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Research Report

False memory for face in short-term memory and neural activity in human amygdala

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ABSTRACT

Human memory is often inaccurate. Similar to words and figures, new faces are often recognized as seen or studied items in long- and short-term memory tests; however, the neural mechanisms underlying this false memory remain elusive. In a previous fMRI study using morphed faces and a standard false memory paradigm, we found that there was a U-shaped response curve of the amygdala to old, new, and lure items. This indicates that the amygdala is more active in response to items that are salient (hit and correct rejection) compared to items that are less salient (false alarm), in terms of memory retrieval. In the present fMRI study, we determined whether the false memory for faces occurs within the short-term memory range (a few seconds), and assessed which neural correlates are involved in veridical and illusory memories. Nineteen healthy participants were scanned by 3T MRI during a short-term memory task using morphed faces. The behavioral results indicated that the occurrence of false memories was within the short-term range. We found that the amygdala displayed a U-shaped response curve to memory items, similar to those observed in our previous study. These results suggest that the amygdala plays a common role in both long- and short-term false memory for faces. We made the following conclusions: First, the amygdala is involved in detecting the saliency of items, in addition to fear, and supports goal-oriented behavior by modulating memory. Second, amygdala activity and response time might be related with a subject's response criterion for similar faces.

1. Introduction

False memory is a phenomenon in which accurate memory formation is disturbed and a novel item is mistaken as a previously seen item in laboratory testing (Schacter and Slotnick, 2004). The processes involved in false memory occur during encoding, and during retrieval where the accuracy of a memory is being monitored (Roediger III et al., 2001).

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The occurrence of false memories was increased in a task developed by Roediger and McDermott (1995), based on earlier work by Deese (1959), called the Deese–Roediger/McDermott (DRM) paradigm. In the original DRM paradigm, subjects are presented with lists of associated words that are related by a critical but unpresented lure word. In a subsequent recognition test, the proportion of old responses to the lure item (recognizing the item as previously presented) was significantly higher than for unrelated and unstudied items. Numerous behavioral (Dodson et al., 2000; Roediger III, 1996; Schacter and Dodson, 2001) and neuroimaging (Abe et al., 2008; Cabeza et al., 2001; Garoff-Eaton et al., 2006, 2007; Gonsalves et al., 2004; Iidaka et al., 2012; Kim and Cabeza, 2007; Okado and Stark, 2003; Schacter et al., 1996, 1997; Slotnick and Schacter, 2004; Umeda et al., 2005) studies have investigated memory distortion by inducing a false memory for items in episodic and long-term memory domains.

False memory for stimuli other than words has been investigated using detailed colored pictures (Koutstaal and Schacter, 1997), photographs (Koutstaal et al., 1999), and faces (Jones et al., 2006; Jones and Bartlett, 2009; Reinitz et al., 1992), all of which are highly memorable items in healthy subjects. False alarm rates for face stimuli, in which familiar and novel faces are combined, are higher than rates for completely novel faces and lower than the hit rates of studied, more familiar faces (Jones et al., 2006; Jones and Bartlett, 2009; Reinitz et al., 1992). In a study using natural face photographs, a conjunction error rate (i.e., false alarms to items composed of studied items) was almost equal to the feature error rate (i.e., false alarms to items composed of half-studied and half-new components) (Jones et al., 2006). These results suggest that memory errors for combined faces are mainly based on familiarity processes in the absence of the precise recollection process used in episodic memory (Jones and Bartlett, 2009).

False memory effects have recently been reported in the short-term memory (STM) domain (Atkins and Reuter-Lorenz, 2008; Coane et al., 2007; Flegal et al., 2010). In these studies, subjects learn sets of several items for a memory test. Immediately after the presentation of a memory set, a probe item is presented and the subject is instructed to indicate whether the probe item was included in the preceding memory set. Prior studies have examined the effect of relatedness on STM by using lists of semantically related items, such as words. There was a significantly higher false-alarm rate for probe items that were semantically related to the preceding memory set (i.e., the lure item) than for those that were not (i.e., a new item). These results indicate that a false memory can occur within a few seconds and there may be a common cognitive process shared between long- and short-term illusory memories. One study investigated the neural correlates of false memory in STM by using functional magnetic resonance imaging (fMRI) and a paradigm with 4-word lists (Atkins and Reuter-Lorenz, 2011). The authors found that activation in the left mid-ventrolateral prefrontal cortex was associated with semantic interference from the preceding word list regarding the decision about the probe word. However, to date, no study has used fMRI and a false memory paradigm to investigate false memory for faces in the STM range.

Theoretical explanations for false memories have been largely related to long-term memory (LTM) because the length of study list items and retrieval tasks are typically longer than the STM range. A brief retention interval between encoding and retrieval associated with STM is expected to minimize false recognition (Flegal et al., 2010). Although a recent study showed that a false memory of words could be induced with both a short and long delay at a similar rate (Flegal et al., 2010), recent findings showed that the effect of encoding manipulation (e.g., depth of the processing procedure) could increase false recognition rates only at the LTM. This suggests that different processes may be operating in STM and LTM conditions (Flegal and Reuter-Lorenz, 2014). Therefore, it is particularly interesting to investigate whether the neural correlates involved in false memories for faces differ between the LTM and STM.

