Hippocampal Activity is Associated with Self-Descriptiveness Effect in Memory, Whereas Self-Reference Effect in Memory Depends on Medial Prefrontal Activity

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ABSTRACT: The self has long been regarded as a unique cognitive structure by virtue of its superior mnemonic abilities. Two separate effects result from this self memory facilitation: self-reference effect and self-descriptiveness effect in memory. Self-reference effect denotes that information processed with reference to the self is better remembered than information processed with reference to others, whereas self-descriptiveness effect indicates that items judged to be self-relevant is remembered better than items judged not to be relevant to self during self-reference task. Although there is a compelling connection between self-reference effect in memory and self mentalization processes indexed by the medial prefrontal activity, the underlying mechanisms of the self-descriptiveness effect in memory have remained underspecified. In the present fMRI study, we used a subsequent memory paradigm to examine the neural correlates of self-descriptiveness and self-reference effect in memory. Participants encoded personality traits while performing self-reference and other-reference task (judged the descriptiveness of the traits to themselves or a famous person ''Bruce Lee''), and then were given a test of recognition memory outside the scanner. It is revealed that the hippocampal activity corresponded with self-descriptiveness effect in memory, but the activity of the medial prefrontal cortex and perirhinal cortex related to self-reference effect in memory. These findings suggested that the memory boost for self-relevant items relies on the enhanced relational binding mechanisms employed during self-relevant items. © 2011 Wiley Periodicals, Inc.

KEY WORDS: self-reference effect in memory; self-descriptiveness effect in memory; hippocampus; medial prefrontal cortex

INTRODUCTION

The self has long been regarded as a unique cognitive structure by virtue of its superior mnemonic abilities (Markus, 1977; Rogers et al., 1977; Symons and Johnson, 1997). Two separate effects result from this

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self memory facilitation: self-reference effect and self-descriptiveness effect. First, information (e.g., trait adjectives) that is processed with reference to the self (e.g., "Does the word HONEST describe you?") is better remembered than information that is processed with reference to others (e.g., "Does the word HONEST describe Ronald Reagan?" Ferguson et al., 1983; Maki and McCaul, 1985). Tasks that permit self-referential processing promote better subsequent memory than tasks that encourage other-referential processing. In the psychological literature, this task-dependent subsequent memory effect is termed as self-reference effect in memory (Symons and Johnson, 1997). Second, the memory boost during self-reference task is also affected by participants' judgments of self-descriptiveness of a particular item. Items judged to be self-relevant (e.g., "Yes, that trait describes me") is remembered better than items judged not to be relevant to self (e.g., "No, that does not describe me," Rogers et al., 1977; Macrae et al., 2004). We henceforth refer to enhanced subsequent memory for self-relevant relative to self-irrelevant information as the self-descriptiveness effect in memory. Although several neuroimaging studies have suggested the linkage between self-reference effect in memory and self mentalization and self reflection processes indexed by the prefrontal activity, especially the medial prefrontal activity (Fossati et al., 2004; Macrae et al., 2004; Benoit et al., 2010), the underlying mechanisms of the self-descriptiveness effect in memory have remained underspecified.

Two putative explanations could be offered for the self-descriptiveness effect in memory. One argues that in the same way as self-reference task promotes memory, self-relevant items, per se, encourage further self-referential processing, i.e., more self mentalization and self reflection processes than self-irrelevant items (Moran et al., 2009), which boosts subsequent memory performance. Supporting this account, medial prefrontal activity indeed corresponds not only to self-referential processing (Kelley et al., 2002; Mitchell et al., 2006; Gutchess et al., 2010), but also to participants' judgment of self-descriptiveness. Specifically, the activity in medial prefrontal cortex (MPFC) and its

adjacent regions increased during items that were responded as self-relevant relative to those endorsed as self-irrelevant (Macrae et al., 2004; Phan et al., 2004; Moran et al., 2006; Moran et al., 2009; Rameson et al., 2010). However, whether additional prefrontal recruitment for self-relevant items will further induce self-descriptiveness effect in memory remain unknown. In other words, whether prefrontal activity contributes more to memory formation of self-relevant items than self-irrelevant items is still undetermined.

Besides, other researchers take a different view. The basis of their argument is that there is nothing special about the self-descriptiveness effect in memory. Rather, the self-descriptiveness effect in memory can be interpreted as an extension of the congruency effect in memory which was observed in various tasks, such as phonemic judgment or semantic judgment (Rogers et al., 1977; Staresina et al., 2009). Congruous items eliciting "yes" answers (e.g., "is ELEPANT animate?") have been found to result in better subsequent memory than incongruous items eliciting "no" answers (e.g., "is TABLE animate?" e.g., Schulman, 1974; Craik and Tulving, 1975; Rogers et al., 1977; Staresina et al., 2009). Unlike incongruous items, the congruous items have a preexisting relationship with the question context. This relationship is thought to prompt additional relational binding processes to combine the context and the item as an integrated unit, which in turn strengthens the memory trace. Similarly, unlike self-irrelevant items, self-relevant items eliciting "yes" responses foster additional relational binding processes as those items can be more readily integrated into a preexisting knowledge. In turn, these relational binding processes strengthen the memory trace and support the enhanced memory for self-relevant items. If this is true, self-descriptiveness effect in memory will be related to some brain regions underlying relational binding, such as the hippocampus (Davachi et al., 2003; Ranganath et al., 2003; Kensinger and Schacter, 2006; Uncapher et al., 2006; Dougal et al., 2007; Qin et al., 2009; Staresina and Davachi, 2009). In addition, descriptiveness effect on subsequent memory will be observed irrespective of the encoding task, i.e., in both self-reference and other-reference tasks.

To our knowledge, one neuroimaging study gave inspiration to the possible mechanism underlying self-descriptiveness effect in memory (Macrae et al., 2004). In this study, participants judged whether a personality trait was self-relevant during encoding and completed a subsequent memory test after that. Macrae et al. (2004) indentified two regions in MPFC which predicted subsequent memory performance and judgments of self-descriptiveness respectively and found that subsequent memory effect (remembered vs. forgotten trials) in both MPFC regions were not modulated by self-descriptiveness judgments. These results implied that self-descriptiveness effect in memory was more likely to be explained by congruency effect. However, given that Macrae et al. (2004) didn't search for MPFC regions exclusively contribute to memory formation of self-relevant items, but not self-irrelevant items, the role of MPFC in self-descriptiveness effect in memory has yet to be tested. Moreover, Macrae et al. (2004) didn't test how subsequent memory effects

in regions other than MPFC, such as hippocampus suggested by congruency effect explanation, were modulated by self-descriptiveness judgment. Thus, the neural correlates for self-descriptiveness effect in memory remain to be specified. Besides, Macrae et al. (2004) study only adopted the self-reference task and did not test whether the descriptiveness effect on subsequent memory is limited to self-reference task, or, as congruency effect, can be broadly applied to other-reference task.

