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Research Report

Incidental encoding of goal irrelevant information is associated with insufficient engagement of the dorsal frontal cortex and the inferior parietal cortex

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ABSTRACT

Previous studies have shown that goal-irrelevant distractors are incidentally encoded into long-term memory. Neuroimaging studies have suggested that the medial temporal and visual association regions are involved in incidental encoding of goal-irrelevant information. However, few studies have investigated prefrontal/parietal influence during the incidental encoding. The present study performed whole brain analysis to identify the brain regions involved in the incidental encoding of goal-irrelevant information. A face working memory (WM) task was administered with insertion of face distractors during the delay period. Following the WM task, a surprise recognition task was given in an MRI scanner. Recognition rate of distractors was higher than that of novel fillers. Recognition time was also faster in distractors than in novel fillers. Neuroimaging results showed less activation to distractors subsequently remembered than those forgotten in the middle and superior frontal regions and the lateral inferior parietal lobe including the angular gyrus and the temporoparietal regions. However, the left anterior hippocampus and the right fusiform gyrus showed greater activation to distractors subsequently remembered. Those findings suggest that insufficient engagement of the dorsal frontal cortex which regulates attentional control and the inferior parietal lobe which functions to reorient attention may allow goal-irrelevant information access to working memory and to be encoded into long-term memory.

1. Introduction

Filtering out goal-irrelevant information is essential to performing goal-directed behaviors. Both behavioral and neuroimaging studies have suggested that attentional control is important to resolving interference from goal-irrelevant information (Conway et al., 1999; de Fockert et al., 2001; Heitz and Engle, 2007; Jha et al., 2004; Theeuwes and Burger, 1998). However, what happens if goal-irrelevant information is not successfully filtered out? Vogel et al. (2005) suggested that participants with low attentional control are more likely to encode task-irrelevant information into working memory. McNab and Klingberg (2008) further demonstrated that participants with high attentional control filtered out goal irrelevant

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information with increased activation in the middle frontal gyrus and the basal ganglia in advance of distractor presentation. Those studies suggest that attentional control plays a major role in filtering out goal irrelevant information. In the other words, inadequate engagement of attentional control allows goal-irrelevant information to be encoded into working memory. In addition to the encoding of goal-irrelevant information into working memory, recent studies shed light on the involvement of attentional control in incidental encoding of goal-irrelevant information into long-term memory (Rissman et al., 2009).

The load theory proposes that increase in cognitive load (such as working memory load) depletes the resources available for attentional control, which depends on the prefrontal cortex (de Fockert et al., 2001; Lavie, 2005; Lavie et al., 2004). Based on this theory, Rissman et al. (2009) manipulated cognitive load, and examined its effect on incidental encoding of goal-irrelevant information into long-term memory. In their study, they prepared two cognitive load conditions (high and low), and required participants to memorize a random sequence of digits in the high load condition and a fixed sequence of digits in the low load condition throughout a delay. Following the presentation of digit stimuli, face and scene stimuli were presented in a mixed order, and participants were instructed to memorize either scene stimuli (scene condition), face stimuli (face condition), or passively view both stimuli (passively view condition). It is notable that participants were required to ignore face stimuli in the scene condition and scene stimuli in the face condition in order to perform the task efficiently. After the task, a surprise recognition of scene stimuli was administered, and the recognition rate of scenes to be ignored was compared with that of novel scenes and that of scenes to be passively viewed between the low load and high load conditions. In the low load condition, the recognition rate of scenes to be ignored was equivalent to that of novel scenes, and lower than those to be passively viewed. In the high load condition, the recognition rate of scenes to be ignored was significantly higher than that of novel scenes, and did not differ from those to be passively viewed. Those results suggest that depletion of resources available for attentional control makes it more difficult to ignore goal-irrelevant stimuli, and allows such information to be encoded into long-term memory incidentally.

Neuroimaging studies have shown that the medial temporal lobe and the posterior perceptual areas are involved in incidental encoding of goal-irrelevant information into long-term memory. Stark and Okado (2003) used an event-related fMRI and had their participants perform two scene recognition tasks. In the recognition phase of the first recognition task, participants saw the scenes they had memorized in the encoding phase as well as novel filler distractors. After the task, participants performed another recognition task outside the scanner and three types of stimuli were presented: scenes participants remembered at the first recognition task, scenes presented as novel distractors at the first recognition task, and scenes never presented in the first recognition task. Stark and Okado (2003) compared brain activity to distractors subsequently recognized with those not recognized in the first phase, focusing on the medial temporal lobe. As a result, several medial temporal regions showed activity in response to distractors subsequently recognized, while such increase was not observed in distractors not-recognized subsequently. The result indicates that medial temporal regions are involved in incidental encoding of goal-irrelevant information. As for the posterior perceptual areas, Rissman et al.'s study described above showed that activation of the regions predicts subsequent recognition performance. Using event-related fMRI, they measured brain activity during the main task, in which participants were required to memorize digits as well as perform the selective attention task described above. Their analysis focused on the activation of the parahippocampal place area (PPA), which shows selective activation to scenes (Epstein and Kanwisher, 1998). In the low cognitive load condition, PPA activation in response to scenes to be ignored did not differ from that scenes to be passively viewed. In the high cognitive load condition, PPA activation to scenes to be ignored was significantly greater than that to be passively viewed. Direct comparison of scenes to be ignored between the high and low load conditions showed that PPA activation in the high load condition was significantly greater than that in the low load condition. Those findings indicate that the posterior perceptual areas, whose activation is shown to be modulated by top–down attention from the frontal and parietal regions, play some role in incidental encoding of goal-irrelevant information.

Although activation of the medial temporal lobe and posterior perceptual cortices is shown to predict subsequent recognition of goal-irrelevant information, prefrontal and parietal cortices could also contribute to incidental encoding of goal-irrelevant information since they are involved in attentional control (Corbetta and Shulman, 2002; Friedman-Hill et al., 2003). Accordingly, the present study investigated how the prefrontal and parietal cortex is involved in incidental encoding of goal-irrelevant information. As previous studies have shown that weak attentional control allows goal-irrelevant distractors to be encoded into working memory and long-term memory (McNab and Klingberg, 2008; Rissman et al., 2009; Vogel et al., 2005), we invited a situation where cognitive resource for attentional control is less available. Furthermore, neuroimaging studies have shown that higher cognitive load consumed resource of the prefrontal and posterior parietal cortex to exert cognitive control (Braver et al., 1997; Cohen et al., 1997; de Fockert et al., 2001). Therefore, we gave high cognitive load (working memory load) prior to exposure of goal-irrelevant distractors, following Rissman et al.'s (2009) study. Here, two experimental hypotheses are proposed. One hypothesis is that goal-irrelevant information is encoded into long-term memory when the prefrontal and the posterior parietal cortex show less activation. This hypothesis is based on the idea that incidental encoding of goal-irrelevant distractor is associated with failure to recruit remaining attentional resources to resolve distractor interference when most of attentional resource is consumed by cognitive load. The other hypothesis is that incidental encoding of distractors is observed when the prefrontal and the posterior parietal cortex show greater activation. This hypothesis is based on the idea that distractors are deeply processed when attentional resources are fully occupied by cognitive load indexed as the greater activation of the prefrontal cortex. To test those hypotheses, we measured brain activity during a face working memory (WM) task with face distractors, using an event-related fMRI. Three face memoranda were given at the encoding period as high cognitive load. During a delay period, three face distractors were presented, and we had participants actively ignore those distractors, requiring them to judge a direction of an arrow presented after the last distractor (Fig. 1). Ten minutes after the WM task, a surprise recognition task was given, where participants were required to judge whether they had seen a face in the WM task regardless of whether it was memoranda or distractor (Fig. 2). Based on the subsequent memory performance, we divided distractors into two categories: distractors remembered and those forgotten. By contrasting brain activity in response to distractors subsequently remembered with that of distractors forgotten, we identified brain regions that are involved in the incidental encoding of goal-irrelevant information. In the present study, we used same type of stimuli (face) for memoranda and distractors, although previous studies have used different types (de Fockert et al., 2001; Lavie, 2005; Rissman et al., 2009). This manipulation was employed because we investigated brain structures for incidental encoding of goal-relevant information as well as intentional encoding of goal-relevant information (see below). In addition, previous studies have shown that congruent type of distractors produced stronger interference, activating the brain regions for cognitive control (Dolcos et al., 2007; Jha et al., 2004; Minamoto et al., 2010). Therefore, this procedure is thought to promote incidental encoding of goal-irrelevant information, demanding more cognitive resource to resolve distractor interference.

