner, 2007; Seeley et al., 2007). For example, Vincent et al. (2007) have found that in anesthetized monkeys, the activity in PCC/precuneus is significantly correlated with the dorsal PFC and lateral temporoparietal cortex (i.e. area 7a and superior temporal gyrus), which is similar to the findings in humans.

As indicated by Tsuchiya and Adolphs (2007), consciousness can be divided by its state, or by its content. The consciousness state refers to the level of consciousness, such as wakefulness, sleep, or coma; whereas the consciousness content refers to what it is we are conscious of. During the conscious state, people can still unconsciously process many kinds of mental activities they are experiencing at that moment, although they may not be aware of what content they process (i.e., unconscious processing) (Christoff et al., 2004; Fransson, 2006). For example, people could unconsciously/automatically perceive the presented stimuli, encode them, and unconsciously retrieve them (Tulving & Schacter, 1990). People could also show preference or prejudice for other people, although they may not explicitly state the reason (Frith & Frith, 2008). There is evidence showing that the default mode network is associated with the unconscious state (e.g., Vincent et al., 2007), but it is unclear whether this network is associated with unconscious processing when normal human subjects perform tasks without awareness.

To address this issue, we manipulated levels of conscious processing in memory retrieval tasks (for reviews, see Schacter et al., 2004; Tulving & Schacter, 1990). After learning the word pairs during encoding, normal human subjects were asked to perform an implicit task (i.e., perceptual identification task) and an explicit task (associative recognition) during retrieval. The two tasks differ in whether subjects *retrieve* information with or without conscious processing. The implicit memory refers to the influence of prior experience on behavior in the absence of conscious awareness during retrieval, whereas explicit memory refers to the retrieval of information by conscious efforts (Schacter et al., 2004). As normal subjects are possible to consciously retrieve information during implicit memory tasks, it is critical to avoid this kind of possible explicit contamination in such studies (Henson, 2003; Schacter et al., 2004). Thus we controlled explicit memory performance at a chance level by using a perceptual encoding task during study, and subsequently by using a perceptual identification task during retrieval (Gabrieli et al., 1997; Yang et al., 2003), in which word pairs were quickly flashed with individually adjusted exposure durations. The behavioral dissociation between the implicit and explicit task was necessary to ensure that the unconscious manipulation was successful thus we could test the difference of baseline versus implicit/explicit task in the default mode regions.

Previous studies have found significant deactivation in the default mode regions during explicit memory tasks (e.g. Daselaar et al., 2004; Marklund et al., 2007; Miller et al., 2008). For example, the PCC exhibits significant deactivation (vs. baseline) during explicit memory, semantic memory, working memory, and attention tasks (Marklund et al., 2007). The PCC and the angular gyrus exhibit greater deactivation for remembered versus forgotten items (Daselaar et al., 2004), but old adults who perform poorly on the memory task do not show this pattern (Miller et al., 2008). The greater the MTL showed deactivation, the better offline memory performance on words and face-name associations for normal subjects (Wig et al., 2008). Alzheimer's patients who have severe memory deficits show less deactivation in the PCC and medial parietal regions (Buckner et al., 2005; Greicius and Menon, 2004). However, whether the implicit task leads to similar deactivation in the default mode regions has not been determined.

The objective of our study was to investigate whether the default mode network is associated with implicit memory task in normal human subjects. To focus on the activity within the default

mode regions, we first analyzed signal changes in regions that showed significant deactivation for each pair type versus fixation baseline in each task, and then found the common deactivated regions for all word pairs by a conjunction analysis. As the regions showing deactivation during the explicit task were consistent with other studies reported in the literature (for reviews, see Gusnard and Raichle, 2001; Shulman et al., 1997), we selected them as regions of interest (ROIs), and tested whether these regions were deactivated during the implicit memory task, and whether the level of deactivation was different between the two tasks. It is generally regarded that the default mode regions are deactivated for external goal-directed tasks, but remain stable when the external demands are minimal (Gusnard and Raichle, 2001; Mazoyer et al., 2001; McKiernan et al., 2003). However, if the external task requires the same or similar cognitive processes that the default network is involved in, these regions would remain active (e.g., Binder et al., 1999; Gusnard et al., 2001). Thus an overlap pattern of brain activation during rest and the cognitive task would be expected, and the signal difference between them would be small. Accordingly, our hypothesis is that if the default mode network is associated with unconscious memory processing, its activity during the baseline would be comparable with that during an implicit memory task, whereas its activity would be significantly decreased during an explicit memory task.

2. Materials and methods

2.1. Subjects

Thirty-three healthy, right-handed subjects (18 male, 15 female), with a mean age 21.58 ± 2.04 years, participated in this study. Fifteen of them (8 male) participated in the fMRI group. Given that speaking aloud may produce excessive head movements, subjects were asked to read word pairs *silently* in the MR scanner. Two subjects' fMRI data were excluded for both tasks because of large head motion. Other two subjects' fMRI data were missing for the explicit task because they were not scanned for this session. A separate behavioral group (18 subjects, 10 male) was selected to perform the same tasks outside of the scanner, except that they read the word pairs aloud during the perceptual identification task. There were no significant gender or age differences between the two groups. All subjects were paid for their participation and gave written informed consent in accordance with procedures and protocols approved by the institutional Review Board of Beijing MRI Center for Brain Research.

2.2. Stimuli

A total of 320 two-character Chinese concrete words were selected to form 160 unrelated word pairs; for example, 玫瑰—磁铁 (rose---magnet), 钥匙—核桃 (key---walnut). Since all Chinese characters correspond to one spoken syllable, each word (two characters) has two syllables. Each character is made up of different types of strokes (i.e., continuous movements), and the number of strokes refers to how many movements a character or a word can be written (e.g., 人 (person) has two strokes; 玫瑰 (rose) has 21 strokes). To control for word familiarity and complexity, all words had medium frequencies (187 ± 90 per million) and a medium number of strokes (17.51 ± 4.56). No obvious semantic, orthographic or phonological relationship existed between two words in each pair.