In the present study, we used a subsequent memory paradigm to examine the neural correlates of self-descriptiveness effect and self-reference effect in memory. Participants were first scanned when they judged the descriptiveness of a list of personality traits to themselves or a famous person (Bruce Lee), and then were given a test of recognition memory outside the scanner. Several analyses were performed for fMRI data. We first identified regions showing main effect of task (i.e., self-reference vs. other-reference tasks) and self-descriptiveness judgment (self-relevant vs. self-irrelevant items) and tested whether the activity of these regions contributed to successful memory formation. Second, we identified regions associated with successful recognition (i.e., remembered vs. forgotten items) and examined whether the subsequent memory effect in these regions was modulated by self-descriptiveness judgment, other-descriptiveness judgment and encoding task. Third, we searched for regions where activity was uniquely associated with successful recognition (1) for self-relevant, but not self-irrelevant items, (2) for other-relevant, but not other-irrelevant items, and (3) under self-reference task, but not other-reference task.

MATERIALS AND METHODS

Participants

Fourteen right-handed volunteers from the university community with normal or corrected-to-normal vision (four males, aged from 20 to 30, $M = 22.64$, SD $= 2.69$) participated in this experiment. None of the participants reported significant abnormal neurological history. All the participants were paid 50 RMB for their participation and gave informed consent before scanning.

Materials

Three hundred two-character adjectives were selected from a pool of normalized Chinese personality trait adjectives (Wang and Cui, 2005) as materials, which were divided into three lists, with 100 words in each list. Lists were counterbalanced for the valence and meaningfulness. Half of the words in each list were positive, the remaining half were negative. Two lists served as learning items in the two tasks and one served as lures during the memory test. Lists were exchanged between tasks across participants, so that trait adjectives that appeared in the self-reference task for one participant appeared in other-reference task for other participants.
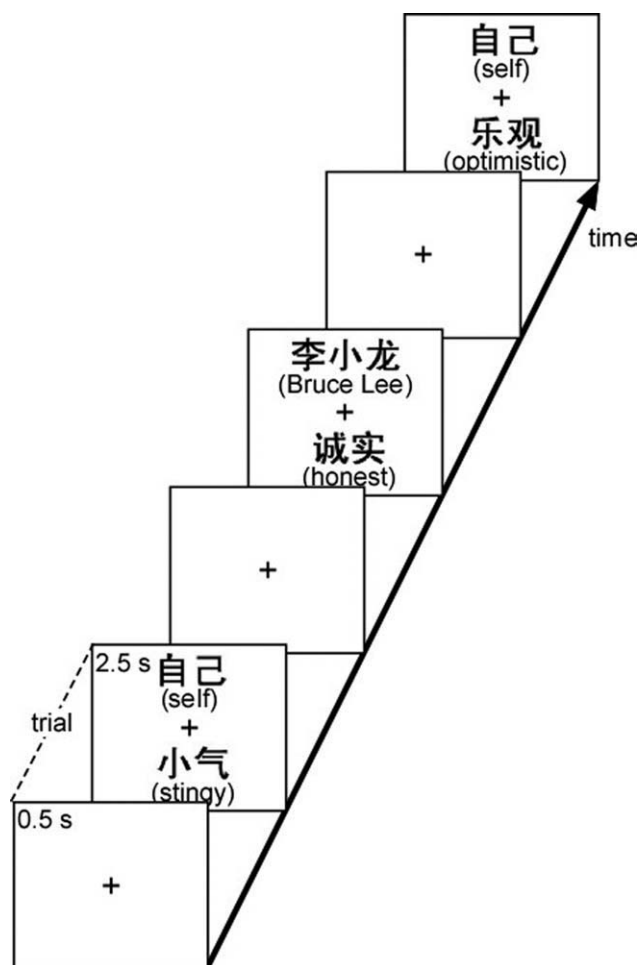
FIGURE 1. Example Encoding Trials. For each encoding trial, a 0.5 s fixation cross was presented at first, followed by a 2.5 s learning item, consisting of a cue word ("self" or "Bruce Lee") presented above a central fixation cross and a trait adjective (e.g., "honest") presented below the central fixation cross. Participants were asked to judge whether the given adjective describes themselves when viewing "self" and whether the given adjective describe Bruce Lee when viewing "Bruce Lee."

Procedure

During the scanned encoding phase, 200 learning items were presented sequentially (Fig. 1). For each encoding trial, a 0.5 s fixation cross was presented at first, followed by a 2.5 s learning item, consisting of a cue word ["self" or "Bruce Lee (famous for his Chinese Kung Fu)"] presented above a central fixation cross and a trait adjective (e.g., "honest") presented below the central fixation cross (Fig. 1). Participants were asked to judge whether the given adjective could describe themselves when viewing "self" and whether the given adjective could describe Bruce Lee when viewing "Bruce Lee." Responses were given via a magnet-compatible button box below participants' right hands. The trials with no responses were excluded from all further analyses. The encoding trials were intermixed with 3 s null trials (60 trials in all), during which a black fixation cross was

presented. All the trials were presented with jittered interstimulus intervals (a fixation cross) from 0 to 1 s.

About 10 minutes after the encoding phase, participants were given a surprise self-paced memory test outside the scanner. 300 trait adjectives were presented sequentially in a random order. Participants were instructed to indicate whether the adjectives was old on a 6-point scale (1: definitely new; 2: probably new; 3: guess it is new; 4: guess it is old; 5: probably old; and 6: definitely old).

fMRI Imaging

Imaging was carried out on a 3T Siemens scanner at the Functional MRI Lab (East China Normal University, Shanghai). Functional images were acquired using a gradient echo echo-planar imaging (EPI) sequence (TR = 2200 ms, TE = 30 ms, FOV = 220 mm, matrix size = 64×64). Thirty-five slices paralleled to the AC–PC line (slice thickness = 3 mm, gap = 0.3 mm) were acquired and covered the whole brain. The first five TRs acquired were discarded to allow for T1 equilibration. Before the functional run, a high-resolution structural image was acquired using a T1-weighted, multiplanar reconstruction sequence (MPR) (TR = 1900ms, TE = 3.42 ms, 192 slices, slice thickness = 1 mm, FOV = 256 mm, matrix size = 256×256).

fMRI Data Analysis

Data preprocessing and statistical analyses were performed with Statistical Parametric Mapping (SPM5, Wellcome Department of Cognitive Neurology, London). During data preprocessing, all volumes were corrected for differences in slice acquisition timing and realigned spatially to the first volume of the first time series. None of participants moved more than 3 mm in any direction during the encoding phase. Then, the resulting images which were resampled to $2 \times 2 \times 2$ mm voxel size were spatially normalized to a standard echo-planar imaging template based on the Montreal Neurological Institute (MNI) reference brain and smoothed with an 8 mm full-width, half-maximum (FWHM) isotropic Gaussian kernel.