A previous study from our laboratory investigated the neuroanatomical substrates of false memories for faces in episodic and long-term memory domains (Iidaka et al., 2012). In that study, the authors applied a modified version of the DRM paradigm that used morphed pictures of faces to induce false memories in an fMRI environment. We found that activity in the amygdala was associated with the sense of familiarity of items despite the experiment involving no emotional facial features. In particular, false responses to items similar to previously seen (old) items evoked a middle-range level of activity in the amygdala; the activity was at a level between that evoked for correct responses to old and new items and that evoked for incorrect responses to old and new items. This indicates that amygdala activity during the processing of false memories falls between correct and incorrect responses to true items, and suggest a possible role for the amygdala in determining the relevance of items with respect to episodic or long-term memory.[1]

The purpose of the present study was to investigate whether false memories for faces in the STM domain could be induced by using the same set of morphed faces as those used in the LTM experiment (Iidaka et al., 2012), and examine which neural correlates were involved in the formation of such illusory memories within a few seconds. To do this, three morphed faces were shown side-by-side to healthy subjects as a memory set for 2.5 s. After an interval of 1.5 s, a probe face was presented for 2.0 s (Fig. 1). Subjects were instructed to memorize three faces in the memory set and make a judgment as quickly and accurately as possible as to whether the probe face had been shown in the previous memory trial (a modified delayed match-to-sample test). There were three different conditions for the probe face: an old face that was presented in the memory set (OLD condition); a lure face that was similar to a face in the memory set (LURE condition); or a new face that had not been presented previously and was not a face similar to the memory set (NEW condition).

There are limited capacities for maintaining objects in memory in the visual STM and working memory (WM)

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[1] In the present study, we used a term “lure” item only for a face picture that was similar to a previously presented item; however, in other memory studies, a new item is also referred to as a “lure” item.

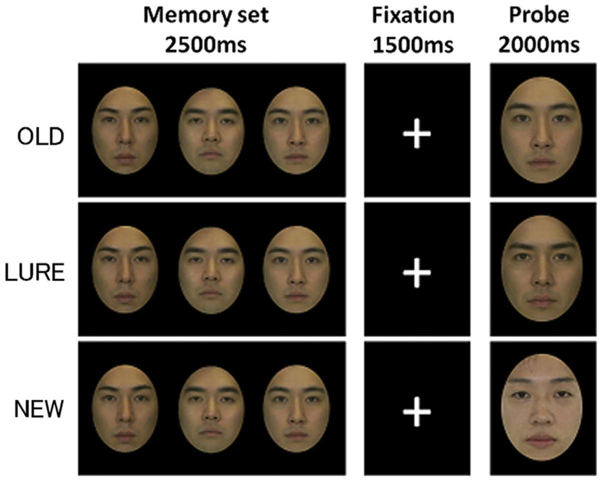

Fig. 1 – Examples of the experimental stimuli. Each memory trial consisted of sequential presentation of a memory set, fixation, and probe faces. The memory set is a combination of three different morphed faces of the same gender and age group. Subjects were instructed to memorize these faces for 2500 ms; no overt response was required. After the presentation of a fixation for 1500 ms, a probe face was presented for 2000 ms. There were three conditions for probe faces: OLD; LURE; and NEW. In the OLD condition, the probe face was a face from the previous memory set in the same trial. In the LURE condition, the probe face was similar to one of the faces in the memory set of the same trial. In the NEW condition, the probe face was a novel face that was not similar to the faces in the memory set. Subjects were instructed to make an old/new judgment as to whether the probe face had been shown in the memory set of the same trial, as quickly and accurately as possible. All faces depicted a neutral emotion. Face pictures shown in this figure are not those used in the present study due to copyright restrictions on the use of the photographs from the database.

domains. In a standard laboratory test, healthy participants are able to memorize three or four simple objects, but the number of objects held in memory could vary depending on the complexity of the stimuli (Luck and Vogel, 2013). Several studies have reported that visual STM capacity for upright faces is greater than for cars and watches and can reach approximately three items in healthy subjects (Curby and Gauthier, 2007; Curby et al., 2009). The superior capacity for upright faces compared with other categories of objects is possibly due to the importance of facial recognition in survival for humans. Theoretically, holistic processing of upright faces that enables us to capture several distinct features (e.g., eyes, eyebrows, nose, and mouth) as a whole would facilitate STM performance (Morgan et al., 2008). Based on these findings, we presented three face pictures simultaneously in the memory set that could be held in the STM domain.

The present study tested the following specific hypotheses. First, we speculated that a probe face that was similar to an old face (LURE condition) could induce a higher false-alarm rate than a new probe face (NEW condition), as shown in previous studies on short-term false memory for words (Atkins and Reuter-Lorenz, 2008; Coane et al., 2007; Flegal et al., 2010). Previous studies have shown that correct responses to lure items were significantly slower than correct responses to studied and unstudied items, indicating that additional processing time was required for the lure items due to high familiarity with these items (Atkins and Reuter-Lorenz, 2008; Coane et al., 2007). Therefore, in the present study, it was predicted that the responses to lure faces would be slower than for correct responses to old and new faces.

It has been proposed that recognition of unknown faces relies mostly on fast familiarity processing, whereas recognition of other types of stimuli (such as words) relies on slow recollection processing (Jones and Bartlett, 2009). Here, we refer to the term “familiarity” as a level of the subjective strength of a visual memory when a probe face was shown to the subject in the STM task. The definition in the present study might be different from other false memory experiments using a standard DRM paradigm where the presentation of list words activates a semantic network involving a critical word. The unfamiliar face pictures used in the present study do not have semantics; therefore, perceptual similarity between faces at encoding and retrieval would increase the occurrence of false memory. In particular, lure items that are shown at retrieval and have high perceptual similarity with an item shown at encoding should produce more “old” responses than a truly new item would. Therefore, we used a proportion of “old” responses for the probe face as an index of subjective “familiarity”. Thus, our second hypothesis was that the neural signature of memory familiarity, as indexed by old minus new responses in fMRI subtraction analysis (Spaniol et al., 2009), would parallel the proportion of old responses for the probe face.

Third, in the previous study using a modified DRM paradigm for morphed faces (Iidaka et al., 2012), we found that the activity in the amygdala showed a U-shaped response curve with regard to item and response conditions. These results suggest that the amygdala activity tracked the saliency (Phan et al., 2002) or relevance (Ousdal et al., 2008) of a stimulus, because both old and new correct conditions are salient and relevant to subjects in terms of mnemonic processing. It is noteworthy that amygdala activity in the false memory condition (that evoked ambiguous and combined feelings with regard to familiarity and novelty) fell between the two extremes. We speculated that this phenomenon would occur in the STM version of the false memory paradigm. If both amygdala activity and reaction time were related to the stimulus ambiguity and saliency, these two measurements would correlate with each other.