All word pairs were divided into two parts, one was used for determining exposure duration (90 pairs), and the other (60 pairs) was used in both behavioral and fMRI study and test sessions. The latter 60 pairs were further divided into three sets, each composed of 20 pairs that were used as old, recombined, and new pairs, respectively. The old and recombined sets were presented in both study and test sessions, and the new set was used as the baseline in the perceptual identification test. Each word and its characters appeared only once in all three sets. Word frequency ($t = .40, p < .69$) and stroke ($t = .48, p < .63$) were not significantly different among the three sets ($p > .05$, for frequency and stroke). The arrangement of the three sets was

counterbalanced across subjects so that each word pair had an equal chance to be an old, recombined and new pair. The remaining 10 pairs were used for practice.

2.3. Task procedure

There were two factors in this study, with word pair type and retrieval task (implicit, explicit) as within-subject factors. The word pairs included three types (old, recombined, and new) in the implicit task, and two types (old and recombined) in the explicit task. We used a mixed-design for the fMRI scanning because pairs were presented in an event-related design for each task, and tasks were performed in a block design.

Subjects were first determined their own optimal exposure durations for word pairs (Yang et al., 2003). They then learned the word pairs in the study session; and retrieved the word pairs during the implicit (i.e., perceptual identification) task and the explicit (recognition) task in the test session (Fig.1). Subjects in the fMRI group were scanned for both the implicit and explicit tasks. To obtain behavioral scores for the implicit task, subjects in the behavioral group performed the same tasks as those in the fMRI group outside of the scanner, except that in the implicit task, they were asked to read aloud the quickly flashed word pairs.

The optimal exposure duration (i.e., how long a word pair was presented) was first determined for each subject. A series of tests, each with 10 unrelated word pairs, was conducted outside of the scanner. Before the presentation of each word pair, a fixation cross (“+”) was displayed on the center of the screen for 500 msec. Then a word pair was presented for a certain duration and masked immediately by an irregular and meaningless drawing consisting of character-like strokes. Subjects were asked to read the word pairs as quickly and accurately as possible. After each 10 pairs, the exposure durations of the word pairs changed according to the subjects' performance. Using this procedure, the exposure duration for each subject was gradually adjusted to yield a correct identification rate of 20% -- 40%.

During the study session, subjects were asked to decide whether the two Chinese words had the same structural configurations. As subjects processed perceptual features of the word pairs, we referred the task as a perceptual encoding task. Each pair was randomly presented for 2 sec and then replaced by “+” on the screen for 2 sec. Then during the implicit task, subjects were asked to silently read the quickly flashed word pairs (i.e., perceptual identification task), following a 3-minute mental arithmetic task (serial subtraction of 7 starting from 1000). Sixty test pairs consisting of old, recombined and new pairs, mixed with 20 masks, were presented with the predetermined exposure duration, and then masked with the character-like strokes. All stimuli were pseudo-randomly assigned to two runs (30 word pairs per run), with no more than three pairs in the same condition (old, recombined, new) were continuously presented. To optimize estimation of the fMRI event-related response, the variable (“jittered”) inter-trial intervals (ITI, mean \approx 6 sec, range = 2-12 sec) were determined by Optseq program (Dale, 1999). As there were additional fixations inserted at the beginning and the end of each run, the whole task lasted for 536 sec (268 sec per run). The run order was counterbalanced across subjects. During the explicit (recognition) task, subjects were asked to make old or recombined judgment as quickly and accurately as possible by button press. There were 20 old pairs and 20 recombined pairs. Each word pair was presented for 2 sec in either the same or different combinations as those in the study session, and then replaced by “+” on the screen. All stimuli were pseudo-randomly assigned, with no more than three pairs in the same condition (old, recombined) were continuously presented. The event-related design was used with a variable ITI (mean \approx 6 sec, range = 2-12 sec). The whole task lasted for 292 sec.

2.4. MRI acquisition

MR data were collected in a Siemens 3 Tesla scanner (Magnetom Trio). Stimuli were presented through a back projector. Subjects viewed the stimuli through a mirror attached to the head coil. Anatomical data were acquired using a high-resolution SPGR (TR = 845 msec, FOV = 22 cm, matrix = 256×256, resolution = $1 \times 1 \times 1.3 \text{ mm}^3$) sequence before the study session. The whole brain functional data were acquired using a gradient echo echo-planar imaging (EPI) sequence (TR = 2 s, TE = 30 ms, flip angle = 90°, FOV = 22 cm, matrix = 64 × 64, resolution = $3.75 \times 3.75 \times 4 \text{ mm}^3$). To better observe the signals in the medial temporal lobe (MTL), oblique slices that were perpendicular to the long axis of the hippocampus were used.

2.5. Data analysis

For the behavioral group, the accuracy and reaction time (RT) data were recorded during both the implicit and explicit tasks; however, because of a malfunction of the microphone, the RTs were only recorded for eight subjects during the implicit task. For the fMRI group, as subjects silently read the quickly flashed word pairs in the scanner, their behavioral data during the implicit task were not recorded. The implicit memory performance was indexed as the difference in accuracy and RT where subjects read the old versus recombined word pairs, and the difference between recombined versus new pairs. The explicit memory performance was indexed as the difference in accuracy and RT where subjects recognized old versus recombined pairs. SPSS was used for behavioral data analysis ($p < .05$, two-tailed).