Statistical analyses were performed using the general linear model implemented in SPM5. Encoding trials were classified into six conditions according to encoding task, participants' descriptiveness judgment at encoding task and participants' performance at subsequent memory tests: (1) SRR, items endorsed as self-relevant in self-reference task and later judged as 4, 5, 6 in memory test; (2) SIR, self-irrelevant items judged as 4, 5, 6; (3) SF, self-relevant and self-irrelevant items judged as 1, 2, 3 were combined together because of the low number of trials; (4) ORR, items endorsed as other-relevant in other-reference task and later judged as 4, 5, 6 in memory test; (5) OIR, other-irrelevant items judged as 4, 5, 6; (6)OF, other-relevant and other-irrelevant items judged as 1, 2, 3 were also combined together. The guess responses were not excluded from further analysis, since participants were able to discriminate old and new items when responding with guess (accuracy: 0.56 ± 0.09, $t(13) = 2.32$, $P < 0.05$). There were, respectively, 43 ± 8, 40

TABLE 1. _____

Behavioral Performance During Encoding and Subsequent Memory Test

	Encoding reaction time (ms)	Test reaction time (ms)	Hit rate (%)
Self-reference task			
Relevant	1,242 (46)	2,069 (173)	90.12 (1.48)
Irrelevant	1,319 (51)	2,448 (316)	82.80 (3.00)
Other-reference task			
Relevant	1,308 (47)	2,841 (331)	72.63 (3.37)
Irrelevant	1,329 (50)	2,621 (250)	69.07 (3.50)

Standard errors are given in parentheses. Average hit rates (%) across participants is shown as a proportion of all valid encoding trials within each condition (2 encoding task * 2 descriptiveness judgment).

$\pm$ 8, 13 $\pm$ 7, 35 $\pm$ 8, 34 $\pm$ 9, 28 $\pm$ 12 trials in the SRR, SIR, SF, ORR, OIR, OF conditions. Each encoding trial was modeled using a canonical hemodynamic response function and its temporal derivative according to six conditions. All the encoding trials were modeled as 2.5 s long events from the onset time of the item. Additional regressors of no interest were created for invalid trials with no responses. Six regressors modeling movement-related variance and one modeling the overall mean during the whole encoding phase were also employed in the design matrix. It should be noted that in this model, we can only contrast the remembered trials to search for regions showing main effect of self-descriptiveness judgment. Thus, we also modeled, in a separate analysis, relevant and irrelevant trials for each task, irrespective of subsequent memory performance, with four types of events (SR: self-relevant, SI: self-irrelevant, OR: other-relevant, OI: other-irrelevant). However, it did not affect the main effect of self-descriptiveness judgment. Parameter estimates (beta estimates in the figures) for each regressor of interest at the single subject level were submitted to the second-level group analysis. Each participant's beta estimates for the six conditions were entered into a flexible factorial ANOVA. The resulting statistical map was thresholded at a voxel-wise p value of $P < 0.001$ and a spatial-extent threshold of 20 contiguous resampled voxels. Anatomic labeling of activations of clusters was performed with the Anatomy Toolbox (Eickhoff et al., 2005). Peak voxels were reported in MNI coordinates.

RESULTS

Behavioral Results

During encoding task, encoding trials with no responses (3.68% $\pm$ 2.85% of trials) were excluded from further analyses. The participants' behavioral performance during encoding and the subsequent memory test is shown in Table 1. A 2 encoding task (Self vs. Other) * 2 descriptiveness judgment (Relevant vs. Irrelevant) ANOVA for reaction time of the encoding trials revealed a significant main effect of descriptiveness judgment ($F(1, 13) = 6.26$, $P < 0.05$) and a significant interaction ($F(1, 13) = 7.15$, $P < 0.05$). This result indicated that the reaction time for relevant items was faster than that for irrelevant items. Further analysis of the descriptiveness effect in the two tasks revealed that the effect did not differ from zero in the other-reference task ($P > 0.05$), but was significantly greater than zero in the self-reference task ($t(13) = 3.18$, $P < 0.01$).

For reaction time during test, a 2 encoding task (Self vs. Other) * 2 descriptiveness judgment (Relevant vs. Irrelevant) ANOVA revealed a significant main effect of task ($F(1, 13) = 27.34$, $P < 0.001$), and a significant interaction ($F(1, 13) = 5.15$, $P < 0.05$). This result indicated that the reaction time for self-referenced items was faster than that for other-referenced items. Further analysis of the task effect revealed that the effect did not differ from zero for irrelevant items ($P > 0.05$), but was significantly greater than zero for relevant items ($t(13) = 4.14$, $P < 0.01$).

Turning to subsequent memory performance during test, hit rates as a proportion of all valid encoding trials within each condition (2 encoding task * 2 descriptiveness judgment) are illustrated in Table 1. Applying repeated-measures ANOVAs, we first observed a significant effect of task on hit rates ($F(1, 13) = 43.84$, $P < 0.001$), indicating the significant self-reference effect in memory. Second, significant effect of descriptiveness was also seen on the hit rates ($F(1, 13) = 7.11$, $P < 0.05$), whereas the interaction was not statistically reliable. These data suggested relevant items were remembered better than irrelevant items across self-reference and other-reference tasks. Consistent with the congruency effect explanation, the descriptiveness effect on subsequent memory was generally observed across self-reference and other-reference tasks.

fMRI Results

We first identified regions showing main effect of self-descriptiveness judgment and encoding task and tested whether the activity of these regions contributed to successful memory formation. Second, we identified regions associated with successful recognition (i.e., remembered vs. forgotten items) and examined whether the subsequent memory effect in these regions was modulated by self-descriptiveness, other-descriptiveness judgment and encoding task. Third, we searched for regions where activity was uniquely associated with successful recognition for self-relevant items or self-irrelevant items. Fourth, given that the behavioral descriptiveness effect on subsequent memory was generally observed across two tasks, we similarly searched for regions showing specific memory effect for other-relevant or other-irrelevant items. Fifth, we searched for regions where activity specifically corresponded with successful recognition during self-reference or other-reference tasks.