Fourth, the significant relationship between the false memory for faces and anterior cingulate cortex (ACC) activation observed in our previous study (Iidaka et al., 2012) indicates that the ACC is involved in handling increasing cognitive demands and reaction time differences when subjects are monitoring conflicts between competing representations (Barch et al., 2001; Carter and van Veen, 2007). A number of studies have shown a significant relationship between activity in the ACC and false memory for words (Garoff-Eaton et al., 2007; Kim and Cabeza, 2007; von Zerssen et al., 2001), shapes (Slotnick and Schacter, 2004), faces (Hofer et al., 2007), and pictures (Duarte et al., 2010; Okado and Stark, 2003).

In line with these findings, we also predicted that the medial prefrontal cortex, including the ACC, would be engaged in the false memory of lure items that have a perceptual resemblance to old items.

2. Results

2.1. *Behavioral data*

The mean proportion [+standard deviation (s.d.)] of old responses for OLD, LURE, and NEW conditions were 0.7 (0.14), 0.32 (0.11), and 0.15 (0.09), respectively (Fig. 2). A one-way repeated measures ANOVA with Greenhouse–Geisser correction showed a significant difference in the proportion of old responses between the conditions ($F(1.3, 23.5)=361$, $p<0.01$). Post-hoc *t*-tests with Bonferroni correction for multiple comparisons revealed that the proportion of old responses significantly differed between each condition ($p<0.01$ for all comparisons). The results that show the subjects made more old responses in the LURE condition than in the NEW condition indicates the occurrence of false memories in the short-term memory range.

RT data were analyzed with a two-way repeated measures ANOVA, which showed no significant main effect of condition ($F(2, 36)=0.75$, $p>0.05$) or response ($F(1, 18)=0.03$, $p>0.05$), but a significant interaction between condition and response ($F(2, 36)=51.7$, $p<0.01$). The interaction effect was most likely due to a significant difference in the mean RT between the old and new responses in both the OLD and NEW conditions ($p<0.01$ for both conditions, post-hoc paired *t*-test), but not in the LURE condition ($p>0.05$, post-hoc paired *t*-test). Subjects had a faster RT for correct responses (i.e., old response to OLD items and new response to NEW items) and a slower RT for incorrect responses (i.e., old responses to NEW items and new responses to OLD items). The RT in the LURE condition was between these two RTs. Therefore, mean RT formed an inverted U-shaped response curve with respect to the experimental condition (Fig. 3). There were significant differences in RT between the old responses to LURE items and old responses to OLD items, and between the new responses to the LURE items and new responses to NEW items ($p<0.01$ in both conditions).

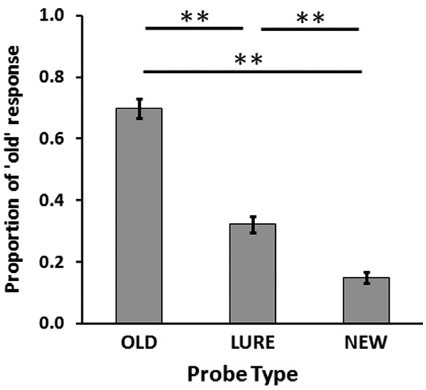

Fig. 2 – The mean (gray column)+s.d. (bar) proportion of old responses in each of the OLD, LURE, and NEW conditions are shown. An ANOVA revealed a significant difference in the proportion of old responses between the conditions ($p<0.01$). The results of the post-hoc test between the conditions with Bonferroni correction are indicated by a double asterisk ($p<0.01$). Subjects had a significantly higher old response rate in the LURE condition than in the NEW condition, indicating the occurrence of false memories in the short-term memory range.

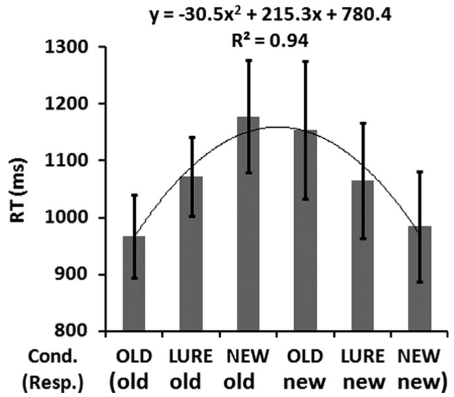

Fig. 3 – The mean (gray column)+S.E.M. (bar) RT are plotted for each of the six experimental conditions. They were sorted with respect to the probe item (OLD, LURE, and NEW) and response (old and new). The mean RT was fitted using the quadric polynomial function. The equation and R^2 value are shown in the figure. The function formed an inverted U-shaped response curve.

2.2. *fMRI data*

The contrast images pertaining to the differences in activation between old and new responses were used for the second-level group analysis. First, we hypothesized that the sense of familiarity, as indexed by the proportion of old responses in each item condition (OLD>LURE>NEW, see Fig. 2), would be associated with the neural correlates of familiarity, as measured by old minus new subtraction of the fMRI data. An ANOVA analysis in SPM8 using the three conditions as factors (contrast value: 1 for OLD; 0 for LURE; and -1 for NEW) was performed. There was a significant relationship between brain activity in the right amygdala and the familiarity; that is, the greatest activity was in the OLD condition, lowest activity in the NEW condition, and activity in the LURE condition was in between of these (Table 2; Fig. 4, top panel). The mean and standard error of the mean (S.E.M.) of parameter estimates extracted from the amygdala (representing the difference between old and new responses) are plotted in Fig. 4 (bottom panel). A region in the right intraparietal sulcus showed a pattern of activity similar to that of the amygdala with regard to the degree of familiarity. In particular, in the right amygdala, the difference in activation between the old and new responses was high for the OLD condition and low for the NEW condition; the difference in activation in the LURE condition was between those for the OLD and NEW conditions.