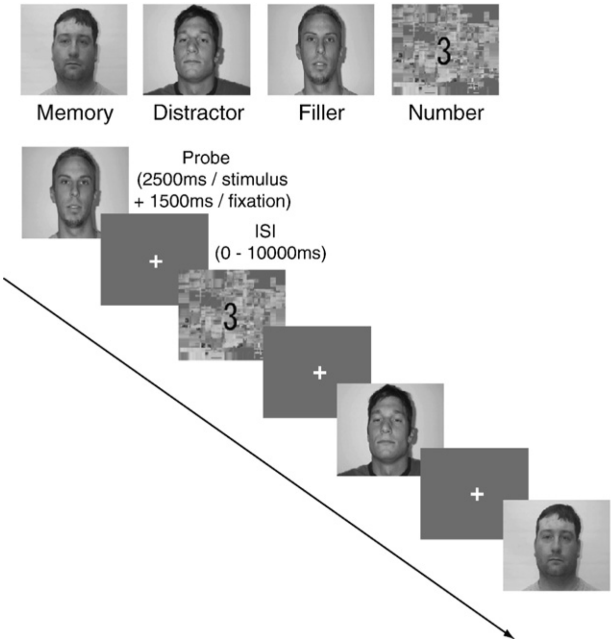

Fig. 2 – Schematic diagram of the subsequent recognition task. A total of 4 stimulus types were prepared: face stimulus presented as a memorandum in the WM task, face presented as a distractor in the WM task, a novel face, and a number. Participants were instructed to judge whether they had seen the face regardless of whether it was a memorandum or a distractor in the WM task. For the number, participants were requested to judge whether it was odd or even.

As the medial temporal lobe and the posterior perceptual areas are reported to be involved in incidental encoding of goal-irrelevant information, we took those regions into consideration. In addition, we specified brain regions related to intentional encoding of goal-relevant information, by comparing brain activity to memoranda subsequently remembered and forgotten. This approach allowed us to elucidate the neural structures mainly related to incidental

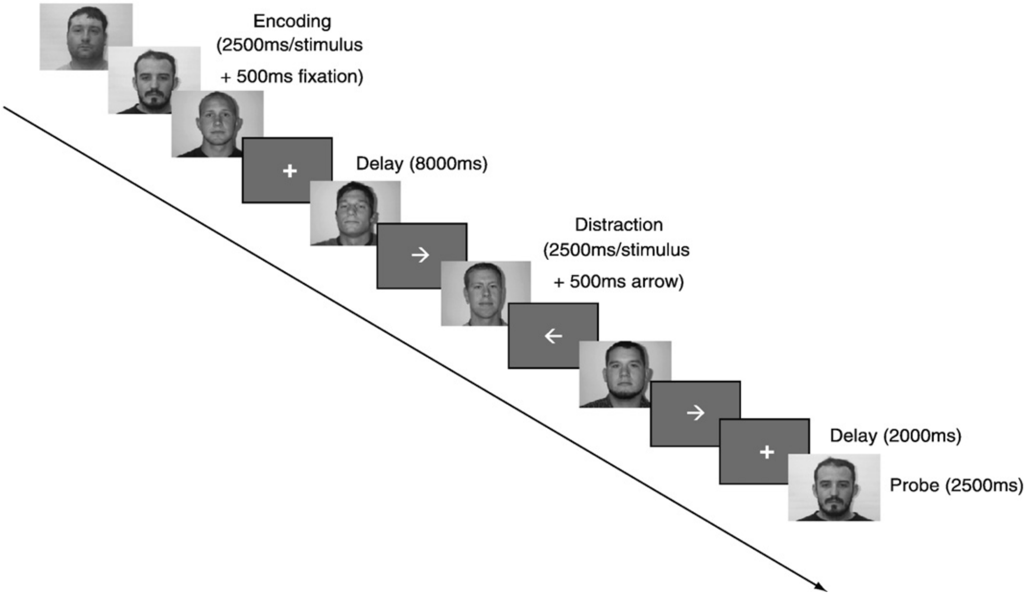

Fig. 1 – Schematic diagram of the working memory task. Following a brief sound, three face memoranda were shown on a screen, with each stimulus being presented for 2500 ms with a 500 ms fixation. After an 8000 ms delay, distractors were presented (2500 ms) along with an arrow stimulus (500 ms), and participants were instructed to judge the direction of the third arrow. A probe stimulus was presented for 2500 ms following a 12,500 ms inter-trial interval.

encoding of goal-irrelevant items. Also, this approach allowed investigation of which neural structures are shared between incidental encoding of goal-irrelevant information and intentional encoding of goal-relevant information.

Furthermore, we explored brain regions functionally connected with the right fugiform gyrus during presentation of distractors subsequently remembered and forgotten. By contrasting connected regions in response to remembered distractors with that to forgotten distractors, we can identify a functional connection which is associated with incidental encoding of goal-irrelevant information.

2. Results

2.1. Behavioral results

2.1.1. The WM task

For judgment of the arrow direction, most participants showed a perfect performance (*M*=19.17 out of 20, *SD*=1.37). Mean reaction time for the judgment was 561.03 ms (*SD*=122.66). Mean accuracy in the face memory was relatively high (*M*=86.04, *SD*=11.16). Mean reaction time to the probe stimuli was 1331.51 (*SD*=239.26).

2.1.2. The subsequent recognition task

Percentages of "yes" responses to each stimulus type and reaction time for "yes" responses are shown in Fig. 3. Regarding the percentage of "yes" responses, participants showed higher percentages of "yes" responses to stimuli used as memoranda in the WM task (memory), followed by that of distractors in the WM task (distractor). Percentages of "yes" responses to novel filler stimuli (filler) were the lowest of all. One-way repeated measure ANOVA yielded a significant main effect of the stimulus type, *F* (2, 46)=71.11, $p<.001$, and the Bonferroni's multiple comparisons showed a significantly greater percentage of "yes" response to memory stimuli than that to distractors and filler stimuli ($p<.001$), and significantly greater "yes" response to distractors than that to fillers ($p<.001$). Averaged d′ of memory stimuli and distractor stimuli is as follows: memory stimuli (*M*=1.09, *SD*=0.64), distractor stimuli (*M*=0.45, *SD*=0.32). Those values were significantly greater than zero ($p<.001$).

Reaction time for the "yes" response to each stimulus type also differed across conditions. Reaction time to memory stimuli was significantly faster than that to distractors and filler stimuli, and reaction time to distractors was faster than that to fillers. One-way repeated measure ANOVA showed a significant main effect of the stimulus type *F* (2, 46)=28.27, $p<.001$, and the post-hoc Bonferroni's multiple comparison yielded a faster reaction time in the memory condition than in the distractor and filler condition ($p<.001$). In addition, the Bonferroni comparison yielded a significant difference between distractor and filler condition, in which reaction time to distractors was significantly faster than that to fillers ($p=.03$).

2.2. fMRI results

2.2.1. Incidental encoding of goal-irrelevant information

The result of whole brain analysis on the incidental encoding was summarized in Table 1. The inferior occipital gyrus was the only region that showed greater activation to distractors subsequently remembered than to those forgotten. However, the frontal, inferior parietal, and temporoparietal regions showed greater activation to distractors forgotten than to those remembered (Fig. 4). Those regions were the bilateral middle and superior frontal gyri (BA 46, 9, 8), the left

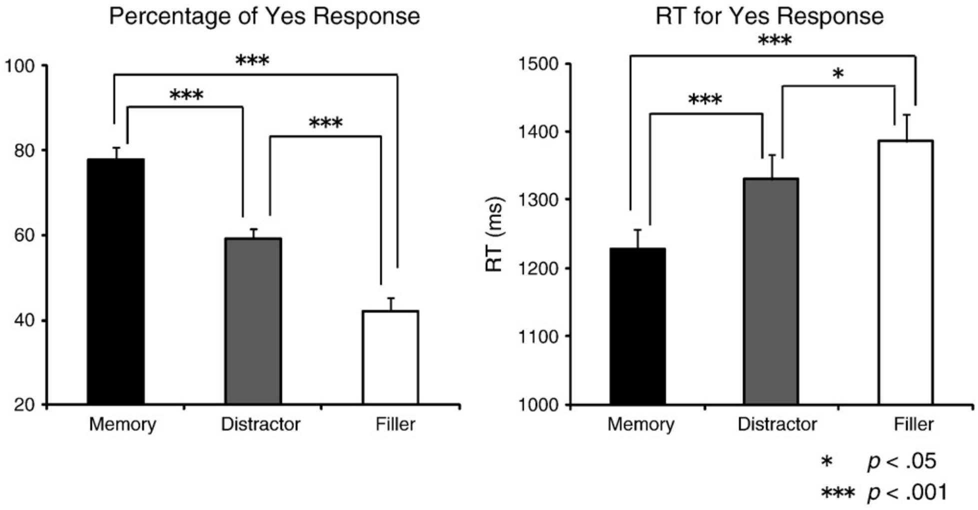

Fig. 3 – Percentage of "yes" responses to each stimulus type (left) and reaction time for "yes" responses (right). Percentage of "yes" responses was highest in the memory condition, while the percentage in the distractor condition was significantly higher than that in the filler condition. Reaction time for "yes" responses was shortest in the memory condition, and the reaction time in the distractor condition was significantly shorter than that in the filler condition.