Effect of self-descriptiveness judgment

To identify regions associated with main effect of self-descriptiveness judgment, we searched for voxels where SRR

Regions Showing Effect of Self-Descriptiveness Judgment and Encoding Task

	Region	Peak activation			*t* Value	Voxels
		X	Y	Z		
Effect of self-descriptiveness judgment (SRR - SIR)						
R	Anterior cingulate cortex	12	30	2	4.80	111
L	Hippocampus	−14	−38	6	4.32	25
L/R	Calcarine gyrus	4	−96	2	3.62	31
Effect of encoding task (SRR + SIR + SF - ORR - OIR - OF)						
L/R	Mid orbital gyrus	0	50	−8	10.56	9,003
R	Superior frontal gyrus	20	54	16	7.17	
L	Middle frontal gyrus	−22	50	28	6.24	
L	Superior frontal gyrus	−16	60	20	4.72	
R	Middle cingulate cortex	2	−14	38	6.59	259
L	Superior temporal gyrus	−58	−48	22	6.03	622
R	Insula lobe	28	20	−20	4.92	97
L	Inferior frontal gyrus	−26	22	−22	4.83	103
L/R	Supplementary motor area	10	22	62	4.62	424
R	Superior medial gyrus	8	28	50	4.58	
L	Inferior temporal gyrus	−56	−62	−14	4.50	102
L	Middle temporal gyrus	−52	−34	4	4.26	148
L	Precuneus	−2	−50	48	3.91	74
L	Caudate nucleus	−8	10	−12	3.91	44
L	Middle orbital gyrus	−28	58	−8	3.79	30

A uncorrected threshold $P < 0.001$ was used in the whole brain volume search and only clusters with 20 or more significant resampled voxels are reported.L, left hemisphere; R, right hemisphere.

trials elicited greater activity than SIR trials. Consistent with previous studies (Moran et al., 2006, 2009; Rameson et al., 2010), a cluster located in the right anterior cingulate cortex within the prefrontal cortex survived from this analysis (Table 2, Fig. 2). In addition to this cluster, activity was also noted in the left hippocampus and medial calcarine gyrus. The reverse contrast reveals no significant activation in the prefrontal cortex.

However, in the present model, we can only contrast the remembered trials to search for regions showing main effect of self-descriptiveness. Thus, we separately modeled relevant and irrelevant trials, irrespective of subsequent memory performance, for each task with four types of events (SR: self-relevant, SI: self-irrelevant, OR: other-relevant, OI: other-irrelevant). A similar contrast was carried out within this model on all the self-referenced trials (SR - SI), which also revealed that the right anterior cingulate cortex (peak xyz: 12, 30, 2), left hippocampus (peak xyz: −12, −40, 8) showed main effect of self-descriptiveness judgment.

Further, to test whether the activity of these regions contribute to successful memory formation, participants' beta estimates in SRR, SIR and SF conditions were extracted from regions-of-interest (ROIs). All the significant voxels in the activated clusters showing effect of self-descriptiveness judgment within 6 mm spherical regions centered on the peak coordinate (right anterior cingulate cortex: 12, 30, 2; left hippocampus: −14, −38, 6; calcarine gyrus: 4, −96, 2) were included in each ROI. ROIs were defined in the same way at the other parts of

the results. Follow-up analysis on beta estimates revealed that the subsequent memory effects (i.e., the difference in activation between remembered and forgotten trials) in the right anterior cingulate cortex were not significant (SRR vs. SF: $t(13) = 1.04$, $P > 0.32$; SIR vs. SF: $t(13) = 1.09$, $P > 0.30$). Similarly, subsequent memory effects in the calcarine gyrus were also not significant ($ts < 1.44$, $Ps > 0.17$). However, the hippocampal activity was related to successful recognition of self-relevant items (SRR vs. SF: $t(13) = 3.16$, $P < 0.01$), but not self-irrelevant items (SIR vs. SF: $t(13) = 1.30$, $P > 0.22$). It is worth mentioning that the additional recruitment of prefrontal cortex (i.e., right anterior cingulate cortex) for self-relevant items relative to self-irrelevant items might not necessarily lead to the general memory enhancement for self-relevant items. Self-descriptiveness effect in memory might depend on the hippocampal activity, which has consistently been linked to relational binding processes (Davachi et al., 2003; Ranganath et al., 2003; Kensinger and Schacter, 2006; Uncapher et al., 2006; Dougal et al., 2007; Qin et al., 2009; Staresina and Davachi, 2009).

Effect of encoding task

Regions demonstrating a main effect of encoding task were identified by contrasting self-referenced trials with other-referenced trials. Consistent with previous studies (Kelley et al., 2002; Fossati et al., 2003; Heatherton et al., 2006; Mitchell
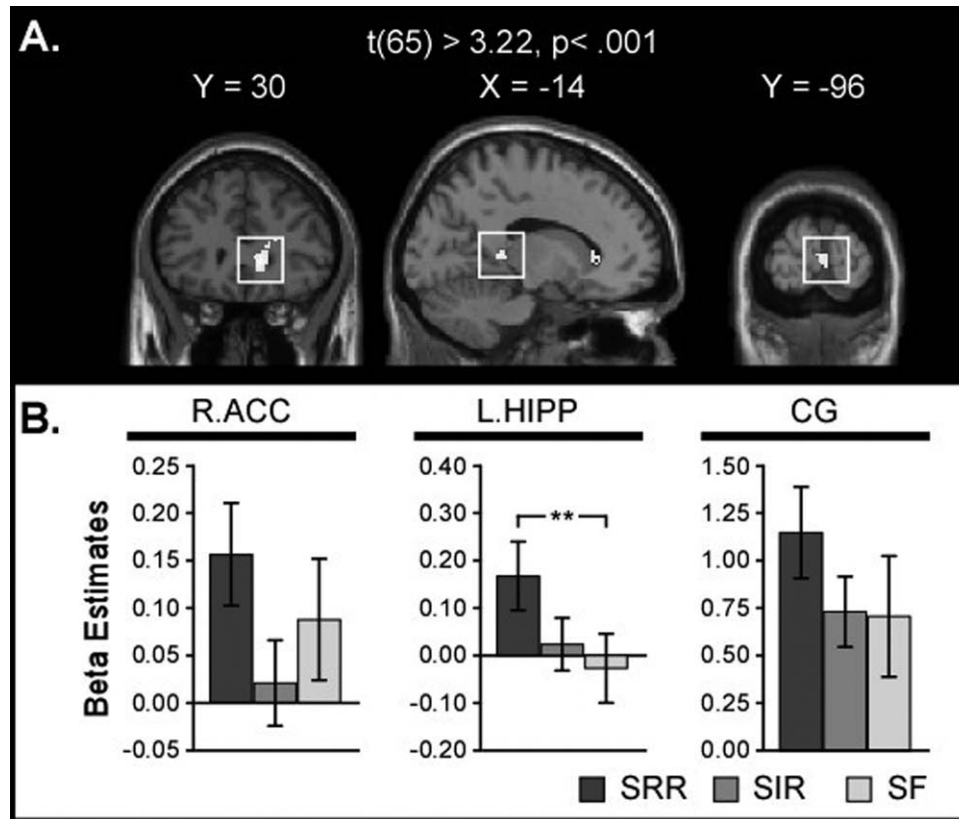
FIGURE 2.   Brain Regions Showing Effect of Self-descriptiveness Judgment. (A) Clusters located in the right anterior cingulate cortex (L.ACC), left hippocampus (L.HIPP) and calcarine gyrus (CG) resulting from the analysis. (B) The hippocampal activity was related to successful recognition of self-relevant items, but not self-irrelevant items. Error bars indicate standard error of the mean. ** $P < 0.01$.