The degree of activation from the baseline fixation condition in all six experimental conditions was extracted from one-sample *t*-tests. This showed that the activity of the right

Table 1 – The mean reaction time data in each condition.

Condition	OLD		LURE		NEW	
Response	Old	New	Old	New	Old	New
RT (ms)	966	1154	1072	1064	1178	984
(s.d.)	(145)	(241)	(138)	(202)	(196)	(194)

Table 2 – Significant results in ANOVA model of fMRI analysis.

Region name	Hem.	Voxels	T value	p Value	x, y, z
Amygdala	Rt.	220	5.69	<0.001	24, 0, −18
Amygdala	Lt.	240	4.57	<0.001	−18, −6, −24
Intra parietal sulcus	Rt.	153	4.39	<0.001	40, −48, 56

Hem.: hemisphere; Rt./Lt.: right/left.
The statistical threshold was set at $p=0.001$, uncorrected and $k=50$ voxels.

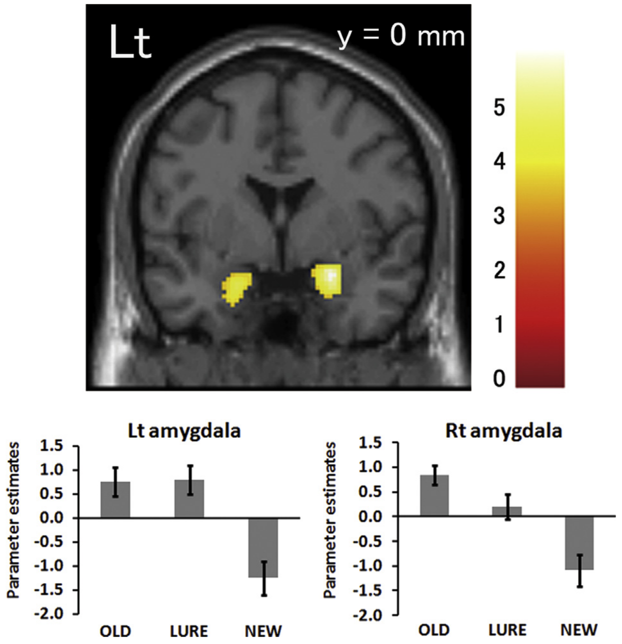

Fig. 4 – *Top*: A significant involvement of the bilateral amygdala in true and false memories for faces in the STM range is shown in the figure. The clusters are superimposed on the coronal section ($y=-0$ mm) of an SPM T1 standard brain. The statistical threshold was set at $p=0.001$, uncorrected for multiple comparisons, and $k=50$ voxels. Detailed information of the clusters is listed in Table 2. The color bar indicates the *T*-values. *Bottom*: The signal extracted from the left and right amygdala in the contrast of old versus new responses is plotted for each condition. The gray column and the bar indicate the mean and S.E.M., respectively. Note that the mean value represents the difference between old and new responses for each probe type.

amygdala formed a U-shaped response curve with regard to the experimental conditions. The degree of activation was high for correct responses (i.e., old response to OLD item and new response to NEW item), low for incorrect responses (i.e., old response to NEW item and new response to OLD item), and activation in the LURE condition was between these two (Fig. 5, right). A two-way repeated measures ANOVA was used to analyze the signal in right amygdala. There was no significant main effect of condition ($F(2, 36)=0.36$, $p>0.05$) or response ($F(1, 18)=0.02$, $p>0.05$), but there was a significant interaction ($F(2, 36)=13.4$, $p<0.01$). The interaction effect was most likely due to a significant difference in the right amygdala signal between the old and new responses in both the OLD and NEW conditions ($p<0.01$ in both conditions, post-hoc paired *t*-test), but not in the LURE condition ($p>0.05$, post-hoc paired *t*-test). The values in Fig. 6 were plotted to investigate the relationship between mean RT and amygdala activity across the experimental conditions. There was a significant negative correlation ($r=-0.93$, $p<0.01$) between mean right amygdala activity (x-axis) and mean RT (y-axis). The results indicate that shorter RTs show higher activity in the right amygdala for the probe faces. In the left amygdala, the correlation between the mean activity and mean RT was at the trend level ($r=-0.78$, $p<0.1$).

The ANOVA, including old minus new contrast for the OLD, LURE, and NEW conditions, revealed a significantly greater activation in three regions of the superior frontal gyrus (SFG, Table 3) for the LURE condition when compared with the OLD condition. In particular, a cluster of significant activation was in the medial part of the prefrontal cortex in a region similar to the activity in the ACC region reported in our previous study on facial false memory in the long-term memory domain (Iidaka et al., 2012). The correlation coefficients between activation in these clusters and differences in RT between old and new responses under the LURE condition were as follows: (1) x, y, z=8, 22, 60, $r=0.31$, $p=0.19$; (2) x, y, z=−6, 24, 46, $r=0.45$, $p=0.06$; (3) x, y, z=18, 62, 28, $r=0.17$, $p=0.48$.

3. Discussion

The present study demonstrates several major findings concerning the behavior and neuroanatomical substrates of short-term false memory for faces in normal human subjects.