Table 1 – Brain coordinates of activation contrasts between distractor forgotten and remembered.

Area	BA	R/L	Talairach coordinates			T-value	Cluster
			x	y	z		
Distractor forgotten–remembered							
Superior frontal gyrus	8	R	14	20	49	4.99	22
Superior frontal gyrus	8	L	−18	22	50	4.03	11
Superior/middle frontal gyrus	9/46	L	−22	55	16	4.43	32
Middle frontal gyrus	46	R	24	57	17	3.95	11
Paracentral lobule	4	L	−8	−16	71	4.27	18
Angular gyrus	39	R	51	−61	33	5.25	34
Precuneus	39	R	2	−48	41	4.88	26
Precuneus	7	R	0	−72	42	4.24	51
Precuneus	5	R	8	−47	63	4.02	46
Inferior parietal lobule	40	L	−63	−32	24	4.50	31
Superior temporal gyrus	22	R	59	−53	23	5.13	27
Middle temporal gyrus	39	L	−46	−61	20	4.85	54
Middle temporal gyrus	21	L	−61	−50	14	6.20	38
Superior occipital gyrus	18	L	−18	−68	29	5.19	39
Midddle cingulate gyrus	23	R	2	−13	43	4.09	20
Posterior cingulate gyrus	26	L	−4	−43	28	4.30	18
Hippocampus	30	L	−20	−28	−7	5.07	22
Cerebellum		R	20	−83	−23	4.82	20
Cerebellum		L	−28	−79	−23	4.28	18
Distractor remembered–forgotten							
Inferior occipital gyrus	19	L	−38	−66	−3	4.82	17

paracentral gyrus (BA 4), the right angular gyrus (BA 39), the left inferior parietal lobule (BA 40), the precuneus (BA 5, 7, 39), the bilateral superior temporal gyri (BA 22), the left middle temporal gyrus (BA 39, 21), the left superior occipital gyrus (BA 18), the right middle cingulate gyrus (BA23), the left posterior cingulate gyrus (BA 26), the left hippocampus, and the cerebellum.

2.2.2. *Intentional encoding of goal-relevant information*

The findings on whole brain analysis of intentional encoding are summarized in Table 2. Activations of the frontal, the superior parietal and the inferior temporal regions were greater for memoranda subsequently remembered than for those forgotten (Fig. 4). Those regions include the left middle frontal gyrus (BA 10), the right middle frontal gyrus (BA 8), the right inferior frontal gyrus (BA 44), the bilateral superior parietal cortex (BA 7), the bilateral inferior temporal gyrus (BA 37, 21), the right precentral gyrus (BA 6), the left supplementary motor area (BA 6), the superior and middle occipital gyrus (BA 39, 19, 18), the left parahippocampal cortex, the left pallidum, and the right cerebellum. The opposite contrast (Memoranda forgotten–Memoranda remembered) did not show brain areas activated above the threshold.

2.2.3. *Fusiform gyrus*

As for the distractors, the right fusiform gyrus (FG) showed a greater activation to distractors subsequently remembered than to those forgotten, while activation of the left FG did not differ between subsequent recognition performances (Fig. 5). Paired t-test showed a significantly greater activation of the right FG to distractors remembered than to those forgotten, $t\ (23)=2.23$, $p=.035$. T-test on the left FG did not demonstrate a significant difference between distractors remembered and forgotten, $t\ (23)=-0.61$, $p>.05$.

Similarly, analysis of the memoranda showed that the right FG showed greater activation in response to memoranda subsequently remembered than to those forgotten, while activation in the left FG did not differ between subsequent recognition performances (Fig. 5). Paired t-test showed a significantly greater activation of the right FG in response to memoranda remembered than to those forgotten, $t\ (14)=3.06$, $p<.01$. T-test on the left FG did not demonstrate a significant difference between memoranda remembered and forgotten, $t\ (14)=0.54$, $p>.05$.

2.2.4. *Hippocampus*

The contrast between distractors subsequently remembered and forgotten (remembered–forgotten) showed greater activation of the anterior left hippocampus whose coordinate of local maxima was (−24, −9, −16) in the Talairach coordinate. Five contiguous voxels with peak activity ($Z=2.63$, $p=.004$ (two-tailed), uncorrected) were obtained (Fig. 6). The opposite contrast (forgotten–remembered) showed significantly greater activation of the posterior bilateral hippocampus. The right hippocampus showed peak activity ($Z=3.33$, $p<.001$, uncorrected) at (20, −26, −7) in the Talairach coordinate, and the left hippocampus showed peak activity ($Z=4.11$, $p<.001$, uncorrected) at (−20, −28, −7).

The contrast between memoranda subsequently remembered and forgotten (remembered–forgotten) showed greater activation of the bilateral anterior and posterior hippocampus (Fig. 6). The right anterior hippocampus showed a peak

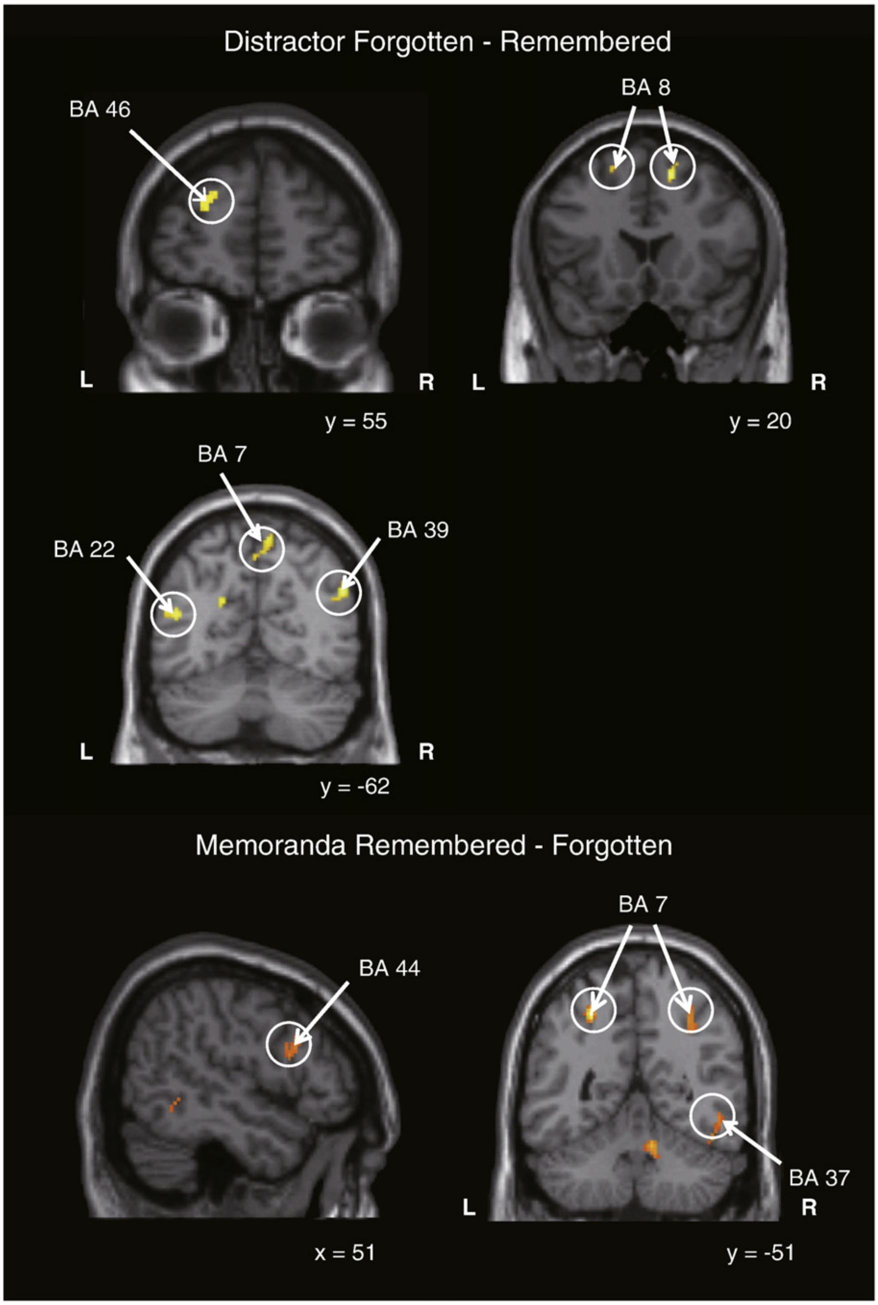

Fig. 4 – Brain activation maps based on the subsequent memory performance. Compared with remembered distractors, forgotten distractors showed greater activation in the middle and superior prefrontal regions, the inferior parietal lobule, the temporoparietal areas, the medial superior parietal cortex and the posterior cingulate cortex (top). As for the memoranda, remembered memoranda showed greater activation in the middle and inferior prefrontal regions, the lateral superior parietal cortex, and the inferior temporal cortex (bottom).

activity ($Z=3.37$, $p<.001$) at (38, −12, −16), and the left anterior hippocampus showed a peak activity ($Z=4.94$, $p<.001$) at (−32, −8, −13), respectively. The right posterior hippocampus showed a peak activity ($Z=3.06$, $p=.001$, two-tailed) at (18, −29, −4), and the left posterior hippocampus showed a peak activity ($Z=2.83$, $p=.002$, two-tailed) at (−28, −27, −4). There was no significant activation detected by the opposite contrast (forgotten–remembered).