The fMRI data were preprocessed and analyzed by the software AFNI (<http://afni.nimh.nih.gov>). The first five EPI volumes before magnetization and intensity remained at a steady state were discarded. The remaining volumes were registered to the nearest volume close to anatomical images to correct subjects' head movement. A spatial smooth with a root-mean-square (RMS) width of 4 mm was applied to all registered volumes. Then all MRI signals in each volume were scaled to percent from the mean before deconvolution analysis. In 3dDeconvolve, a time window of 6 TRs (12 sec) was selected with which to model the hemodynamic response of each stimulus. Altogether 18 regressors of interest (3 pair types, 6 TRs) were applied for the perceptual identification task, and 12 regressors of interest (2 pair types, 6 TRs) were applied for the explicit task, each with an additional 6 regressors of non-interest motion parameters. The averaged β weights of the hemodynamic response function (HRF) in the second to fourth time points (2–8 sec, corresponding to peak BOLD signal changes) were used to estimate the amplitude for each condition (vs. fixation) (e.g., Beauchamp et al., 2004).

After transforming functional HRF for each subject to the standard stereotaxic coordinates of the Talairach and Tournoux (1988) atlas, three approaches were adopted in the group analysis to determine the relationship between the default network and different tasks. First, to determine the difference between experimental conditions and the baseline, a voxel-wise mixed-effect model of ANOVA was adopted in each task, with word pair type (old, recombined, and new pairs in the implicit task; old and recombined pairs in the recognition task) as a fixed factor. We examined the BOLD signal changes for each stimulus type (vs. baseline). As the word pairs were retrieved in either the implicit or explicit task, we then applied a conjunction analysis to find the common regions that showed significant deactivation for all word pair types (vs. baseline) in each task, that is, the common deactivation for the old, recombined, and new pairs in the implicit task, and the common deactivation for the old and recombined pairs in the explicit task. To compare between tasks, we also adopted conjunction analysis to determine the common deactivation for the old and recombined pairs in the implicit task.

Second, to determine the differences between the two tasks, a separate voxel-wise mixed-effect model of ANOVA was adopted, with pair type (old, recombined) and task (implicit, explicit) as fixed factors. As new pairs were only presented in the implicit task, they were not included as a condition. The different activity of implicit versus explicit memory across pair types in the default mode regions was used as the index of task difference. For the above two approaches, to ensure that the deactivation could be detected for the implicit task and reduce type-II errors, the criterion of $p < .05$ was adopted as the level of significance. Monte Carlo simulations were then used to correct for multiple comparisons and to determine how large a cluster of voxels was needed to be significantly meaningful ($\alpha < .05$).

Third, to further investigate whether the regions that showed deactivation in the explicit task showed similar activity in the implicit task, a region of interest (ROI) analysis was applied. Functional ROIs were defined as those regions that showed significantly greater deactivation for both the old and recombined pairs (vs. the fixation, $p < .05$, corrected) in the explicit task. Then the time series for each subject from these ROIs was extracted and averaged for each task. SPSS was used to analyze the ROI data ($p < .05$, two-tailed). Among the tests, a one-sample test was used to obtain the difference in signal changes for each pair type (vs. baseline) in each task; and a repeated measure ANOVA was used, with pair type (old, recombined) and task (implicit, explicit) as within-subject factors, to obtain task difference. Similar to the voxel-wise analysis, the task difference was indexed as the main contrast of tasks. In addition, the main contrast of pair types, and the interaction between pair type and task could be obtained.

3. Results

3.1. Behavioral results

We first report results from the behavioral group, then move to results from the fMRI group (Table 1). For the behavioral group, subjects encoded the word pairs with the accuracy of $.80 \pm .16$. They showed significant priming effects in the perceptual identification task, as they identified more old items or associations than new items or associations. The old pairs were identified more accurately than the recombined pairs ($t(17) = 2.17, p < .05$), with no significant difference in RTs ($t(7) = .13, p < .9$). The recombined pairs were identified more accurately ($t(17) = 5.04, p < .001$) and quickly ($t(7) = 2.6, p < .05$) than the new pairs. On the other hand, subjects' recognition performance was at a chance level, as there was also no significant difference between old and recombined pairs either for accuracy ($t(17) = .82, p < .42$) or for RT ($t(17) = 1.01, p < .33$). The mean d' ($-.53 \pm .86$) was not significantly different from chance level ($d' = 0, t(17) = 1.62, p < .12$). These results showed a behavioral dissociation between the implicit task and explicit task. Moreover, as subjects could not distinguish the old and recombined items, their priming effects shown in the implicit task are not due to possible explicit contamination.

Although we did not record behavioral performance in subjects from the fMRI group, their performance during encoding ($.80 \pm .08$) and explicit memory task was similar to that of the behavioral group (Table 1). Subjects had chance level of recognizing old and recombined pairs, with no significance between them for accuracy ($p < .73$) and RT ($p < .89$). The mean d' ($.27 \pm .92$) was not significantly different from chance level ($t(10) = .99, p < .35$). These data are important as they indicated that explicit influence on the implicit task is controlled due to their low explicit performance, thus priming effects were not the result of conscious retrieval of studied word pairs. In addition, the recognition performance in the two groups was similar for accuracy ($t(27) = .99$ for old, $t(27) = .44$ for recombined pairs, $p < .3$), RTs ($t(17) = .09$ for old, $t(17) = .71$ for recombined pairs, $p < .5$), and d' ($t(27) = .002, p < .1$). The post hoc inquiry showed that subjects attended to all stimuli and silently read the presented pairs in the implicit task. Given that both groups had similar levels of explicit memory, and there was no group

difference for the subject population, we assume that subjects performed the implicit task in the scanner as others did outside of the scanner.

In addition, as previous studies indicate that task difficulty influences the activity in the default mode network (e.g., Gould et al., 2006; McKiernan et al., 2003), we tested whether the accuracy was different between the two tasks in the behavioral group. Note that it was not appropriate to match reaction times between the two tasks, as the two tasks required different demands and responses (silent naming for the implicit task, and button press for the explicit recognition task). With respect to different pairs, the accuracy for both old ($t(17) = 2.50, p < .02$) and recombined ($t(17) = 2.15, p < .05$) pairs was higher in the implicit task than that in the explicit task. However, the overall accuracy ($.55 \pm .24$ for old, recombined, and new pairs in the implicit task; $.48 \pm .23$ for old and recombined pairs in the explicit task) was comparable across the two tasks ($t(17) = 1.92, p > .05$).