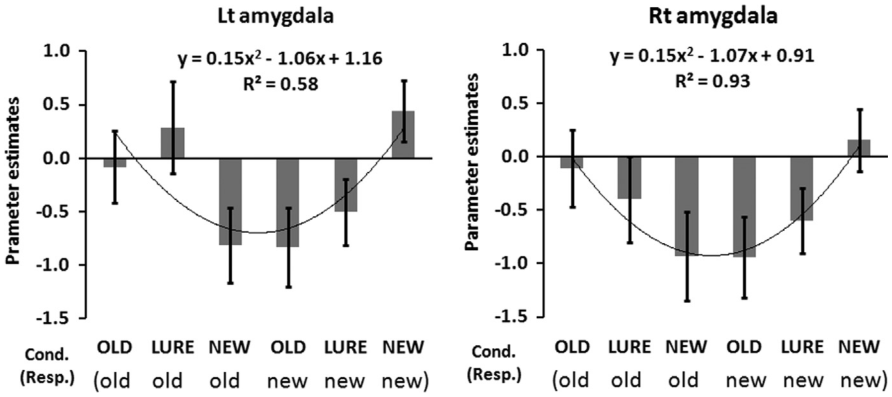

Fig. 5 – The mean (gray column)+S.E.M. (bar) of the left and right amygdala activity are plotted for each of the six experimental conditions. They were sorted with respect to the probe item (OLD, LURE, and NEW) and response (old and new). The mean amygdala activity was fitted using the quadric polynomial function. The equation and R^2 value are shown in the figure. The function formed a U-shaped response curve. Note that the mean value represents activation from the baseline fixation condition for each probe type (OLD, LURE, and NEW) and response (old and new).

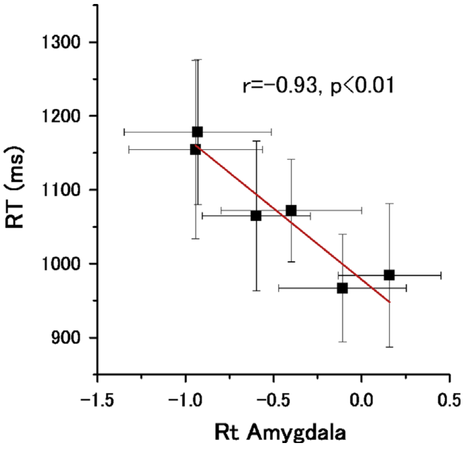

Fig. 6 – The mean (black square) right amygdala activity (*x*-axis) and RT (*y*-axis) for each of the six experimental conditions are plotted. The horizontal bars indicate the S.E.M. of the right amygdala activity for each condition, and the vertical bars indicate the S.E.M. of the RT for each condition. A regression line (shown in red), Pearson's correlation coefficient, and *p* value are shown in the figure. There was a significant negative correlation between the mean amygdala activity and mean RT across conditions.

First, our procedure using a modified delayed match-to-sample task successfully evoked false memories for faces in the fMRI environment. Although one fMRI study has focused on false memory for words (Atkins and Reuter-Lorenz, 2011), this is the first fMRI study to investigate false memory for faces in the STM range. The behavioral results of the present study clearly demonstrate that the proportion of old responses to the lure probe face was significantly higher than that of the new probe faces; these results confirm the occurrence of a false memory for the morphed faces within a few seconds.

Second, the RT analysis revealed that subjects' RTs were significantly slower for the lure probe faces in both correct and incorrect responses than for the correct responses to both the old and new faces. This matches the results of previous studies showing that false-alarm rates for lure items were longer than for hits of old items and correct rejections of lure items took longer than correct rejections of new items (Atkins and Reuter-Lorenz, 2008; Coane et al., 2007). Even when subjects judged a lure face as an old face, indicating that it was indistinguishable from a true memory in terms of accuracy level, there was still a significant difference in the RT level. This also holds true for correct rejections of lure and new items. The additional processing time that is required for memory judgments of lure items compared with the old and new items may suggest that the perceptual similarity of the lure item makes it more difficult to judge than an item that had not been active in STM as discussed in a study of semantic false memory (Atkins and Reuter-Lorenz, 2008).

In a theoretical framework designed from false memory experiments that used a standard DRM paradigm, activation/monitoring theory suggests that during encoding of list items, participants automatically activate the related information of the items through inferential processes, and during retrieval they actively monitor the familiarity of items (Roediger III et al., 2001). The time required to reject related lures is increased because correct rejection of these items requires a control process that resolves interference that is induced by the semantic familiarity of these items (Atkins and Reuter-Lorenz, 2011). If an item that was related to but not included in the memory list has been activated during encoding, presentation of such an item increases the occurrence of false memories during retrieval. However, the present results showing slower RTs for false alarms to the lure faces are not necessarily consistent with this view because there should be no semantic network activated during encoding; rather, perceptual similarity of lure faces with the old faces required extensive monitoring from the subject when compared with unrelated items during retrieval.

The third, and most important finding, is that activity in the right amygdala was significantly associated with a sense of familiarity to the probe faces across conditions. Specifically, activity levels in the right amygdala were greatest when subjects' responses were correct, lowest when responses

Table 3 – Significant results in ANOVA model of fMRI analysis.

Region name (BA)	Hem.	Voxels	T value	*p* Value	x, y, z
LURE versus OLD					
Superior frontal gyrus (6)	Rt.	64	4.18	0.001	8, 22, 60
Superior frontal gyrus (8)	Lt.	283	4.12	0.001	−6, 24, 46
Superior frontal gyrus (10)	Rt.	91	4.05	0.001	18, 62, 28

Hem.: hemisphere; Rt./Lt.: right/left; BA: Brodmann area.
The statistical threshold was set at $p=0.001$, uncorrected and $k=50$ voxels.

were incorrect, and between the highest and lowest when LURE items were presented. These findings replicate the results of our previous study that used the DRM paradigm and the same set of morphed faces in episodic and long-term memory domains (Iidaka et al., 2012), and likely to be due to the critical role the amygdala plays in detecting the saliency (Phan et al., 2002) and relevance (Ousdal et al., 2008) of a stimulus. The old and new correct conditions are salient and relevant to the subjects in terms of mnemonic processing within the STM (the former involves familiarity and the latter novelty); therefore, the level of amygdala activity in the experimentally induced false-memory condition fell between these two extremes. The results of the repeated measures ANOVA also showed that the right amygdala successfully discriminated between the old and new responses for both OLD and NEW conditions, but not for the LURE condition. This indicates that activation of the right amygdala could differentiate between correct and incorrect memories for items other than lure items. The negative amygdala activity, below the baseline activity, in the present study is most likely because the present study used an STM task and baseline activity was continuously elevated throughout the experiment.