2.2.5. *Correlation between recognition memory of distractors and brain activity*

Correlation analysis was performed between recognition memory of distractor items (d′) and brain activation. Nine ROIs were selected based on a priori hypothesis that the frontal, parietal and inferior temporal lobes are involved in incidental encoding of goal-irrelevant information; the bilateral middle frontal gyri (BA46), the bilateral superior frontal gyri

Table 2 – Brain coordinates of activation contrasts between memorandum forgotten and remembered.

Area	BA	R/L	Talairach coordinates			T-value	Cluster
			x	y	z		
Memorandum remembered–forgotten							
Middle frontal gyrus	10	L	−28	57	6	5.57	16
Middle frontal gyrus	8	R	30	8	51	5.39	29
Inferior frontal gyrus	44	R	53	19	23	4.91	44
Precentral gyrus	6	R	46	1	26	5.81	32
Supplementary motor area	6	L	−6	−1	57	5.4	18
Superior parietal cortex	7	R	26	−58	51	4.95	49
Superior parietal cortex	7	R	34	−54	54	3.94	73
Superior parietal cortex	7	L	−26	−48	48	9.67	27
Inferior temporal gyrus	21/37	R	46	−51	−14	4.99	30
Inferior temporal gyrus	37	L	−44	−56	−1	5.61	45
Middle occipital gyrus	19/39	R	38	−71	26	6.58	56
Middle occipital gyrus	39	L	−40	−79	21	5.65	69
Middle occipital gyrus	18	R	34	−87	6	5	41
Calcarine	18	R	18	−91	6	6.22	22
Parahippocampal cortex	37	L	−22	−39	−5	6.34	28
Pallidum		L	−22	2	−3	4.68	27
Cerebellum		R	12	−34	−20	4.51	
Cerebellum		R	12	−67	−19	5.54	20
Cerebellum		R	28	−59	−12	4.93	29

(BA8), the right angular gyrus (BA39), the right precuneus (BA7), the left inferior parietal lobule (BA 40), and the bilateral fusiform gyri (FG). The coordinates of the ROIs were determined by the whole brain contrast (Distractor forgottten–Distractor remembered), except for the bilateral FG which was anatomically defined. All the ROIs were created with 4 mm radius so that we can mostly cover the largest cluster (middle temporal gyrus; BA39) obtained in the contrast between distractors forgotten and remembered. The center of the ROI was located at the peak coordinates reported in Table 1, and the brain activation during the distractor period is included for the first correlation analysis. When subsequently forgotten distractors were presented, we found a significant positive correlation in the right fusiform gyrus (FG), and significant trends toward positive correlation in the left middle frontal gyrus (BA46) and the left FG (Fig. 7). On the other hand, when subsequently remembered distractors were presented, significantly positive correlation was observed in the bilateral FG. Other regions were not correlated with recognition memory of distractors, as shown in Table 3.

In addition, we examined correlation between recognition memory of distractors and activation of the bilateral FG during presentation of memoranda. Assuming that activation of the FG during memoranda encoding reflects individual cognitive load, it is possible that individuals with high cognitive load showed higher recognition memory of distractors as they have little attentional resource to resolve distractor interference. To perform the analysis, we generated a new statistical model, which included 4 covariates: *encoding* with duration of 9 s, *delay* (middle time point between encoding and distraction with duration of 0 s), *distraction* with duration of 9 s, and *probe* with duration of 3 s. Signal change during encoding phase was extracted by MarsBaR, and correlation coefficient was computed. As the result, we found a significant positive correlation between activity of the bilateral FG during encoding phase and recognition memory of distractors, $r=.54$, $p<.01$ for the right FG, and $r=.62$, $p<.01$ for the left FG.[1]

2.2.6. *Functional connectivity analysis*

Fig. 8 illustrates the brain regions functionally connected with the right fusiform gyrus (FG) when distractors subsequently forgotten were presented. The specific coordinates and *t*-values are provided in the supported material. Those regions are the lateral prefrontal regions, posterior parietal regions, inferior temporal regions, and occipital regions. They are mostly overlapped with ones reported in the previous study examining the functional connectivity while ignoring distractors (Gazzaley et al., 2007). Similar pattern of the connectivity was observed when remembered distractors were presented.

When comparing the functional connectivity in response to forgotten distractors with that in response to remembered distractors, the left middle/inferior frontal gyrus (BA 46/45) showed a stronger connectivity when forgotten distractors were presented than when remembered distractors were presented (Fig. 8). Stronger connectivity in response to forgotten

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[1] We also performed a correlation between FG activity during distraction and recognition memory of memoranda. This analysis was performed based on the hypothesis that stronger activation of the FG during distraction impairs episodic encoding of memoranda; therefore a negative correlation was predicted. The result did not show a significant correlation: $r=.27$, $p>.05$ for the right FG, and $r=.14$, $p>.05$ for the left FG. We also computed a partial correlation between FG activation during distraction and recognition of memoranda, controlling the effect of activation during memoranda encoding as it could be co-varied with activation during distraction. The result showed a non-significant negative correlation in the right FG ($r=-.27$, $p>.05$) and non-significant correlation in the left FG ($r=.05$, $p>.05$). Although the correlation coefficient in the right FG showed a negative direction, it is non-significant. Therefore, the null result indicates that FG activation during distraction cannot predict episodic encoding of memoranda.

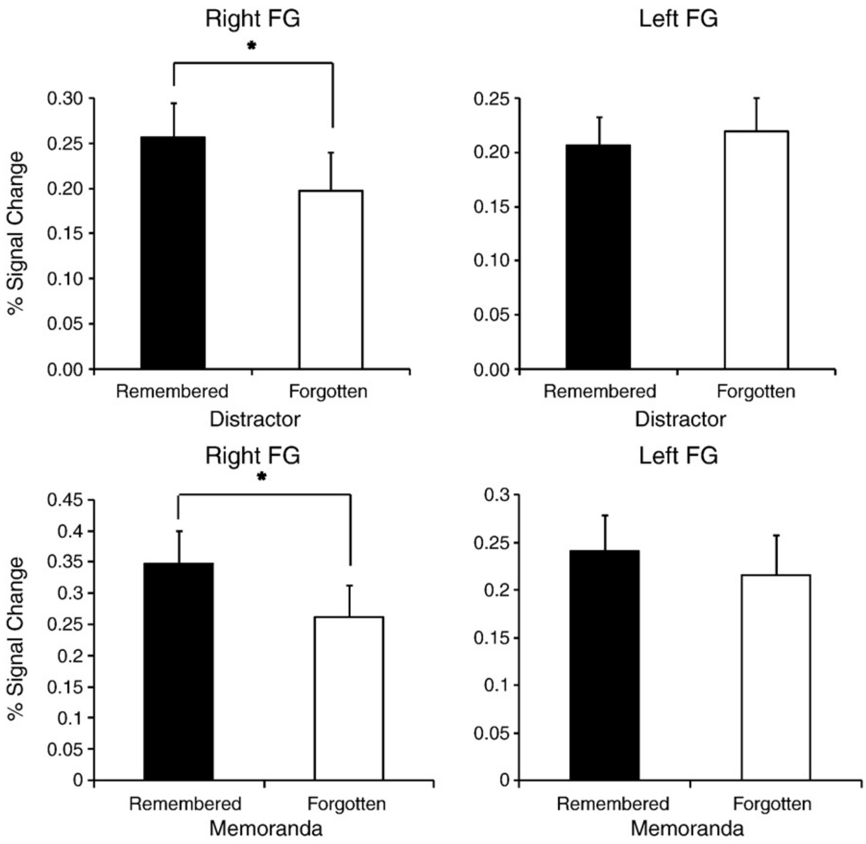

Fig. 5 – Activation in the bilateral fusiform gyrus (FG) during presentation of distractors and memoranda. The right FG showed greater activation in response to distractors subsequently remembered than to those forgotten (top left), whereas activation of the left FG did not differ across conditions (top right). Similarly, the right FG showed greater activation in response to memoranda subsequently remembered than to those forgotten (bottom left), whereas activation of the left FG did not differ across conditions (bottom right).

distractors was also found in the frontal cortex, precuneus, and subcortical regions (Table 4). On the other hand, the superior temporal gyrus and the cerebellum showed stronger connectivity in response to remembered distractors.