et al., 2006; Moran et al., 2006; D'Argembeau et al., 2005, 2007, 2008; Benoit et al., 2010; Gutchess et al., 2010; Rameson et al., 2010), several regions including bilateral ventral, dorsal and medial prefrontal cortex exhibited main effect of self-referential encoding (Table 2). The reverse contrast reveals no significant activation in the prefrontal cortex. To test whether the activity of these regions contribute to successful memory formation, participants' beta estimates in the six conditions were extracted from ROIs. ROIs in the mid orbital gyrus (0, 50, −8), superior frontal gyrus (right: 20, 54, 16; left: −16, 60, 20), left middle frontal gyrus (−22, 50, 28), right middle cingulate cortex (2, −14, 38), left superior temporal gyrus (−58, −48, 22), right insula (28, 20, −20), left inferior frontal gyrus (−26, 22, −22), supplementary motor area (10, 22, 62), right superior medial prefrontal gyrus (8, 28, 50), left inferior temporal gyrus (−56, −62, −14), left middle temporal gyrus (−52, −34, 4), left precuneus (−2, −50, 48), left caudate nucleus (−8, 10, −12) and middle orbital gyrus (−28, 58, −8) were defined as 6 mm spherical regions centered on the peak or local maximum coordinate, including all the significant voxels in the activated clusters. Follow-up analysis on beta estimates for self-reference task revealed that only the subsequent memory effects in the left superior frontal gyrus (SRR vs. SF: $t(13) = 2.21$, $P < 0.05$; SIR vs. SF: $t(13) =$

2.47, $P < 0.05$) and subsequent memory effect in the left middle temporal gyrus for self-irrelevant items (SIR vs. SF: $t(13) = 2.58$, $P < 0.05$) were significant. As for other-reference task, activations in all the ROIs for remembered trials were not significant higher than forgotten trials ($ts < 1.71$, $Ps > 0.11$), indicating that additional recruitment of prefrontal cortex during self-reference task was associated with memory enhancement that accompanied self-referential processing.

Subsequent memory effect

Data analyses revealed greater activation in regions including left medial and lateral prefrontal cortex, bilateral perirhinal cortex and left middle temporal gyrus during remembered trials relative to forgotten trials by contrasting [(SRR + SIR + ORR + OIR) - 2(SF + OF)] (Table 3). These results conformed to prior demonstrations of medial and lateral prefrontal activation during successful memory formation for self knowledge (Macrae et al., 2004) and perirhinal cortex activation during item recognition (Davachi et al., 2003; Ranganath et al., 2003; Kirwan and Stark, 2004; Uncapher et al., 2006; Staresina and Davachi, 2009; Zhu et al., 2010). Further, middle temporal gyrus engagement was consistent with the critical role of middle temporal gyrus in semantic memory encoding (Fletcher and

TABLE 3.

Regions Showing Subsequent Memory Effect

	Region	Peak activation			t Value	Voxels
		X	Y	Z		
L	Inferior frontal gyrus	−38	34	−14	5.36	648
L	Superior medial gyrus	−8	62	26	4.85	285
L	Perirhinal cortex	−24	4	−28	4.45	145
L	Middle temporal gyrus	−58	2	−30	4.25	176
L	Caudate nucleus	−8	14	8	4.16	70
R	Perirhinal cortex	30	6	−32	4.04	33
R	Fusiform gyrus	36	−60	−10	4.02	57
R	Linual gyrus	12	−42	−6	3.97	49
L	Inferior temporal gyrus	−46	−50	−10	3.90	25
R	Cuneus	14	−92	8	3.78	27
L	Linual gyrus	−12	−90	−12	3.71	31

A uncorrected threshold $P < 0.001$ was used in the whole brain volume search and only clusters with 20 or more significant resampled voxels are reported. L, left hemisphere; R, right hemisphere.

Tyler, 2002; Ojemann et al., 2009). Participants' beta estimates in the six conditions were further extracted from ROIs in all the activated clusters (6 mm sphere centered on the peak) to calculate the contrast values of remembered vs. forgotten trials in 2 encoding task * 2 descriptiveness conditions. Follow-up analysis on the contrast values demonstrated that a marginal significant main effect of encoding task on the subsequent memory effect in the left medial prefrontal cortex (−8, 62, 26) ($F(1, 13) = 4.47$, $P = 0.05$), but not in other regions ($Fs < 3.76$, $Ps > 0.07$), probably indicating that medial prefrontal activity was related to self-reference effect in memory. Further, paired t-tests revealed that the contrast values of remembered vs. forgotten trials for self-relevant items were not significantly different from those for self-irrelevant items in all the ROIs ($ts < 2.05$, $P > 0.06$). Similarly, the difference of contrast values between other-relevant and other-irrelevant items in all the ROIs was also not statistically reliable ($ts < 1.87$, $P > 0.09$). The findings conformed with those of Macrae et al. (2004) demonstrating that the subsequent memory effect in prefrontal cortex was not modulated by self-descriptiveness.

Memory effect selective to self-relevant or self-irrelevant items

The above analysis revealed that self-descriptiveness effect in memory was not associated with more self mentalization and self reflection processes indexed by prefrontal activity. To identify regions showing self-descriptiveness effect in memory, we searched for regions that exhibited subsequent memory effects associated selectively with self-relevant items, but not self-irrelevant items by two steps. First, a contrast was computed to identify voxels where activity elicited by SRR trials was greater than activity elicited by SF trials. To remove voxels that also exhibited a subsequent memory effect for self-irrelevant items, this contrast was then exclusively masked with the corresponding contrast of "SIR - SF" (thresholded at $P < 0.05$). A cluster located in the hippocampus survived from the analysis (Table 4, Fig. 3). These results suggested that the medial prefrontal cortex did not selectively contribute to memory formation for self-relevant items and behavioral self-descriptiveness effect in memory was related to the activity of the left hippocampus in the medial temporal lobe which is engaged in relational memory formation irrespective of encoding task (Davachi et al.,

TABLE 4.