Predominant involvement of the amygdala in the detection of stimulus saliency has been previously reported in studies that used tasks relating to other domains of mental processing. Several reviews have shown that the human amygdala is activated in response to both positive and negative emotional stimuli (Costafreda et al., 2008; Fusar-Poli et al., 2009; Phan et al., 2002; Wager et al., 2003); similar patterns have also been observed in the primate amygdala (Paton et al., 2006). In other studies using fMRI and an evaluation task of face trustworthiness, both extremely trustworthy and untrustworthy faces elicited significant activation in the amygdala (Said et al., 2009; Todorov, 2008; Todorov et al., 2011). Furthermore, amygdala activation is elicited by a threatening avoidance cue, in addition to a rewarding cue, that predicts monetary loss or gain (Schlund and Cataldo, 2010). These results indicate that amygdala function is mostly subjective and dependent on each person's contextual interpretation of a stimulus rather than a common view that it tracks emotional arousal – in particular, specialization for processing fear, threats, or other emotionally negative stimuli. Therefore, it is believed that the amygdala plays a role in detecting features of salient stimuli in several areas of human emotion and cognition that stress the contextual and goal-dependent value of a stimulus (Adolphs, 2010).

The recently developed motivation salience hypothesis proposes that the amygdala is sensitive not only to threat detection but also to motivational relevance (Cunningham et al., 2010). In this hypothesis, a primary function of the amygdala is to indicate what is important in any particular situation and then modulate the necessary and appropriate perceptual, attentional, autonomic, and cognitive processes (Cunningham et al., 2011). The authors of an fMRI study that adopts this hypothesis investigated amygdala activity in response to the names of famous people and found that amygdala activity showed a U-shaped response in terms of the stimulus valence, similar to the response curve observed in the present study (Cunningham et al., 2008). These notions fit with the results of the present study showing that the most relevant conditions (i.e., old responses to an old probe face and new responses to a new probe face) had high amygdala activity because these responses were highly discriminable for the subjects. The new responses to old probes and old responses to new probes, both of which had low amygdala activity, would be the least relevant in terms of familiarity because the subjects failed to recognize the items, even with a short delay. Similar response patterns observed in the right intraparietal sulcus (Table 2), which is associated with attention to salient stimuli (Mesulam, 1999), may support the present results.

An alternative explanation for the characteristic responses of the right amygdala would be related to the signal detection theory (Snodgrass and Corwin, 1988). For example, if we assume that the familiarity of three types of probe faces is normally distributed, it is likely that the distributions would overlap in the order of OLD>LURE>NEW. It would also be predicted that a subject's response criterion for his/her memory of a probe face would reside somewhere within the distribution of the LURE faces. Within the three distributions, the old response to the OLD face and the new response to the NEW face is the farthest from the subject's criterion. In contrast, the old response to the NEW face and the new response to the OLD face would be the closest to the criterion. This means that old and new responses to the LURE face would fall between the two distributions. With regards to the distance from the subject's response criterion, this alignment mimics the amygdala activity that was shown in the present study. It is also likely that the response furthest from the criterion would be the fastest, while the response closest to the criterion would be the slowest, and this was also shown in the present study.

Fourth, there was a significant negative relationship between the mean RT and mean amygdala activity across the six experimental conditions, indicating that shorter RTs are associated with stronger amygdala activity. This result is predictable because both the RTs and amygdala activity followed an inverted U-shaped curve (Figs. 3 and 5, respectively) when they were plotted as functions of the conditions. The mean RTs for hits on old probe faces and correct rejections of new probe faces were shorter than for lure probe faces. These results indicate that the stimulus saliency of old and new probe faces caused these differences when they were correctly recognized as old and new, respectively. Amygdala activity is also believed to track stimulus saliency, as discussed in the previous section; therefore, the negative correlation between the two measurements is most likely a reflection of the saliency of the probe face in terms of STM, conferred by the encoding and retrieval of face stimuli.

Fifth, we observed significant involvement of the medial frontal cortices in the LURE condition. In particular, the peak voxel in the SFG (x, y, $z=-6$, 24, 46) found in the present study was close to a cluster in the ACC (peak voxel at x, y, $z=4$, 14, 34) that was found in our previous study on false memory for faces in the long-term memory domain (Iidaka et al., 2012). In the previous study, the ACC appeared to engage in the false recognition of LURE items that had a perceptual resemblance to the OLD items. It has been proposed that these results occurred because the DRM paradigm and morphed faces caused a response conflict between the items. Several reviews in the literature have shown that the medial prefrontal cortex (including the ACC) is involved in handling increasing cognitive demands and RT differences when subjects are monitoring conflicts between competing representations (Barch et al., 2001; Carter and van Veen, 2007). Greater cingulate cortex activity associated with memory paradigms has been reported in fMRI studies that evoked a tip-of-tongue state in subjects (Maril et al., 2001) and that investigated the neural correlates of retrieval-related forgetting (Kuhl et al., 2007), both of which induce response conflict in the subjects. There was no significant relationship between the medial prefrontal activity in the false memory for faces and the difference in RT for LURE items in the present study; however, the positive correlation was nearly significant ($r=0.45$, $p=0.06$) in the medial SFG (shown in Fig. 7). This finding partially replicates the significant correlation between ACC activity and RT difference under the LURE condition in the previous study (Iidaka et al., 2012).

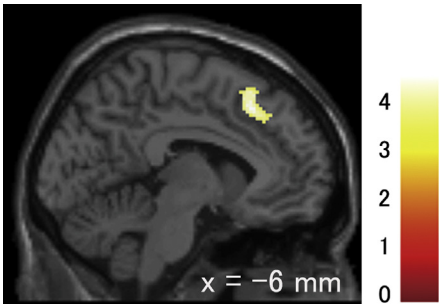

Fig. 7 – Significant involvement of the medial superior frontal gyrus (x, y, $z=-6$, 24, 46) in the false memory for faces in short-term memory is shown. The clusters are superimposed on the coronal section ($y=-6$ mm) of an SPM T1 standard brain. The statistical threshold was set at $p=0.001$, uncorrected for multiple comparisons, and $k=50$ voxels. Detailed information of the cluster is listed in Table 3. The color bar indicates T-values.