3. Discussion

The present study investigated the neural structures related to incidental encoding of goal-irrelevant information. As a result, several brain regions showed smaller activation in response to distractors subsequently remembered, compared with those forgotten. Those regions were the bilateral superior and middle frontal gyri, the medial superior parietal cortex, the inferior parietal lobule, the temporoparietal regions, and the posterior cingulate cortex. Interestingly, those regions are mostly overlapped with those reported in the previous studies, which investigated the neural structures related to unsuccessful memory encoding, using an incidental memory paradigm (Otten and Rugg, 2001; Wagner and Davachi, 2001). The authors interpreted the finding as indicating that activation of those regions reflects impaired encoding of information due to diversion of the cognitive resource to process task-irrelevant information or task-irrelevant thoughts, resulting in negative effects on subsequent memory performance. However, impaired encoding is not always aversive but rather useful in some occasions, and one such occasion is filtering out of goal-irrelevant information. Our findings support the idea that activation of these regions helps us in avoiding the encoding of goal-irrelevant information. In other words, less engagement of those regions may encode goal-irrelevant information into long-term memory. In fact, the right fusiform gyrus (FG) and the left anterior hippocampus showed greater activation in response to distractors remembered than to those forgotten, indicating that remembered distractors underwent more processing through those regions.

Neural correlates of the intentional encoding of goal-relevant information were also examined for contrast with those of incidental encoding of goal-irrelevant information. The results showed that following neural structures demonstrated greater activation in response to memoranda subsequently remembered than to those forgotten: the bilateral middle and the right inferior frontal gyri, the bilateral superior parietal cortex, and the bilateral inferior temporal cortex. Activation of those regions is consistent with previous literature, which investigated the neural structures supporting successful episodic encoding (e.g., Kelley et al., 1998; Kirchhoff et al.,

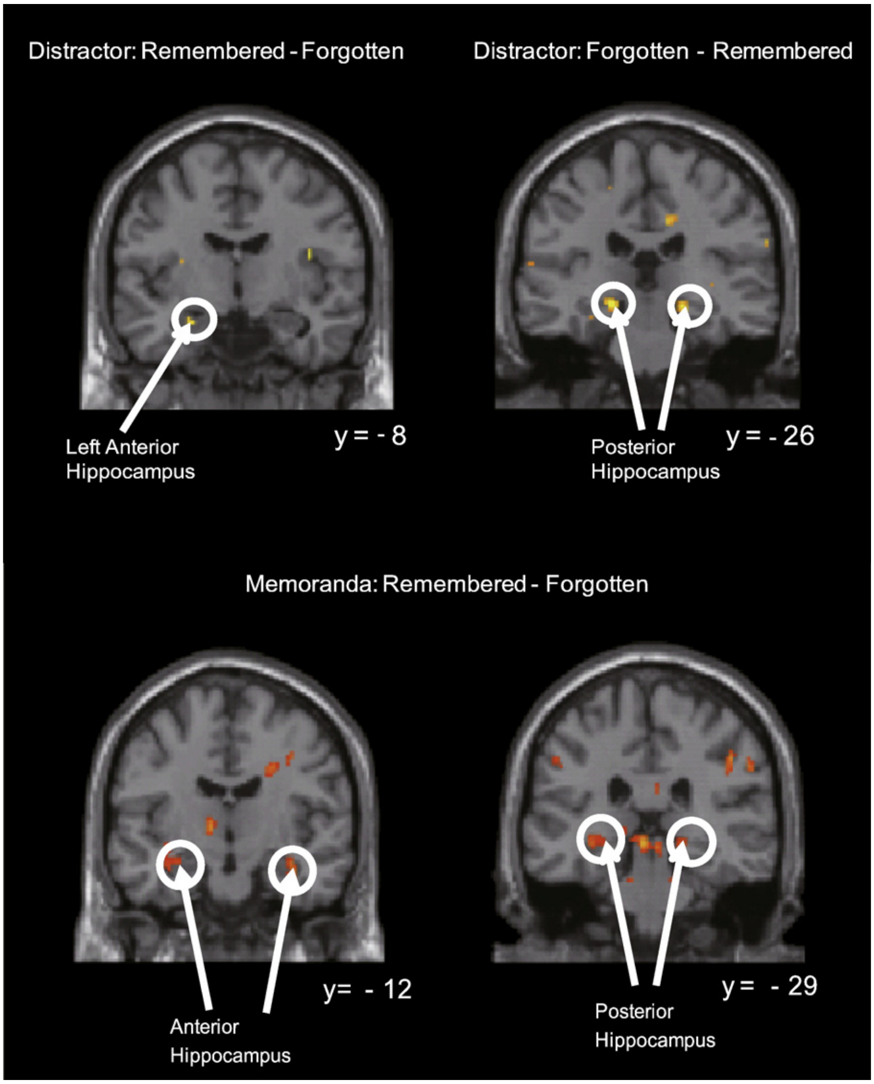

Fig. 6 – Activation in the hippocampal area during presentation of distractors. The left anterior hippocampus showed greater activation in response to distractors subsequently remembered than to those forgotten (top left). The bilateral posterior hippocampus showed greater activation in response to distractors subsequently forgotten than to those remembered (top right). The bilateral anterior and posterior hippocampus showed greater activation in response to memoranda subsequently remembered than to those forgotten (bottom).

2000; Wagner et al., 1998). In addition, the right FG and the bilateral anterior and posterior hippocampus showed greater activation in response to memoranda remembered than to those forgotten, suggesting that the remembered memoranda were processed more deeply than those forgotten. Thus, the prominent difference between the incidental encoding of goal-irrelevant information and the intentional-encoding of goal-relevant information seems to be that the incidental encoding is brought by less activation of the dorsolateral prefrontal, the inferior parietal and the tempроparietal areas, while the intentional encoding is supported by greater activation of the lateral prefrontal, the superior parietal, and the inferior temporal cortex. However, posterior perceptual areas and some portion of the medial temporal lobe can be recruited in both incidental encoding of goal-irrelevant information and intentional encoding of goal-relevant information.

3.1. *Cognitive load and distractor processing*

Lavie's load theory predicts that high cognitive load makes it more difficult to ignore goal-irrelevant information, and Rissman et al. (2009) found that high cognitive load allows such information to be encoded into long-term memory. Using high cognitive load, the present study found that distractors were discriminated from novel fillers in the subsequent recognition task. In addition, analysis of reaction time shows that participants made a faster response to goal-irrelevant information than novel filler stimuli when they made "yes" response. Thus, those results support the hypothesis that high cognitive load impairs resolution of distractor interference, and distractors that failed to be ignored are likely to be encoded into long-term memory. Additional correlation analysis showed significant positive correlation between

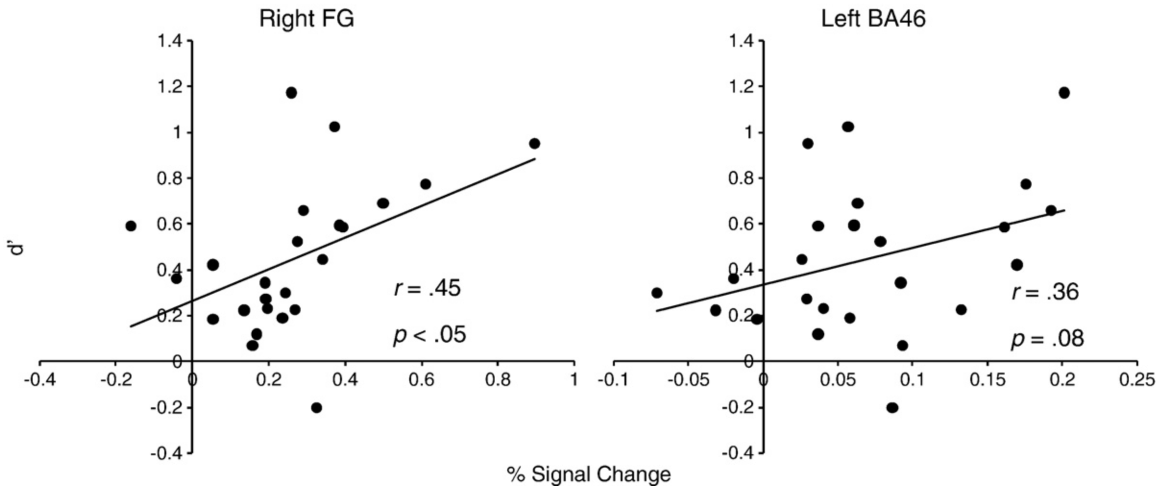

Fig. 7 – Correlation between recognition memory of distractors and brain activity. Activity of the right fusiform gyrus (FG) is positively correlated with distractor recognition in response to distractors subsequently forgotten. A significant trend toward positive correlation was observed between activity of the left middle frontal gyrus and distractor recognition when forgotten distractors were presented.

activation of the bilateral fusiform gyrus (FG) during memoranda encoding and recognition memory of distractors. Assuming that activation of the FG during memoranda encoding reflects individual cognitive load, higher cognitive load makes it difficult to resolve distractor interference, leading incidental encoding of those distractors. However, direct manipulation of cognitive load is required to discuss the effect of cognitive load on incidental encoding of goal-irrelevant distractors, as the previous study did (Rissman et al., 2009).