Regions Showing Memory Effect Selective to Self-Relevant and Self-Irrelevant Items

	Region	Peak activation			t Value	Voxels
		X	Y	Z		
Memory effect selective to self-relevant items: (SRR - SF) masked by (SIR - SF)						
L	Hippocampus	−34	−28	−6	3.91	20
Memory effect selective to self-irrelevant items: (SIR - SF) masked by (SRR - SF)						
R	Fusiform gyrus	32	−60	−10	3.89	41

A uncorrected threshold $P < 0.001$ was used in the whole brain volume search and only clusters with 20 or more significant resampled voxels are reported. L, left hemisphere; R, right hemisphere.
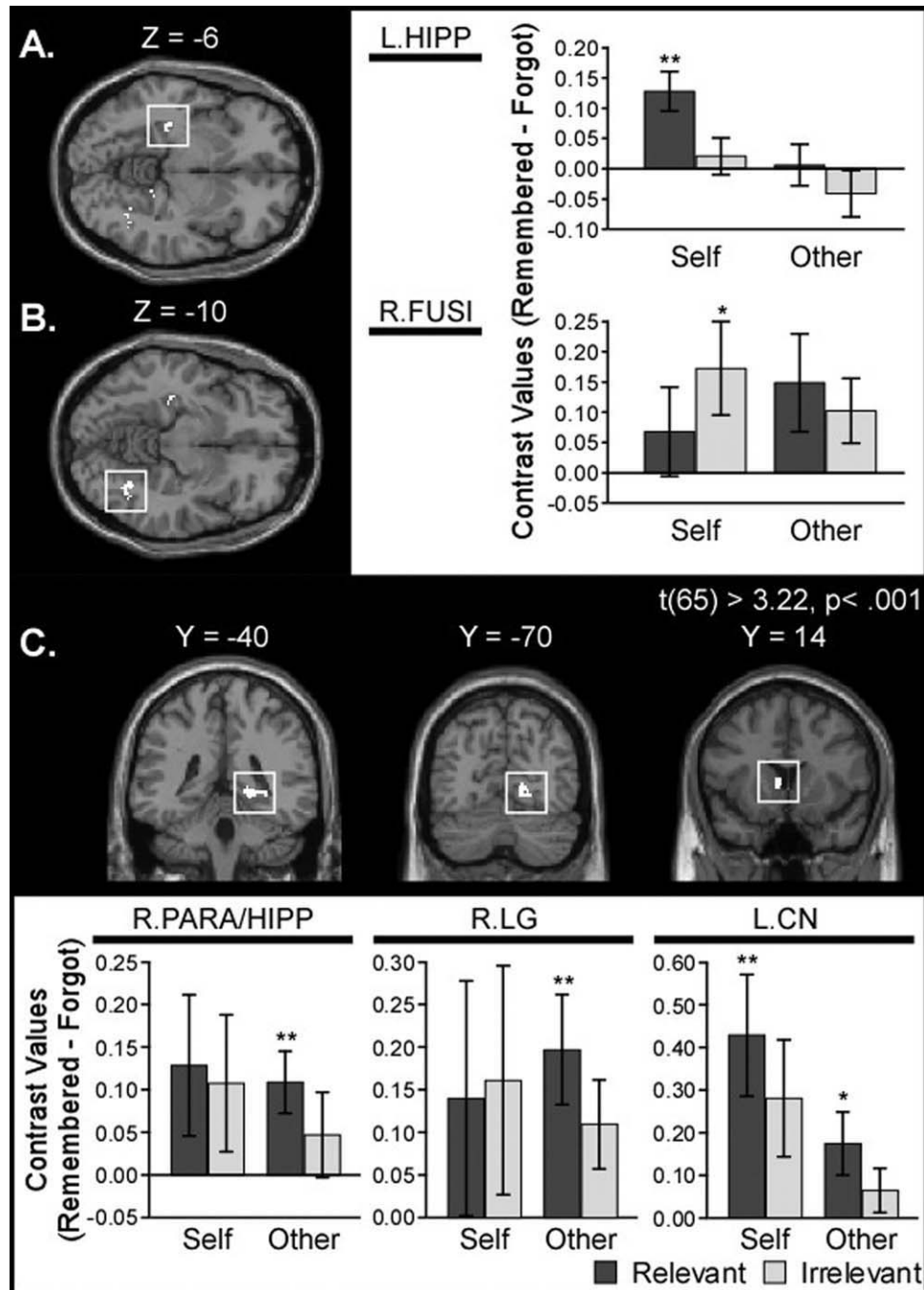
Hippocampus

FIGURE 3. Brain regions showing memory effect selective to self-relevant, self-irrelevant and other-relevant items. (A) A cluster located in the left hippocampus (L.HIPP) showing memory effect selective to self-relevant items. (B) A cluster located in the right fusiform (R.FUSI) showing memory effect selective to self-irrele-vant items. (C) Clusters located in the right parahippocampal gyrus/hippocampus (R.PARA/HIPP), right lingual gyrus (R.LG) and left caudate nucleus (L.CN) showing memory effect selective to other-relevant items. Error bars indicate standard error of the mean. * *P* < 0.05, ** *P* < 0.01.

2003; Ranganath et al., 2003; Kensinger and Schacter, 2006; Uncapher et al., 2006; Dougal et al., 2007; Qin et al., 2009; Staresina and Davachi, 2009). A similar analysis was employed to identify regions that exhibited subsequent memory effects selective to self-irrelevant items. A cluster located in the right fusiform emerged in this analysis (Table 4, Fig. 3).

Memory effect selective to other-relevant or other-irrelevant items

Given that the descriptiveness effect on subsequent memory was generally observed across two tasks at behavioral level, one could ask whether the self-descriptiveness effect and other-descriptiveness effect in memory would rely on similar regions

Hippocampus

TABLE 5.

Regions Showing Memory Effect Selective to Other-Relevant and Other-Irrelevant Items

		Peak activation				
	Region	X	Y	Z	*t* Value	Voxels
Memory effect selective to other-relevant items: (ORR - OF) masked by (OIR - OF)						
L	Caudate nucleus	−6	14	6	4.05	30
R	Linual gyrus	14	−70	0	3.93	25
R	Parahippocampal gyrus	20	−40	−2	3.91	39
R	Hippocampus	30	−40	−2	3.81	
Memory effect selective to other-irrelevant items: (OIR - OF) masked by (ORR – OF)						
	No regions					

A uncorrected threshold $P < 0.001$ was used in the whole brain volume search and only clusters with 20 or more significant resampled voxels are reported.L, left hemisphere; R, right hemisphere.

which are responsible for relational binding. Next, to clarify the neural correlates of the other-descriptiveness effect in memory, we searched for regions showing memory effect selective to other-relevant, but not other-irrelevant items by two steps. Two contrasts (ORR - OF and OIR - OF) were carried out and masked by each other at a threshold of $P < 0.05$. Consistent with self-descriptiveness effect in memory, although no region exhibited memory effect selective to other-irrelevant items, regions including the right parahippocampal gyrus/hippocampus exclusively contributed to memory formation for other-relevant items (Table 5, Fig. 3).