4. Conclusion

The present study showed that false memory for faces could be experimentally induced in the STM domain by using morphed face stimuli in an fMRI environment. There was a significant, but partial, involvement of the amygdala in the illusory retrieval of faces within a few seconds after encoding the faces. The response of the right amygdala in the STM domain showed a remarkable similarity with the response observed in episodic and long-term memory retrieval, indicating that long- and short-term memory for faces share common neural mechanisms with regard to amygdala activity. The neural substrates for face memory on the continuum from correct responses to incorrect responses, with the illusory memory condition in between, relate to the notion that the amygdala tracks stimulus saliency and relevance. The amygdala is involved in detecting saliency in relation to the motivation of current goals and in modulating the processing of long- and short-term memory for faces. Alternatively, amygdala activation, as well as the RT, could be associated with the distance between memory judgment and a subject's response criterion for probe faces.

5. Experimental procedures

5.1. *Subjects*

Participants were 19 right-handed healthy subjects (9 men, 10 women; mean age=19.9 years, s.d.=1.7 years) with normal or corrected-to-normal vision. Written informed consent was obtained from each participant prior to the experiment. The study was approved by the ethics committee of the National Institute for Physiological Sciences and the Nagoya University School of Medicine.

5.2. *Stimuli*

A set of morphed faces used in the previous fMRI study (Iidaka et al., 2012) served as experimental stimuli in the present study. In short, these faces were created by morphing two different individuals' faces of the same gender and age using computer software. The faces depicted a neutral emotion. The set of morphed faces contained four similar faces for each facial image. The manipulation of facial similarity was validated by a pilot study that used a different group of subjects from those who had participated in the fMRI experiment. The total number of morphed faces used in the present study was 289. The detailed method used to create the stimuli is described in our previous study (Iidaka et al., 2012).

In the memory set (Fig. 1), three different faces were presented side-by-side on the screen. These faces were selected from the same gender and age group among the morphed faces. We created 30 memory sets with only male faces and 30 memory sets with only female faces, resulting in

60 memory sets. Each memory set was presented three times through the two scan sessions, but only once for each of the OLD, LURE, and NEW conditions. Gender and age groups were counterbalanced across the two scan sessions. In the OLD condition trials, one of the three faces shown in the memory set also served as the probe face. The probe face was randomly chosen from the left, middle, or right position of the memory set. In the LURE condition trials, the probe face had a similar appearance as one of the three faces, but had not previously been shown in the memory set of the same trial. In the NEW condition trials, the probe face was a novel face that had not been shown in the memory set of the same trial and was not similar in appearance to any of the three faces of the memory set, but belonged to the same gender and age group as the memory set.

Each probe face was unique in each trial throughout the two scan sessions, with the exception of some of the faces in the LURE and NEW conditions. Some probe faces were used two or three times during the experiment due to the limited number of face photos available in the set of morphed faces, but shown only once in each scan session as much as possible. Prior to the scan, the participants were instructed to attend to the faces in each trial, but not to try to remember faces shown in earlier trials as there was no memory test after the scan. This was to reduce the chance that multiple presentations of the same faces during the two sessions affected the occurrence of false memory. This manipulation resulted in the presentation of 289 faces in the memory set and/or as a probe face throughout the experiment.[2]

5.3. *Experimental procedure*

During the experiment, subjects performed a delayed match-to-sample task for faces (see Fig. 1). One trial consisted of the sequential presentation of a memory set (duration, 2500 ms), fixation (1500 ms), and probe face (2000 ms). The interval between each memory trial was jittered between 2500 ms and 4500 ms, with a mean of 3500 ms. The fixation was shown during the inter-trial interval. Thirty OLD, 30 LURE, and 30 NEW memory trials were randomly presented to the subject during one scan session. The scan session was repeated using a different set of stimuli after this. Thus, the full experiment comprised of 60 OLD, 60 LURE, and 60 NEW trials. Subjects were instructed to memorize the three faces in the memory set and make a judgment as quickly and accurately as possible as to whether the probe face had been shown in the previous memory trial. Responses were made using the subject's right index and middle fingers. No overt response was required for the memory set.

Subjects' responses were measured using an MRI-compatible response box held in their right hand. The proportion of old responses was entered into a repeated measures one-way ANOVA with condition (OLD, LURE, and NEW) as a factor (Bonferroni correction for multiple comparisons was applied at the threshold of $p=0.05$). The mean (+s.d.) proportion of old responses are plotted in Fig. 2. Reaction time (RT) was entered into a repeated measures two-way ANOVA with condition (OLD, LURE, and NEW) and response (old and new) as factors (significance was set at $p=0.05$). A post-hoc *t*-test was conducted between the old and new responses separately for each condition. The mean (+s.d.) RT for each condition is listed in Table 1. Mean RT was plotted as a function of the experimental condition and curve-fitted by using a quadric polynomial function (Fig. 3). Post-hoc *t*-tests of the RT between the six conditions were conducted (significance was set at $p=0.05$).

5.4. *fMRI acquisition and preprocessing*

Functional images of the brain were obtained during the two sessions in an axial-oblique position by using a 3-T MRI scanner (Allegra, Siemens, Erlangen, Germany) equipped with single-shot echo planar imaging (EPI; TR=2.3 s, TE=30 ms, flip angle=80°, 64 × 64 matrix, 36 slices, voxel size=3 mm × 3 mm × 3 mm) sensitive to blood oxygen level-dependent (BOLD) contrast. Three hundred and ninety eight (all sessions and subjects) images were obtained in each session. After discarding the first 4 images, successive images were subjected to analysis. A high-resolution anatomical T1-weighted image was also acquired (MPRAGE; TR=2.5 s, TE=4.38 ms, flip angle=8°, 256 × 256 matrix, 192 slices, voxel size=0.75 mm × 0.75 mm × 1 mm) for each subject. The data were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK). First, the signal in each slice was temporally realigned to the middle slice using sinc interpolation and all volumes were spatially realigned to the mean volume. The resliced volumes were then normalized to standard Montreal Neurological Institute (MNI) space using a transformation matrix obtained from the normalization process of the mean EPI image of each subject to the EPI template image. The normalized images were spatially smoothed using an 8 mm Gaussian kernel.