3.2. fMRI ANOVA results

There were two different patterns in brain activity (vs. baseline): activation and deactivation. The activation results are reported in a separate paper (Yang et al., 2008), and the deactivation results are reported in detail in this paper. Some regions were activated for different types of word pairs, in both implicit and explicit tasks. For example, the occipital cortex, bilateral fusiform gyrus, the prefrontal cortex, and the medial temporal lobe (MTL) showed significant above-baseline activation for word pairs. In addition, we found functional dissociations between subregions of the MTL in implicit and explicit tasks, showing that the parahippocampal region was more activated in the associative priming task, and both the parahippocampal and hippocampus were activated in the associative recognition task (for details, see Yang et al., 2008).

In addition, brain regions in the default mode network showed significant deactivation. During the explicit recognition task, there was significant deactivation in a wide range of regions for the old pairs and the recombined pairs when compared with the fixation baseline (Table 2, Fig. 2). The location of these regions was similar to that reported in the literature for the default mode network (Gusnard and Raichle, 2001; Mazoyer et al., 2001; Shulman et al., 1997). Using the conjunction analysis, seven common deactivated areas for the old and recombined pairs were identified in the PCC/precuneus, bilateral angular gyrus (BA39), vmPFC, left dPFC, and bilateral MTG (BA21) (Table 3). Of all the regions, the PCC, bilateral angular gyrus, and the vmPFC showed the largest clusters of deactivation. All these regions were extracted as ROIs for further analysis. Note that we did not find significant activation in the default regions during the explicit memory task, although some studies on explicit memory report such activation (vs. baseline) in the default mode network (e.g., Shannon and Buckner, 2007; Wheeler and Buckner, 2007).

During the implicit task, the number of the deactivated regions was fewer than during the recognition task. These regions included the bilateral angular gyrus, bilateral insula and the left MTG for each stimulus type (Table 2, Fig. 3). Although other regions exhibited deactivations (e.g., PCC/precuneus and the left dPFC for the old and new pairs, and vmPFC and right MTG for the old pairs), these deactivations did not survive correction ($p < .05$, uncorrected). The conjunction analysis showed that the common deactivated regions for the three types of word pairs were in the left angular gyrus (-54, -58, 24) and the right insula (36, -4, 3). The common deactivated regions for the old and recombined word pairs were additionally found in the left insula (-40, -21, 14). Several brain regions also showed activations, e.g., PCC (-7, -43, 42) for old pairs and precuneus (1, -60, 36) for the new pairs, but they did not survive for correction. These data suggest that the activation in the default network is sustained during the implicit task when compared with the baseline.

Using voxel-wise ANOVA (with task and pair type as factors), a significant difference was found between the two tasks (Fig. 4). There was greater deactivation in the PCC, right angular gyrus, vmPFC, bilateral dPFC, and the right MTG during the explicit task than during the implicit task. Note that the left angular gyrus and the left MTG did not show significant difference between tasks. Thus, the explicit task differs from the implicit task in its significant deactivation in the default mode regions.

3.3. ROI analysis results

We obtained similar results with the ROI analysis as those from the ANOVA analysis (Table 3). Given that the activation patterns of most ROIs were similar, we selected four largest ROIs (PCC/precuneus, vmPFC and the bilateral angular gyrus) as examples for illustration in Fig. 5. By using a one-sample t-test ($p < .05$), we found that for each pair type, these ROIs showed significant deactivation during the explicit task when compared with the baseline; whereas the activation in these ROIs was sustained during the implicit task. One exception was that the activation in the left angular gyrus was reduced during the implicit task ($p < .05$ for all three word pairs, Fig. 5). These data suggest that activation in these default regions, except in the left angular gyrus, is modulated according to whether the task requires conscious retrieval.

We also tested the task difference in the default regions by the ROI analysis. Consistent with the results from the ANOVA, there was significant task difference in most of these ROIs. Using a repeated measure ANOVA (task and word pair type as within-subject factors), we found that there was greater deactivation for the explicit task than for the implicit task in the PCC, vmPFC, bilateral dorsal MFG, right angular gyrus and the right MTG. Similarly to the voxel-wise analysis, we did not find significant difference between tasks in the left angular gyrus ($F = 3.56$, $p < .09$) and the left MTG ($F = 4.32$, $p < .06$) (Fig. 5 for the left angular gyrus as an example). In addition, the main effect of word pair type and the interaction between task and pair type were not significant for any of the ROIs ($p > .05$), except the PCC ($F = 6.75$, $p < .03$) and the right MFG ($F = 8.38$, $p < .02$) showed significant interaction, as task difference for the recombined pairs were greater than for the old pairs.

To determine whether task difficulty influences the results in the default network, as the overall correct percentage was comparable across the two tasks in the behavioral group, we averaged the time series across all word pairs in each task (old, recombined and new for the implicit task, and old, and recombined pairs for the explicit task), and compared them between tasks. By doing this, we found the similar results in these ROIs as the main effect of the task. Specifically, there was a significant task difference for the PCC, vmPFC, bilateral dPFC, right angular gyrus, right MTG, but no significant difference for the left angular gyrus ($t = 1.72$, $p < .12$) and left MTG ($F = 2.04$, $p < .07$). Thus, task difficulty did not affect the activity patterns of the default network during the two tasks.