3.2. *The prefrontal cortex and attentional control*

The dorsal prefrontal cortex (BA8, 9, 46) showed smaller activation to distractors remembered than those forgotten. As those regions are shown to exert attentional control (Corbetta and Shulman, 2002; du Boisgueheneuc et al., 2006), incidental encoding of goal-irrelevant distractors can be brought by insufficient involvement of attentional control. Therefore, our results support the first hypothesis proposed at the beginning of the paper; failure to recruit remaining attentional resource under high cognitive load (as indexed by reduced PFc activation) is associated with incidental encoding of goal-irrelevant information. The reduced PFc activation was obtained possibly because the effect of cognitive load was equivalent for both types of distractors (remembered and forgotten distractors), depleting same amount of PFc resource in the present study. In that case, residual PFc resource for cognitive control was also equivalent for both types of distractors, and this resource can be consumed to resolve distractor interference. If so, more activation of the PFc enables participants to filter out distractors while holding memoranda. In other words, insufficient activation of the PFc allow distractors to be encoded into long-term memory. However, if magnitude of cognitive load was apparently different between two conditions (high load vs. low load), it would be plausible to hypothesize that greater PFc activation reflected as the depletion of attentional resource is associated with incidental encoding of goal-irrelevant distractors, considering the previous finding that greater PFc activation by higher cognitive load increased distractor interference (de Fockert et al., 2001). Thus, further research directly manipulating cognitive load is required to test the second hypothesis.

In the left dorsolateral prefrontal cortex (BA46), a marginally positive correlation was observed between activation of the region and recognition memory of distractors when forgotten distractors were presented, while such correlation was not observed when remembered distractors were presented. This result raises the possibility that individuals with higher recognition memory required more attentional control to resolve distractor interference when they successfully filtered out goal-irrelevant distractors. In contrast, when remembered distractors were presented, all participants might fail to resolve distractor interference, which may eliminate the positive correlation between the BA46 and the recognition memory of distractors. Although it seems counterintuitive that positive correlation was observed between the recognition memory of distractors and the activity of the left BA46, a previous study investigating interference resolution showed that individuals with higher interference showed stronger activation of the ventrolateral prefrontal cortex (Nee et al., 2007). Their interpretation of the result was that participants with greater conflict face more selection demands, requiring more

Table 3 – Correlation coefficient between subsequent distractor recognition and brain activity.

	L BA46	R BA46	R BA8	L BA8	R BA39
Distractor forgotten	$.36^{\dagger}$	.18	.18	.15	.32
Distractor remembered	.05	.05	.08	.09	.30

	R BA7	L BA40	R FG	L FG
Distractor forgotten	.06	.06	$.45^{*}$	$.37^{\dagger}$
Distractor remembered	.16	.25	$.41^{*}$	$.59^{*}$

$^{*}p<.05$, $^{\dagger}p<.10$.

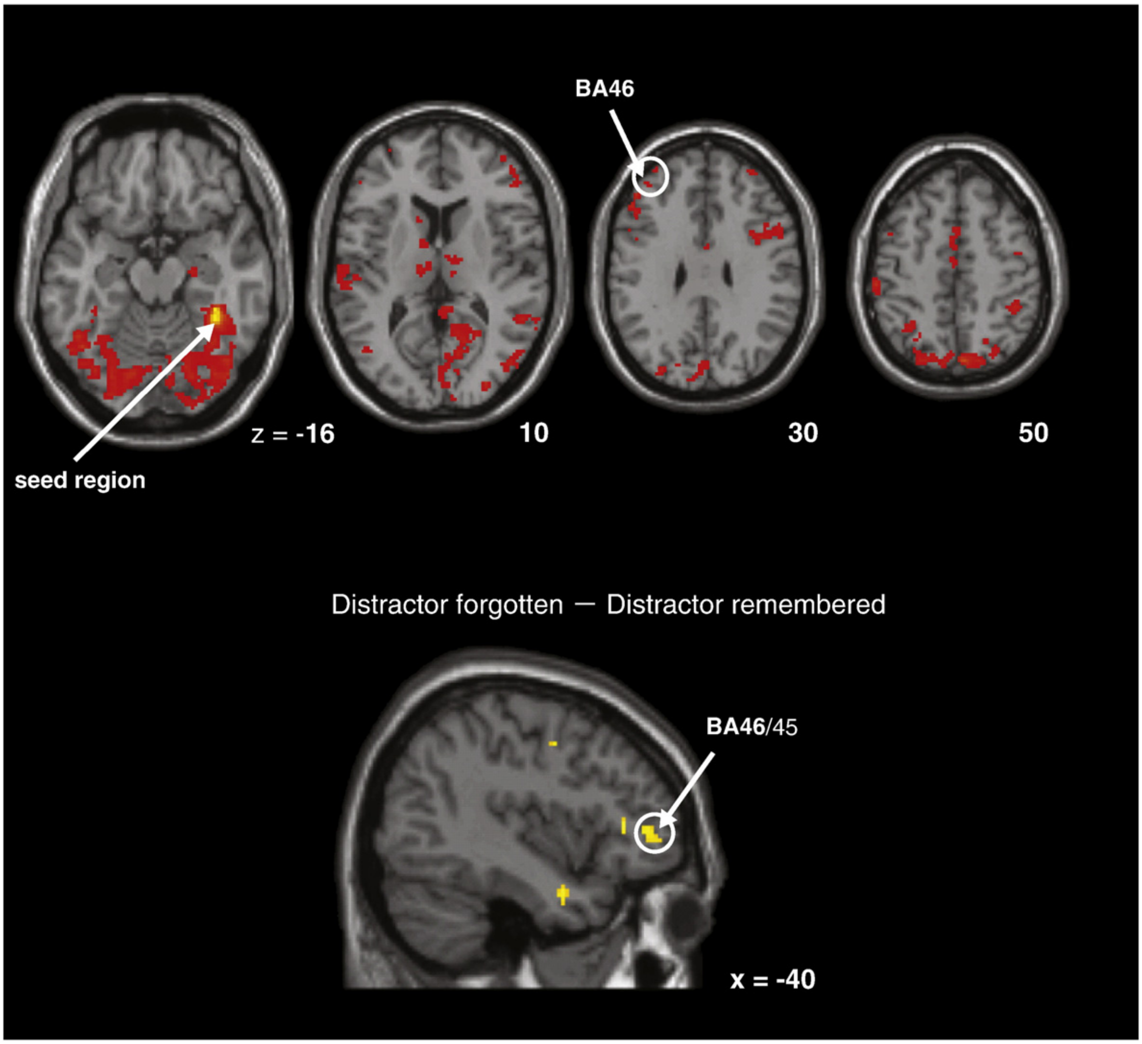

Fig. 8 – Brain regions functionally connected with the right fusiform gyrus during distractor presentation. In response to forgotten distractors, the right fusiform gyrus (FG) functionally connected with the lateral prefrontal cortex, frontal cortex, posterior parietal cortex, inferior temporal cortex, occipital cortex, and several subcortical regions (top). The functional connectivity between the right FG and left middle/inferior frontal gyrus was stronger in response to forgotten distractors than those remembered (bottom).

activation of the ventrolateral prefrontal cortex. This interpretation can be applied to the present result; participants with higher recognition memory received more distractor interference as reflected by the activation of the fusiform gyrus, and they might require more attentional control to resolve the interference. However, once again, positive correlation in the left dorsolateral prefrontal cortex was significant trend so that this result must be carefully interpreted.

The connectivity analysis showed that the functional connectivity between the right fusiform gyrus and the left middle/inferior frontal gyrus was stronger when forgotten distractors were presented than when those remembered were presented. The stronger connectivity in response to forgotten distractors may reflect efficient maintenance of memory items in working memory, preventing goal-irrelevant distractors from accessing to working memory. In fact, previous study found that coordinated activity between the left ventrolateral prefrontal cortex and the visual association cortex reflects efficient maintenance of goal-relevant information and interference resolution of goal-irrelevant information (Jha et al., 2004), supporting our interpretation. In other words, when the connectivity between the regions was weak, goal-relevant information held in working memory may be more vulnerable to distracting information.