Memory effect selective to self-reference or other-reference tasks

Analyses of encoding task effects and subsequent memory effects suggested that medial prefrontal activity was related to self-reference effect in memory. Besides, Macrae et al. (2004) demonstrated that memory formation of self-reference informa-

tion engaged medial temporal brain regions. To confirm these hypotheses, we first searched for regions where activity was uniquely associated with successful recognition during self-reference or other-reference tasks. Two contrasts (SRR + SIR - 2SF and ORR + OIR - 2OF) were carried out and masked by each other at a threshold of $P < 0.05$. As displayed in Table 6, the right lingual gyrus exhibited memory effect selective to other-reference task, whereas regions including medial and lateral prefrontal cortex, left perirhinal cortex exclusively contributed to memory formation during self-reference task (Fig. 4). Second, we computed a memory * task interaction contrast [(SRR + SIR - 2SF) - (ORR + OIR - 2OF)] to examine regions underlying self-reference effect in memory. Table 7 displays all the activated clusters in the whole brain, including lateral and medial prefrontal cortex, left perirhinal cortex and left middle temporal gyrus. These results further assured that self-reference effect in memory depended on the activity of medial prefrontal cortex and perirhinal cortex within medial temporal gyrus.

TABLE 6.

Regions Showing Memory Effect Selective to Self-Reference and Other-Reference Tasks

		Peak activation				
	Region	X	Y	Z	*t* Value	Voxels
Memory effect selective to self-reference task: (SRR + SIR - 2SF) masked by (ORR + OIR - 2OF)						
L	Inferior frontal gyrus	−42	32	−12	5.46	887
L/R	Superior frontal gyrus	−14	60	24	5.05	228
L	Middle temporal gyrus	−54	−4	−18	5.04	306
L	Perirhinal cortex	−26	4	−30	5.04	490
L	Caudate nucleus	−14	22	2	4.33	107
L	Rectal gyrus	−6	42	−24	4.08	99
L	Linual gyrus	−8	−88	−14	3.76	43
Memory effect selective to other-reference task: (ORR + OIR - 2OF) masked by (SRR + SIR - 2SF)						
R	Linual gyrus	16	−66	−2	4.18	39

A uncorrected threshold $P < 0.001$ was used in the whole brain volume search and only clusters with 20 or more significant resampled voxels are reported.L, left hemisphere; R, right hemisphere.
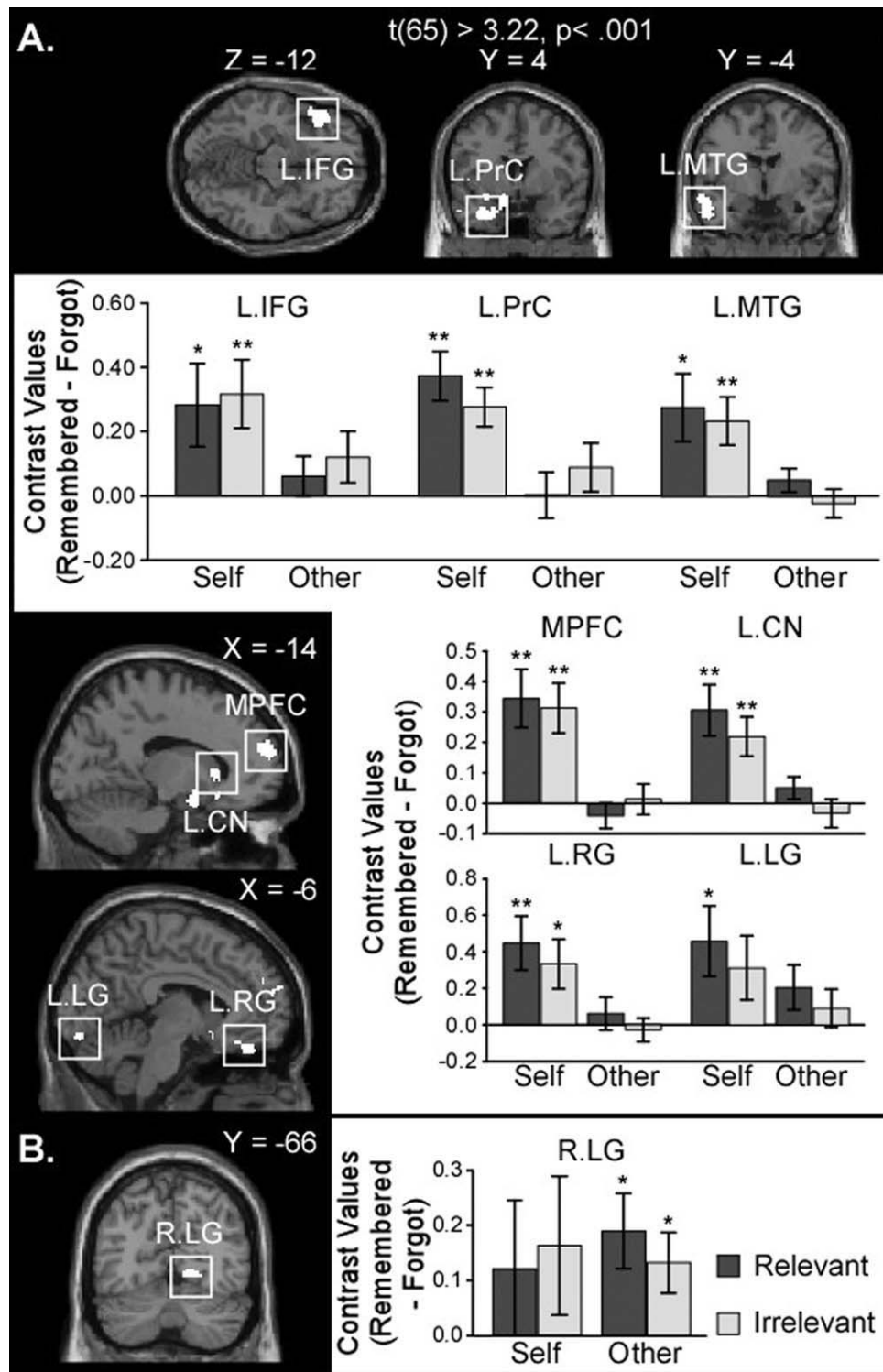
Hippocampus

FIGURE 4. Brain regions showing memory effect selective to self-reference and other-reference tasks. (A) Clusters located in the left inferior frontal gyrus (L.IFG), left perirhinal cortex (L.PrC), left middle temporal gyrus (L.MTG), medial prefrontal cortex (MPFC), left caudate nucleus (L.CN), left rectal gyrus (L.RG) and left lingual gyrus (L.LG) showing memory effect selective to self-reference task. (B) A cluster located in the right linual gyrus (R.LG) showing memory effect selective to other-reference task. Error bars indicate standard error of the mean. * $P < 0.05$, ** $P < 0.01$.

TABLE 7.