5.5. *First-level analysis*

After preprocessing, statistical analysis of the data obtained for each subject was conducted using the general linear model. At the first level (a fixed-effects model), each event was modeled as a hemodynamic response function. High-pass-frequency filters (128 s) were applied to the time-series data. An autoregressive AR(1) model was used to estimate the temporal autocorrelation. The images were scaled to a grand mean of 100 overall voxels and scans within a session. In the present study, we explored the difference in neural response to the probe face because veridical and illusory memories were evoked by judgment of the probe face. The following conditions for the probe face were separately modeled as regressors: (1) old response to OLD item; (2) new response to OLD item; (3) old response to LURE item; (4) new response

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[2] One probe face for the NEW condition and three probe faces for the LURE condition also served as probe faces in different trials for the NEW and LURE conditions, respectively. Each of the seven probe faces for the NEW condition were also used in two different trials throughout the two scan sessions, once in the memory set for each of the OLD and LURE conditions. In addition, each of seven probe faces for the NEW condition were used in the memory set of a different trial for the NEW condition, but not in the memory sets for the OLD and LURE conditions, due to a replacement of some faces in memory sets for the NEW condition.

to LURE item; (5) old response to NEW item; and (6) new response to NEW item. In addition, one regressor for the onset of the memory set and six regressors for movement parameters obtained during the realignment were entered in the design matrix.

The parameter estimates for each condition and for the differences between the conditions were computed from the least mean square fit of the model to the time-series data. Images of the parameter estimates representing event-related activity at each voxel were created for each condition and subject. In particular, we used the contrast between the old and new responses for each condition (i.e., OLD, LURE, and NEW) in the main analysis because the activity indicated by these contrast images reflects the neural correlates of familiarity in memory items (Schacter and Slotnick, 2004; Spaniol et al., 2009).

5.6. *Second-level analysis*

At the second level, the contrast images of each subject were entered into a group analysis (a random-effects model). The contrast images pertaining to the differences in activation between old and new responses were used for the group analysis. First, we hypothesized that the sense of familiarity, as indexed by the proportion of old responses in each item condition (OLD > LURE > NEW, see Fig. 2), would be associated with the neural correlates of familiarity as measured by the old minus new subtraction of the fMRI data. To test this, we performed an ANOVA analysis in SPM8 by using the three conditions (OLD, LURE, and NEW) as factors and the degree of familiarity as a contrast (contrast value: 1 for OLD; 0 for LURE; and -1 for NEW). A significant positive relationship between activity and these values was investigated; that is, brain regions where the activity was the greatest for the OLD condition, the lowest for the NEW condition, and between the two conditions for the LURE condition were determined. Significance was set at $p=0.001$, uncorrected for multiple comparisons, and $k=50$ voxels. The results are listed in Table 2. The significant result with respect to the amygdala is shown in Fig. 4 (top panel). In addition, to measure neural activity from the baseline fixation condition in each of the six experimental conditions (i.e., old response to OLD item, old response to LURE item, old response to NEW item, new response to OLD item, new response to LURE item, and new response to NEW item), separate one-sample *t*-tests were conducted for these analyses.

A signal was extracted from the significant cluster in the amygdala (10 mm spherical VOI at x, y, $z=24$, 0, -18; -18, -6, -24), as identified by the ANOVA investigating the relationship between neural activity and degree of familiarity. A principal eigenvariate of parameter estimates in a given volume of interest (VOI) was computed using a function implemented in SPM8. The mean (±S.E.M.) of the value associated with old minus new subtraction across subjects and for each item type were plotted (Fig. 4, bottom panel). Furthermore, to explore the relationship between the amygdala activity and experimental condition, activation from the baseline fixation condition was extracted from the separate one-sample *t*-tests for each of the six conditions (10 mm spherical VOI at x, y, $z=24$, 0, -18; -18, -6, -24) by using a VOI function in SPM8. The mean value was plotted as a function of the experimental condition and curve-fitted by using a quadric polynomial function (Fig. 5).

The right amygdala signal for each of the six conditions was entered into a repeated measures two-way ANOVA with condition (OLD, LURE, and NEW) and response (old and new) as factors (significance was set at $p=0.05$). Post-hoc *t*-tests of the amygdala signal between the six conditions were conducted. Furthermore, to investigate the relationship between neural activity and response time, the mean (+S.E.M.) right amygdala activity (data shown in Fig. 5) and RT (data shown in Fig. 3) are plotted in Fig. 6. The Pearson's correlation coefficient between mean RT and mean amygdala activity was computed (significance was set at $p=0.05$).

To investigate the brain region involved in processing false memories for faces, the LURE condition was contrasted with the OLD condition using an ANOVA model in SPM8. The contrast images pertaining to the subtraction between old and new responses for OLD and LURE items were used for the analysis. The statistical threshold was set at $p=0.001$, uncorrected for multiple comparisons, and $k=50$ voxels. The results are listed in Table 3; the significant cluster in the superior frontal gyrus (SFG) is shown in Fig. 7. To explore the relationship between activation and RT, the signal was extracted from the clusters listed in Table 3 (10 mm spherical VOI at x, y, $z=8$, 22, 60; -6, 24, 46; 18, 62, 28). A principal eigenvariate of parameter estimates in a given VOI was computed using a function implemented in SPM8. The Pearson's correlation coefficient between activity (old minus new contrast) and the RT (old minus new in the LURE condition) was computed (statistical threshold was set at $p=0.05$).

Conflict of interest

There is no conflict of interest.

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