3.3. *Posterior parietal cortex and episodic encoding*

According to Uncapher and Wagner (2009), activation of the lateral posterior parietal cortex (PPC) during episodic encoding predicts subsequent memory performance. Specifically, increased activation of the dorsal PPC, which encompasses the superior parietal lobe and the intraparietal sulcus, is associated with memory success. However, activation of the ventral PPC, which includes the inferior parietal lobe, the supramarginal gyrus, temporoparietal junction and the angular gyrus, correlated with subsequent memory failure.

Table 4 – Brain coordinates of functional connectivity contrasts between distractors forgotten and remembered.

Area	BA	R/L	Talairach coordinates			T-value	Cluster
			x	y	z		
Distractor forgotten–remembered							
MFG/IFG	45/46	L	−42	43	2	3.24	27
Inferior frontal gyrus	45	L	−38	31	6	3.69	17
Supplementary motor area	6	R	12	3	68	3.4	18
Precentral gyrus	6	R	14	−14	65	3.2	21
Precentral gyrus	6	L	−34	−2	42	3.16	22
Paracentral lobule	6	L	−12	−14	67	3.49	41
Paracentral lobule	4	L	−12	−24	68	3.59	26
Precuneus	2	L	−16	−40	63	3.42	29
Middle cingulate cortex		R	4	−21	43	3.4	23
Cingulate gyrus		R	38	−29	5	3.3	17
Lingual gyrus	27	R	6	−38	7	3.31	24
Caudate		L	−12	10	12	3.81	86
Putamen		L	−22	14	10	3.73	
Parahippocampal Gyrus	37	R	26	−33	−3	3.27	22
Distractor remembered–forgotten							
Superior temporal gyrus	38	R	46	16	−23	3.28	21
Cerebellum		L	−8	−34	−13	3.22	17

Literature on attention has shown that the dorsal PPC supports the allocation of goal-directed attention (Corbetta and Shulman, 2002), which could promote encoding of episodic information into long-term memory. Given that, our finding on intentional encoding can be interpreted as indicating that more goal-directed attention was allocated to memoranda subsequently remembered, which could enhance episodic encoding of those items. As for the ventral PPC, it is proposed that the region functions to mediate attentional reorienting in a domain-general way (Corbetta et al., 2008). This includes attentional reorientation from external stimulus feature to introspective thoughts, which can be related to the forgetting process because less attention is directed to external stimulus (Wagner and Davachi, 2001). In the present study, greater activation of the angular gyrus and the middle and inferior temporal gyrus was observed when items subsequently forgotten were presented. Assuming that the ventral PPC reorients attention from the external environment to internal representation, participants in our study might reorient their attention from the distractor faces to their internal thoughts or representation (possibly internally-generated representations of relevant faces), in order to reduce distractor interference. Activation of the posterior cingulate cortex and the precuneus also supports this interpretation since those areas constitute one portion of the default mode network, which is hypothesized to contribute to internal mentation (Buckner et al., 2008). The internal representation might be maintained in the posterior hippocampus, which showed greater activation in response to distractors forgotten than to those remembered, since the regions has been proposed to hold goal-representation in working memory (Duncan et al., 2009). Taken together, activation of the ventral PPC may help to avoid encoding goal-irrelevant information by disengaging attention from the external distractors to internal thoughts or internally-generated representation. In other words, failure of such attentional reorientation may yield encoding of goal-irrelevant information into long-term memory. This is one possibility and further study is required to test this hypothesis.

Although we suggest that the ventral PPC helps participants reorient their attention from face distractors toward internal representation of face memoranda, there is an alternative account that activation of the ventral PPC had participants to reorient their attention from face distractors toward arrow stimuli, not toward the internally represented faces. It is difficult to reject the possibility with the present dataset; however, the functional connectivity result may support our interpretation, given that the coordinated activity between the visual association cortex and the lateral prefrontal cortex helps maintain target information with resolving interference of goal-irrelevant distractors (Jha et al., 2004). As the functional connectivity was stronger when forgotten distractors were presented, participants may direct their attention toward target faces held in working memory, which might be initiated by the ventral PPC.

3.4. *Conclusion*

The present study investigated neural structures related to incidental encoding of goal-irrelevant distractors. Contrasting brain activation between the distractors subsequently remembered and those forgotten showed less activation of the dorsal frontal cortex, the lateral inferior parietal lobule, the precuneus, the middle cingulate cortex when distractors were remembered. However, the right FG and the left anterior hippocampus showed greater activation. Those findings suggest that insufficient attentional control regulated by the dorsal frontal cortex and failure of attentional reorientation controlled by the inferior parietal lobule may allow goal-irrelevant information to be encoded into long-term memory.

4. Experimental procedures

4.1. *Participants*

Twenty-nine Japanese college students (mean age=22.04, *SD*=2.58, 15 females) participated in the present study. All participants reported normal or corrected to normal vision, and were right handed except for one who was left handed. Before the experiment, an experimenter gave a detailed description of the study to all participants, and each participant provided informed consent. The study protocol was approved by the Advanced Telecommunications Research Institute International prior to the experiment. Five participants were excluded from data analysis. Two were removed due to failure of data collection, one could not complete the experiment due to poor physical condition, one showed large head motion (>2.0 mm), and one showed deviated brain activities in the left fusiform gyrus (3SDs away from the mean).

4.2. *Stimuli and procedure*

Experimental stimuli were projected onto a screen through a mirror mounted on a head radiofrequency coil. Stimuli subtended a visual angle of 9° on a gray background. One-hundred ninety face pictures were retrieved from the Productive Aging Laboratory (Minear and Park, 2004), University of Texas at Dallas (http://agingmind.cns.uiuc.edu/facedb/) and the Psychological Image Collection at Stirling, University of Stirling Psychology Department (http://pics.psych.stir.ac.uk/). Faces were of female and male adult Caucasians with neutral facial expressions. Pictures were converted to grayscale so that participants could not use color information as a memory cue. In addition, numbers were used in a subsequent recognition task. A number was projected onto scrambled faces, which were fabricated with an image-editing software, Photoshop (Adobe Systems, Inc., San Jose. CA).

The experiment consisted of two parts: a face working memory (WM) task and a subsequent surprise recognition task. Before being scanned, participants performed practice trials of the WM task until they fully understood the procedure. Fig. 1 illustrates a schematic diagram of the WM task. At the beginning of a trial, a brief beep sound (11.25 kHz) was given, which warned participants to prepare for a trial. Three faces were presented on the screen (2500 ms per stimulus with a following fixation of 500 ms), and participants were instructed to memorize and remember those faces during the trial. A delay of 8000 ms followed the faces, and another set of three faces (2500 ms) were presented with arrows (500 ms). Those faces were completely irrelevant to the task and participants were instructed to ignore them, but to judge direction of the third arrow, thus participants needed to count arrows while ignoring face distractors. Another delay of 2000 ms was inserted prior to a probe stimulus, and participants were required to judge if the probe matched one of the faces they had been instructed to remember. The inter-trial interval between trials was 12,500 ms. A total of 20 trials were performed with half of them match trials. In non-matching trials, novel faces, which were not used for distractor stimuli, were presented. In order to eliminate the effect of stimuli, faces for memoranda and distractors were counterbalanced across participants. Stimulus presentation and response retrieval was regulated with Presentation (Neurobehavioral Systems, Inc., Albany, CA).

A subsequent recognition task was performed 10 min after the WM task. A schematic diagram of the recognition task (Fig. 2) was presented on the screen of the scanner, and an experimenter gave instructions to participants through an audio transmission device. Instruction was repeated until participants showed sufficient understanding of the task. Four different stimuli were prepared in the task (Fig. 2). Those were faces used as memoranda in the WM task, faces used as distractors in the WM task, faces never shown in the WM task, and numbers (1–10) mounted on scrambled faces. All stimuli were presented for 2500 ms with the following 1500 ms fixation, and the inter stimulus interval (ISI) was varied between 0 and 10,000 ms. Order of trials and duration of ISI was determined by “Optsec2” (http://surfer.nmr.mgh.harvard.edu/optseq/). In the task, a face was presented on the screen and participants were instructed to judge whether they had seen a face in the previous WM task regardless of whether it was memoranda or distractor. When a number was presented, participants were asked to judge whether the number was odd or even. Stark and Squire (2000) recommended this task to measure the baseline activity of the medial temporal lobe. A total of 200 trials were performed: 50 trials of faces as memoranda in the WM task, 60 trials of faces as distractors in the WM task, 60 trials of faces as novel stimuli, and 40 trials of numbers. Ten faces were removed from memoranda presented in the WM task because they were presented twice as probe stimuli in match trials.