4. Discussion

In this study, we investigated whether the default mode network is associated with unconscious processing in normal human subjects. There were two main findings. First, in most regions of the default mode network, the level of activation during an implicit task was comparable with that during a fixation baseline. The task difference was significant in that an explicit task elicited strong deactivation in the default mode regions. Thus, the activity in the default network is sustained and less disrupted when an implicit task is performed, but is suspended when explicit retrieval is required. Second, the left angular gyrus and the insula exhibited comparable deactivation during both tasks. These data suggest that the activation in these default regions, except in the left angular gyrus and the insula, is modulated according to whether the task requires conscious memory retrieval.

We used memory retrieval tasks to manipulate levels of conscious processing in this study. Several steps were adopted to ensure that the implicit task was sufficient to represent a type of unconscious processing. First, during the implicit task, the word pairs were presented very briefly with predetermined duration. Thus subjects had little chance to consciously process these pairs. Second, subjects were asked to read the word pairs, rather than asked to consciously retrieve the studied word pairs. Using this strategy, the previous study experience would facilitate more accurate reading of old pairs than recombined and new pairs. Third, by employing a perceptual encoding task, a possible explicit contamination to the implicit task was controlled (Yang et al., 2008). The results confirmed that these steps were successful in dissociating the implicit memory task from the explicit memory task. Subjects had higher accuracy for old versus recombined and old versus new word pairs in the implicit task, but their explicit memory performance remained at the level of chance. These manipulations were important given that explicit contamination was a critical confounding factor in previous studies of implicit memory (for reviews, see Henson, 2003; Schacter et al., 2004).

The novel finding of the study was that during the implicit memory, the level of activation was comparable with that during the fixation baseline. It supported our hypothesis that when an external task requires the same or similar cognitive processes as that in the default network is involved, the signal difference between rest and the cognitive task would be small (e.g., Binder et al., 1999). There may be similar unconscious processing during the baseline as during the implicit task, which leaves these activities sustained when subjects performed the implicit task. Although the implicit task demands a goal-directed response (i.e., to silently read the presented word pairs), the performance does not require conscious involvement, and does not disrupt the on-going unconscious processing. In contrast, as the explicit task demands conscious effort to retrieve the information, the unconscious activity in the network was disrupted. Even though the explicit performance was low, to prevent conscious contamination to the implicit task, the deactivation was similar to other studies of explicit memory in regions such as the PCC and angular gyrus (e.g., Daselaar et al., 2004), suggesting that the deactivation is related to retrieval mode/effort process in explicit retrieval.

It has been proposed that the function of the default network is to build models and process information that represents self and social cognition (for reviews, see Buckner and Carroll, 2007; Schilbach et al., 2008). These functions are closely associated with memory processes to provide the foundation on which functions are built (Buckner and Carroll, 2007). During the resting state, the default mode regions may continuously and spontaneously encode internal thoughts and self-representations, consolidate recent memory traces, retrieve representations in memory and flexibly generate predictions about the present and relevant future (Bar, 2007; Buckner and Carroll, 2007; Hassabis et al., 2007; Schilbach et al., 2008). Note that not all of these memory processes require conscious demands (Wig et al., 2008); thus, when subjects unconsciously retrieve word pairs during the implicit task, these processes are sustained and are not disrupted.

In addition, other studies support the view that the default mode network is associated with unconscious processing. For example, in a study by Binder et al. (1999), the resting state and a semantic task exhibit similar activation in the default mode regions. The default network is also sustained and minimally disrupted by sensory processing tasks with limited conscious processing (e.g., Greicius and Menon, 2004; Mazoyer et al., 2001). When subjects perform an object recognition task, the retrosplenial is activated versus fixation (Bar and Aminoff, 2003). The more practiced the task (Mason et al., 2007) and the more static and predictable the task (Binder et al., 1999), the less conscious processing is required, and the less deactivation is found in the default network. A recent study also showed that young subjects and old adults have similar activity in the default network during a repetition priming task (Soldan et al., 2008). Taken together, our study and these data provide evidence that the default mode network

is associated with continuous, unconscious processing in normal, alert human beings. In future study, we could further test whether there is correlation between less deactivation in the default mode regions and behavioral performance in the implicit task. One approach is to collect behavioral data and neuroimaging data using the same group of subjects while they perform implicit and explicit tasks in the scanner (e.g., Schott et al., 2005).

Our findings regarding explicit memory are consistent with previous studies that find significant deactivation in the default mode regions during explicit tasks (e.g., Daselaar et al., 2004; Marklund et al., 2007; Miller et al., 2008). There is also the view that the default mode regions are activated (vs. baseline) by conscious memory processing (for reviews, see Buckner and Carroll, 2007; Schilbach et al., 2008). For example, the precuneus, medial and lateral parietal cortices are activated during explicit recognition (Wheeler and Buckner, 2004), and the PCC, mPFC, and lateral parietal regions are activated for memory retrieval success or recollection (e.g., Hassabis et al., 2007; Shannon and Buckner, 2004). However, our results are not contradictory to this view. It seems that there are complicated relationships between default activation and memory processing, because when an external memory task is performed, activation in the default network could be activated/sustained or deactivated. Although the precise mechanisms remain to be elucidated (Morcom and Fletcher, 2007), recent studies suggest that different regions of the default network may be involved in different memory processes (e.g., encoding vs. retrieval, remembering vs. familiarity, etc), which leads to different responses versus baseline (e.g., Daselaar et al., 2006; Marklund et al., 2007). For example, in the Daselaar et al. (2006) study, subjects perform an old/new word recognition task, and then rate their confidence for the response to dissociate memory recollection and familiarity processes. The study found that the anterior angular gyrus and the ventral PCC are *deactivated* and associated with memory recollection, whereas the dorsal angular gyrus and precuneus are *activated* and associated with memory familiarity. Marklund et al. (2007) also found deactivation in the PCC, but activation in ACC, when subjects perform a word recognition task. Therefore, in addition to conscious/unconscious memory retrieval, the decreased and increased patterns may also be related to different memory task demands, and default mode subregions.