Regions Underlying Self-Reference Effect in Memory

	Region	Peak activation				
		X	Y	Z	*t* Value	Voxels
L	Perirhinal cortex	−32	2	−32	4.75	140
L	Superior frontal gyrus	−14	60	20	4.72	184
L	Superior medial gyrus	−12	62	12	4.37	
L	Middle temporal gyrus	−54	−4	−18	4.60	138
L	Putamen	−22	14	0	4.38	175
L	Temporal pole	−46	24	−18	4.00	123
R	Precuneus	8	−46	72	4.00	41
L	Superior orbital gyrus	−18	20	−14	3.93	40
R	Putamen	30	4	−2	3.74	25
L	Rectal gyrus	−4	34	−16	3.72	27

A uncorrected threshold $P < 0.001$ was used in the whole brain volume search and only clusters with 20 or more significant resampled voxels are reported.L, left hemisphere; R, right hemisphere.

DISCUSSION

The present study had four main results. First, memorial advantage for relevant items was evident across the self-reference task and the other-reference task. And, the beneficial effect of descriptiveness in both tasks depended, in part, on hippocampal activity. This important finding highlights that item descriptiveness promotes successful memory formation through some common processes that were shared across the two tasks and were independent of explicit self-referential processing. As their attempt to explain the impact of self-descriptiveness on memory formation, Rogers et al. (1977) speculated that relevant items lead to enhanced relational binding as those items can be more readily integrated into a preexisting cognitive network and consequently strengthen the memory trace. Indeed, the hippocampus has been held to play a key role in binding various episodic details irrespective of encoding task (Davachi et al., 2003; Ranganath et al., 2003; Kensinger and Schacter, 2006; Uncapher et al., 2006; Dougal et al., 2007; Qin et al., 2009; Staresina and Davachi, 2009). This may suggests that the memory boost for relevant items relies on the enhanced relational binding mechanisms employed during relevant trials.

Second, in the self-reference task, activity in the anterior cingulate cortex within prefrontal cortex showed the effect of self-descriptiveness judgment. Combined with recent studies which have demonstrated that the prefrontal cortex was more responsive to self-relevant items than self-irrelevant items in both the explicit self-reference task (Moran et al., 2006, 2009; Rameson et al., 2010) and the implicit encoding task (e.g., passive viewing or social desirability judgment, Moran et al., 2009; Rameson et al., 2010), it is suggested that the prefrontal cortex is likely to play a role in encouraging further self-referential processing for self-relevant stimuli.

Third, there was no evidence that activity in the prefrontal cortex contributed differentially or disproportionately to memory formation for self-relevant items and self-irrelevant items.

Although anterior cingulate cortex within prefrontal cortex displayed greater activation for self-relevant items, it was not more engaged in mnemonic encoding for self-relevant items and not associated with memory enhancement for self-relevant items at behavioral level. Upon closer examination, these neural and behavioral discrepancies might be broadly explained by the task demands in the present study. The present study explicitly required participants to relate individual items to the self. This explicit self-referential processing, even for self-irrelevant items, engages self mentalization and self reflection indexed by the prefrontal activity (Johnson et al., 2002; Macrae et al., 2004), which is likely to attenuate the superiority of self-relevant information at neural level. This idea is supported by the current data which demonstrates that the prefrontal region exhibiting the effect of self-descriptiveness judgment was much smaller than that showing the effect of self-referential encoding and the subsequent memory effect in the prefrontal cortex was not modulated by self-descriptiveness judgment. Nevertheless, the self-descriptiveness effect in memory at the behavioral level was related to some medial temporal region which has been activated during memory formation in various tasks, i.e., the hippocampus in the present study.

By contrast, it might be the case that in some implicit tasks that do not explicitly refer to the self, self mentalization and self reflection might be triggered automatically only for self-relevant stimuli, which would lead to the self-relevant superiority in memory. Consistently, pervious studies where directly referring the self was not a part of task demands demonstrated the superiority of self-relevant information both at behavioral and neural level. At the behavioral level, highly self-relevant information exhibited better recognition (Cunningham et al., 2008) and more precise eyewitness testimony memory (Block et al., 2009). At neural level, passively viewing self-relevant information activated massive medial prefrontal regions relative to self-irrelevant information (Moran et al., 2009). Whether this additional recruitment of medial prefrontal cortex for self-relevant stimuli in implicit tasks selectively contributes to memory formation of self-relevant items remain to be tested.

Fourth, the activity of medial prefrontal cortex and perirhinal cortex was associated with the self-reference effect in memory. This result is consistent with previous studies suggesting that the medial prefrontal cortex and medial temporal gyrus were engaged in encoding and retrieval of information in self-reference task (Fossati et al., 2004; Macrae et al., 2004; Benoit et al., 2010). In particular, the activity of medial prefrontal cortex and medial temporal cortex at encoding had predicted whether a self-referenced personality trait would later be remembered or forgotten (Macrae et al., 2004), and medial prefrontal cortex was previously shown to be more responsive to hits for self-referenced items than correct rejection of new items during retrieval (Fossati et al., 2004; Benoit et al., 2010). However, although there is a compelling relation between medial prefrontal cortex and self-referential processing (Kelley et al., 2002; Mitchell et al., 2006; Gutchess et al., 2010), this region is not exclusively recruited while referencing the self. Specifically, the medial prefrontal cortex has shown a comparable activation during both self- and other-reference tasks (Schmitz et al., 2004; Ochsner et al.,

2005), a pattern that is consistent with simulation theory, which postulates that people often make judgments about others by referring to the self (Gallese and Goldman, 1998; Frith and Frith, 1999). Therefore, the medial prefrontal cortex probably also contributes to mnemonic encoding of other-referenced information. Merely demonstrating medial prefrontal activity contributed to memory formation of self-referenced information (Macrae et al., 2004) can not lead to the conclusion that medial prefrontal modulation to be a critical neural correlates for self-reference effect in memory. Nevertheless, the present study revealed that the medial prefrontal cortex was more related to successful memory formation in self-reference task relative to other-reference task. The results of the present study, combined with previous studies (Fossati et al., 2004; Macrae et al., 2004; Benoit et al., 2010), converged on the conclusion that the medial prefrontal activity predicts the self-reference effect in memory.

CONCLUSIONS

In sum, the results of the present study suggested that the activity of medial prefrontal cortex and perirhinal cortex at encoding was associated with better memory for self-referenced items and further demonstrated that the relationship of the prefrontal cortex to subsequent memory could be equally strong for self-relevant and self-irrelevant items. However, hippocampal activity selectively contributed to successful recognition of self-relevant items, but not self-irrelevant items. And, this memorial advantage for relevant items was across tasks, which implied that the self-descriptiveness effect in memory relies on some common mechanisms shared across tasks, such as enhanced relational binding mechanisms employed during relevant items. Taken together, the current results reveal that hippocampal activity was associated with self-descriptiveness effect in memory, whereas the activity of medial prefrontal cortex and perirhinal cortex was related to the self-reference effect in memory.

Acknowledgments

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