4.3. *fMRI data acquisition*

Functional images were obtained using a 1.5-T MRI scanner (Shimadzu-Marconi Eclipse, Shimadzu Corp., Kyoto, Japan). Head motions were minimized with a forehead strap and comfortable padding around the participant’s head. Functional images (467 images in the WM task and 637 images in the subsequent recognition task) sensitive to blood oxygen level-dependent (BOLD) contrasts were acquired by a single-shot echo-planar imaging sequence (TR = 2000 ms, TE = 48 ms, flip angle = 80°, 64 × 64 at 3 mm in-plane resolution, 7-mm thickness, 20 contiguous oblique axial slices parallel to the AC–PC line). After the experimental scans, anatomical images were collected for all participants (TR = 12 ms, TE = 4.5 ms, flip angle = 20°, voxel size = 1 × 1 × 1 mm).

4.4. *fMRI data analysis*

Here we report the fMRI results during the WM task since we focused on brain activity during that task. The fMRI results of the recognition task will be presented elsewhere. Imaging data were analyzed with SPM5 (Wellcome Trust Center for Imaging, London, UK) running on Matlab 7.30 (Mathworks Inc., Sherbon, MA). Six initial dummy scans were discarded to eliminate nonequilibrium effects of magnetization and the remaining scans were included in the following analysis. Head motion was corrected and coregistration of functional images with anatomical images was performed. Coregistered images were normalized onto a common brain space (the MNI template), and smoothed with a Gaussian filter (full width half maximum = 4 mm). A relatively small parameter of smoothing was employed, as recommended in the previous literature (Stark and Okado, 2003), which investigated involvement of the medial temporal lobe in incidental encoding of goal-irrelevant information.

In modeling the functional images, we employed a high-pass filter (1/128 Hz) to cut off baseline drifts and an autoregression model (1) to correct the temporal correlated data. Seven regressors were convolved with the canonical HRF (Hemodynamic response function). Those regressors were memoranda subsequently remembered and forgotten, middle of the delay between encoding and distractors, distractors subsequently remembered and forgotten, probe stimulus, and inter-trial interval. A total of four contrasts were created in each participant: 1) distractors remembered–distractors forgotten, 2) distractors forgotten–distractors remembered, 3) memoranda remembered–memoranda forgotten, and 4) memoranda forgotten–memoranda remembered. As for the group-level analysis, a random effect model was created in each contrast. One sample *t*-test was performed in each contrast, with a statistical threshold $p<.001$ (uncorrected) with an extent threshold $k>10$. Although we used the extent threshold, we also computed the FWE-corrected extent threshold ($p<.05$), considering a risk of type I error. The corrected threshold was simulated by the script provided by John Ashburner (SPM-compatible code available at http://www2.warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/scripts/spm/johnsgems5/CorrClusTh.m), taking the smoothness of each contrast ("forgotten distractor–remembered distractor" and "remembered memoranda–forgotten memoranda") into account. The result showed that the corrected threshold of the contrast (forgotten distractor–remembered distractor) was 57 voxels, and that of the contrast (remembered memoranda–forgotten memoranda) was 46 voxels. In addition, we simulated the corrected extent threshold by masking the dorsolateral frontal and the posterior parietal regions based on our hypothesis that those regions are involved in incidental encoding of distractors. The mask image included the bilateral superior and middle frontal gyri and the superior and inferior parietal regions which were retrieved from the AAL ROI package (Tzourio-Mazoyer et al., 2002) embedded in MarsBaR. The obtained corrected extent threshold was 32 voxels. Therefore, it should be noted that, as for the contrast of "distractor forgotten vs. distractor remembered", clusters whose voxel size was less than 32 voxels in the dorsolatereal and posterior parietal cortices can be false positive results and that other regions with less than 57 voxels have a risk of type I error. As for the contrast "memoranda remembered vs. memoranda forgotten", clusters whose voxel size was less than 46 voxels have the risk of type I error. It should be noted that 9 participants were removed from the analysis of the intentional encoding dataset because those participants showed high recognition performance of memoranda and less than 9 items subsequently forgotten. For incidental encoding, all participants were included for the analysis. Since inter-stimulus intervals were fixed in presenting memoranda and distractors, there was a possibility that our model could not estimate the respective contributions of each stimulus to the hemodynamically blurred fMRI signal. Therefore, we obtained correlation coefficients between regressors of distractors subsequently remembered and those of forgotten, and correlation coefficients between regressors of memoranda subsequently remembered and those of forgotten in each participant. Mean correlation coefficients between regressors of distractors subsequently remembered and those of forgotten were .27 (*SD*=.05, range: .20–.36). Mean coefficients between regressors of memoranda subsequently remembered and those of forgotten were .19 (*SD*=.07, range: .08–.30). Since obtained correlation coefficients were similar to that of experimental design (+.33), which randomly varies ISIs (Henson, 2006), our model made it possible to estimate brain activation in response to each covariate. In addition, we extracted an FIR time courses of the bilateral FG to see whether timecourse plots of each type of distractor has a sensible shape. An averaged FIR timecourses of the bilateral FG in response to the presentation of distractors remembered and those forgotten are provided in a supported material, which showed a sensible shape. To report brain coordinates, we transformed MNI coordinates into Talairach coordinates, using a non-linear transform of MNI to Talairach (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach).

4.5. *Region of interest (ROI) analysis*

The ROIs of the fusiform gyrus (FG) were determined anatomically. The center of coordinate of the FGs was determined (the right FG: 39, −40, −16 and the left FG: −37, −42, −16), referring to a previous study (Grill-Spector et al., 2004). ROIs of the FG were created with a 4 mm radius. It should be noted that the FGs in the present study are putative since we specified the area in accordance with the coordinates provided by the previous study, not with individual localized coordinates. Extraction of ROI data and computation of percent signal change in each ROI was performed, using MarsBaR (Brett et al., 2002). A paired *t*-test was performed to compare the FG activation in response to distractors remembered with those forgotten. Likewise paired *t*-test was performed to compare the FG activation to remembered memoranda with those forgotten. A statistical threshold of $p<.05$ was used as alpha-level. The analyses were performed, using STATISTICA (StatSoft, Inc., Salsa, OK).

4.6. *Analysis on hippocampus*

In order to investigate the involvement of the hippocampus in the incidental encoding of goal-irrelevant information and the intentional encoding of relevant information, whole brain analysis was performed, using a relatively low statistical threshold ($p<.005$, uncorrected) with five contiguous voxels. This is because previous studies found that signal-to-noise ratio in the medial temporal lobe is relatively low (Davachi and Wagner, 2002; Duncan et al., 2009; Schacter et al., 1999), and they used a threshold ($p<.005$, uncorrected) with five contiguous voxels. As for the left hippocampus, we used the threshold of $p<.005$ (one-tailed) with five contiguous voxels for the region. This is because we had a priori hypothesis that the left hippocampus is involved in both intentional and incidental encoding based on previous literature (Rugg et al., 1997).

4.7. *Functional connectivity analysis*

To estimate the functional connectivity, we performed the beta-series correlation analysis developed by Rissman et al. (2003) and widely used in the other studies (Clapp et al., 2010; Gazzaley et al., 2007). As we found the main effect of memory performance in the right FG, we selected the region as the seed voxels. In order to perform the analysis, we constructed a new GLM design matrix, in which each individual event was coded with a unique covariate. As a result, a total of 160 covariates of interest (60 memory items, 60 distractor items, 20 delay, and 20 probe items) were entered into the GLM, which yield a unique set of 160 beta values of each voxel in the brain. The beta values were then sorted based on recognition performance of memory items and distractors items (1. memory items remembered, 2 memory items forgotten, 3 distractor items remembered, and 4. distractor items forgotten), followed by beta values of delay and probe phase (5. delay phase and 6. probe phase). Correlation coefficient between the right FG and the other brain regions was calculated so that we can investigate the interaction between brain regions during incidental encoding and successful filtering of goal-irrelevant distractors. As our primary interest was the cognitive process during distractor processing, we focused on the functional connectivity during distractor processing (distractors remembered and those forgotten). Seed correlation maps were created by computing correlation between the seed's beta series (averages across the FG seed voxels) and that of all brain voxels. Two correlation maps were generated: one for the distractors remembered and the other for those forgotten. To normalize the data, an arc-hyperbolic tangent transformation was applied to the obtained correlation coefficients of all the brain voxels, which allowed us to compare magnitude of the functional connectivity in random-effect contrast. The statistical threshold of $p < .005$ (two-tailed) with 15 contiguous voxels was employed for the contrast, following the previous study (Gazzaley et al., 2007).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.brainres.2011.10.034.

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