Several issues need to be addressed in future studies. First, many cognitive and social functions could be unconsciously processed, e.g., attitude, prejudice, and self-representation (for reviews, see Frith and Frith, 2008). However, as many previous tasks do not specify whether subjects retrieve information consciously or unconsciously, it is unclear whether these social processes render similar dissociation between implicit and explicit processing in the default network. One hypothesis is that at least conscious processing is not necessary for some tasks. As an example, the mPFC is activated even when subjects make indirect self-judgment (e.g., pleasant/unpleasant ratings of pictures) (Gusnard et al., 2001). Second, as we used an event-related fMRI design, subjects were prepared for the next stimulus during the fixation. According to the distinction between stimulus-oriented and stimulus-independent processes (Gilbert et al., 2007), the default network shown in our study was more driven by a stimulus-oriented process. Whether the stimulus-independent process is modulated by conscious involvement needs further investigation.

Some may be concerned that the difference between the implicit and explicit tasks is not due to consciousness manipulation, but instead due to task difficulty or response requirements. The task difficulty has been identified to modulate the level of deactivation in many regions of the default network (e.g., Gould et al., 2006; McKiernan et al., 2003). For example, using an auditory detection task, McKiernan et al. (2003) manipulate difficult levels of stimulus presentation rate, target discriminability, and short-term memory load. The results showed that the more difficult a task, the more deactivation is shown in regions such as the MFG, bilateral ACC, and the PCC. We could not fully exclude the possible influence from task difficulty,

because the two tasks in our study were only matched for accuracy. Given that the two tasks had different response requirements, it is inappropriate to match the RTs. Nevertheless, there is little possibility that the difference in task difficulty accounts for our results, for three reasons. First, for studies that have shown task difficulty effects, even in the easiest tasks, all regions in the default mode network show significant deactivation (vs. baseline) (e.g., Gould et al., 2006; McKiernan et al., 2003). It is different from our data in that in the default mode regions, the level of activation during the implicit task was comparable with that during the baseline. If task difficulty is accounted for in our results, there should have been significant deactivations even for the implicit task; however, we found the opposite. This is important, because it indicates that the level of conscious memory retrieval, but not the level of task difficulty, modulates the activation in the default network in our study.

Second, when we controlled the two tasks having comparable accuracy, the default mode regions still showed significant task difference except for the left angular gyrus and left MTG. The dissociation between implicit and explicit memory is usually manipulated by task demands and instructions. As the two memory systems differ in the way that the information is retrieved, response requirements are usually different (for reviews, see Henson, 2003; Schacter et al., 2004; Tulving and Schacter, 1990). Given that we used typical manipulations adopted from other studies in the implicit memory field, at least our results shed light on implicit memory studies using these manipulations. Third, task difficulty manipulations do not affect the deactivation of all regions in the default network, and the deactivation in some regions is not influenced by some task difficulty manipulations. For example, stimulus presentation rate does not influence the deactivation levels in any regions of the default network except the left ACC (McKiernan et al., 2003). These evidences raise the possibility that in addition to task difficulty, other factors, e.g., conscious processing may influence the activation in the default network. It is unclear whether consciousness and task difficulty interact with each other to modulate the activation in the default mode network. Further studies are needed to address this issue, with consciousness and task difficulty independently manipulated.

Unexpectedly, we found that the left angular gyrus and the insula exhibited significant deactivation during the implicit task, and the task difference did not reach significance. This is an interesting finding as the activation pattern for these regions was different from that of other default mode regions. Previous studies have indicated that they subserve linguistic and emotional functions. Specifically, the angular gyrus is associated with conceptual/semantic processing (e.g., Binder et al., 1999; Marklund et al., 2004; Schilbach et al., 2008), word generation (Gusnard and Raichle, 2001; Schulman et al., 1997) and inner speech (Mazoyer et al., 2001). For example, the angular gyrus is activated during rest versus tone, and semantic versus tone, but there is no significant difference between rest and semantic conditions (Binder et al., 1999). The activity in the angular gyrus, especially the left side, is stable in different conditions, e.g., it remains active during the loss of consciousness (Fiset et al., 1999; Laureys et al., 1999), by aging and Alzheimer's disease, and its deactivation does not vary by task difficulty (McKiernan et al., 2003), and attention (Fox et al., 2006). In our study, subjects encoded the word pairs by their perceptual/orthographical associations, by which their explicit performance was controlled to the level of chance. Note that all words were emotionally neutral. During both memory tasks, subjects relied on the perceptual associations to either silently read the word pairs in the implicit task, or judge whether the word pairs were old or recombined in the explicit task. Therefore, it seems that the linguistic and emotional processes that these regions subserve are disrupted by both implicit and explicit processing, leading them to be consistently deactivated.

Our data suggest that implicit memory may be characteristic of the sustained activity in the default mode network. Converging evidence from neuropsychological and neuroimaging studies has found dissociations between implicit and explicit memory (e.g., Donaldson et al.,

2001; Merikle and Reingold, 1991; Schott et al., 2005; but see Berry et al., 2006). Implicit processing has been shown to be associated with repetition suppression of neural activity in neuroimaging studies, i.e., old/repeated items elicit weaker BOLD change when compared with new items (for reviews, see Grill-Spector et al., 2006; Schacter et al., 2004). The sustained default mode network may be another important feature to distinguish implicit from explicit processing in neural mechanisms. Given that the control of explicit contamination is critical to explore the neural mechanisms of implicit processing (Henson, 2003; Schacter et al., 2004), our data may provide a new approach with which to determine whether explicit contamination is controlled. It would also be of interest to investigate whether there is deactivation in the default mode regions under possible conditions of explicit contamination in the future.

In conclusion, our results showed that in most regions of the default mode network, the level of activation during an implicit task was comparable with that during the fixation baseline, except in the left angular gyrus and the insula. These data provide evidence that the default-mode network is associated with unconscious processing when human subjects perform implicit tasks.

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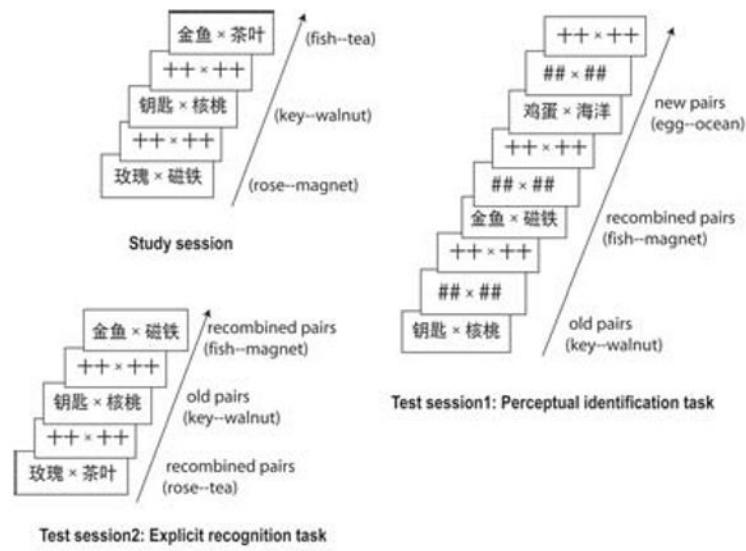


Fig. 1. Illustration of the study and test sessions. In the study session, unrelated Chinese word pairs were presented and subjects made a perceptual encoding judgment. During the perceptual identification task, three types of unrelated word pairs (old, recombined and new) were presented with pre-determined duration in an intermixed order. During the recognition task, word and recombined word pairs were presented, and subjects made an old/recombined pair judgment.

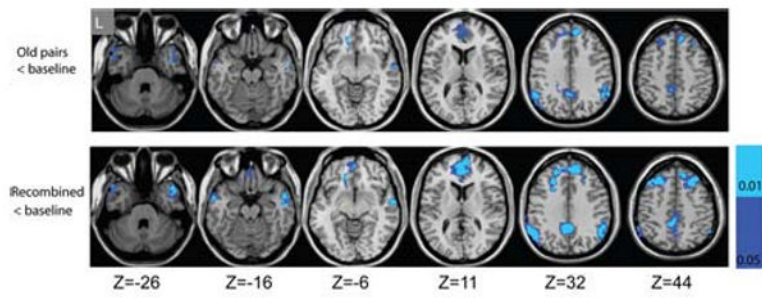


Fig. 2. Brain regions showed significant deactivation for old pairs and recombined pairs when each was compared with the fixation baseline in the recognition task.

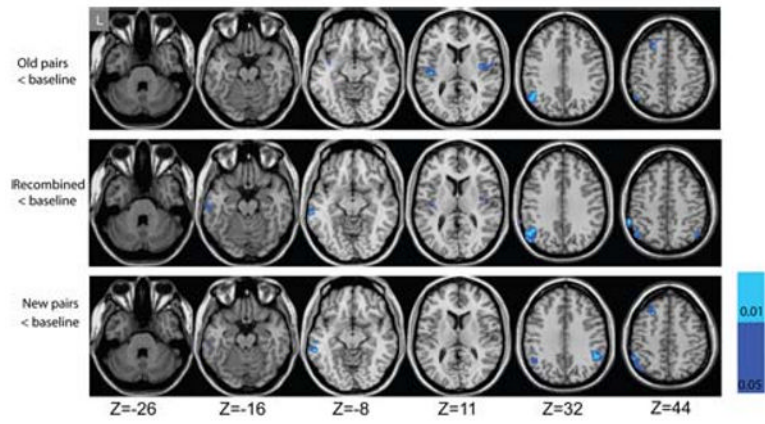


Fig. 3. Brain regions showed significant deactivation for old, recombined and new pairs when each was compared with the fixation baseline in the perceptual identification task. Note that the deactivation was fewer and smaller in the implicit task than that in the explicit task.

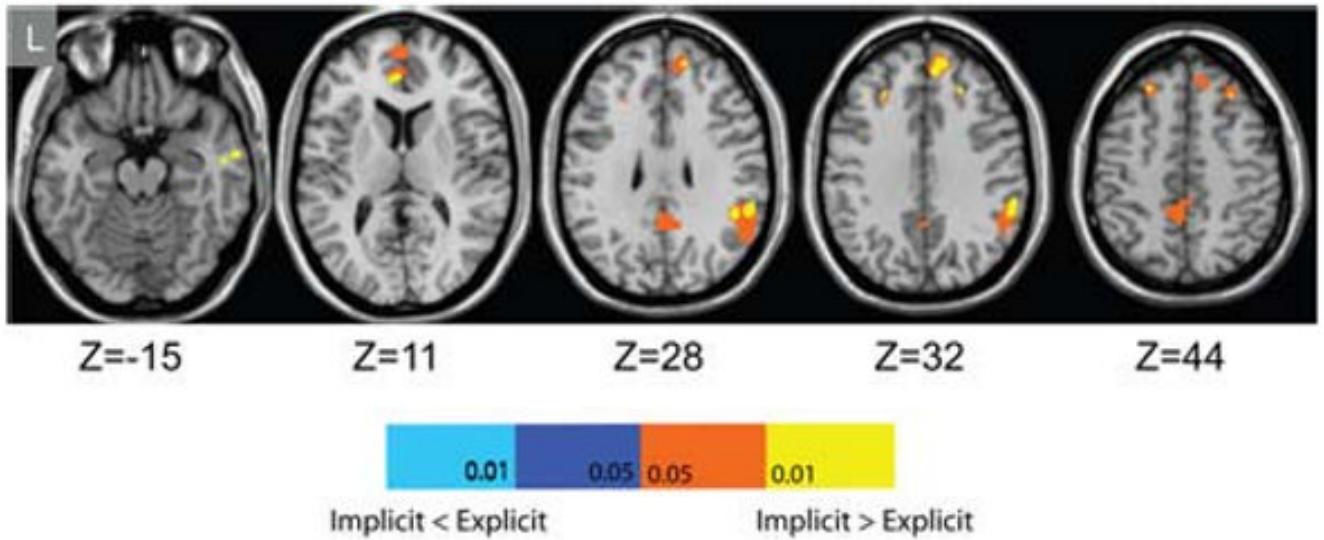


Fig. 4. Task difference within the ROIs using voxel-wise analysis. The explicit task elicited stronger deactivation than the implicit task in the vmPFC, PCC, the bilateral angular gyrus, dmPFC, and the right MTG. Note that no region within the default network showed stronger activation during the explicit task than during the implicit task.

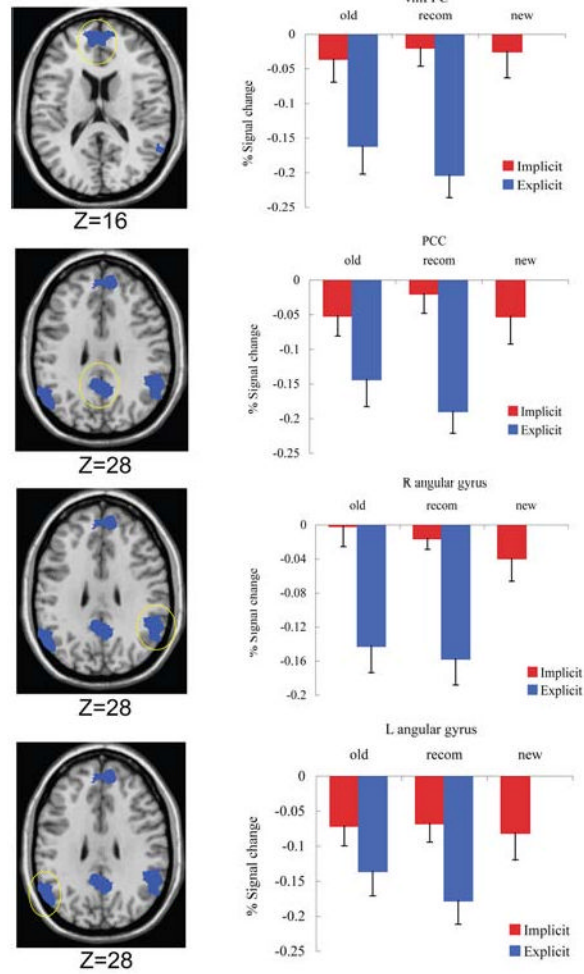


Fig. 5. ROI analysis for the vmPFC, PCC, and the right and left angular gyrus. The bars show signal changes (mean \pm SEM) in each ROI, which are circled in yellow. The activation of the vmPFC, PCC, and the right angular gyrus was sustained during the implicit task, but decreased during the explicit task. The activation of the left angular gyrus was decreased during both tasks.

Table 1
Behavioral data for the perceptual identification task and the associative recognition task (M±SD)

Task	Accuracy			RT (msec)		
	Old	Recom	New	Old	Recom	New
Perceptual identification	.67±.22	.61±.21	.38±.17	866±120	863±151	964±185
Behavioral group	.51±.20	.43±.27		1290±168	1326±182	
fMRI group	.43±.25	.47±.27		1248±152	1261±170	

Table 2

Regions showing deactivation in two tasks ($p < .05$, corrected)

L/R	Region	t-value	x	y	z
Explicit task					
Old					
	vmPFC	-8.82	11	47	32
	PCC	-6.40	-34	-37	2
R	Angular gyrus	-5.45	50	-55	27
L	Angular gyrus	-6.60	-51	-55	30
R	MTG	-4.36	58	-9	-12
L	dPFC	-3.47	-14	25	47
L	MTG	-3.76	-46	12	-26
Recombined					
	mPFC	-13.30	13	46	31
	PCC	-10.24	-4	-52	30
L	Angular gyrus	-8.87	-50	-58	33
R	Angular gyrus	-5.55	47	-56	35
L	MTG	-6.72	62	-7	-5
R	MTG	-5.18	-55	1	-15
Implicit task					
Old					
R	Insula	-6.00	30	-7	21
L	Angular gyrus	-5.76	-44	-53	30
L	Insula	-4.79	-41	-22	14
L	dPFC	-3.66	-20	21	44
Recombined					
L	Angular gyrus	-5.46	-45	-57	36
L	MTG	-4.51	-62	-30	-9
R	Angular gyrus	-4.41	47	-55	26
R	Insula	-5.23	37	-11	26
New					
L	Angular gyrus	-3.40	-53	-45	41

L/R	Region	t-value	x	y	z
R	Angular gyrus	-4.20	49	-48	31
L	MTG	-5.55	-56	-37	-7

Note: L: left hemisphere; R: right hemisphere; MTG: middle temporal gyrus; dPFC: dorsal prefrontal cortex; mPFC: medial prefrontal cortex; vmPFC: ventrolateral prefrontal cortex; PCC: posterior cingulate cortex

Table 3
ROI regions defined by the conjunction analysis in the recognition task (p < .05, corrected)

Region	Old						Recombined							
	t-value	x	y	z	t-value	z	t-value	x	y	z	t-value	x	y	z
vmPFC	-8.82	11	47	32	-13.30	13	46	31						
PCC	-4.07	2	-54	25	-10.24	-4	-52	30						
L Angular gyrus	-6.60	-51	-55	30	-8.87	-50	-58	33						
R Angular gyrus	-5.45	50	-55	27	-5.55	47	-56	35						
R MTG	-4.36	58	-9	-12	-6.32	51	1	-15						
L dPFC	-3.47	-14	25	47	-10.01	-22	30	34						
L MTG	-3.76	-46	12	-26	-5.18	-55	1	-15						