Remembering the specific visual details of presented objects: Neuroimaging evidence for effects of emotion

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Abstract

Memories can be retrieved with varied amounts of visual detail, and the emotional content of information can influence the likelihood that visual detail is remembered. In the present fMRI experiment (conducted with 19 adults scanned using a 3 T magnet), we examined the neural processes that correspond with recognition of the visual details of negative and neutral items. Results revealed that a region of the left fusiform gyrus corresponded with retrieval of visual details for both negative and neutral items. Activity in the amygdala and orbitofrontal cortex, in contrast, was related to retrieval of visual details only for negative items. Activity in these regions corresponded only with successful recognition, and not with false recognition, providing strong evidence that limbic engagement during retrieval does not correspond merely with a person's belief that detail has been recognized. Rather, limbic engagement appears to relate specifically to the successful recognition of information.
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1. Introduction

Memories can be retrieved with varying amounts of visual information. Some memories include precise visual details, whereas others lack visual specificity. There have been extensive discussions about whether emotional memories are remembered with more visual detail than non-emotional ones (Adolphs, Denburg, & Tranel, 2001; Kensinger, Garoff-Eaton, & Schacter, 2006), and if so, what retrieval processes correspond with emotion's influence on the visual specificity of memory. The extant neuroimaging data have suggested that emotional items can be associated with less visual activity at retrieval than neutral items (Dolcos, LaBar, & Cabeza, 2005; Sharot, Delgado, & Phelps, 2004; but see Fenker, Schott, Richardson-Klavehn, Heinze, & Duzel, 2005), and these findings have been taken as evidence that emotional memories do not contain the same perceptual detail as non-emotional memories (Sharot et al., 2004). How-

ever, because these prior neuroimaging studies assessed only participants' subjective beliefs about the vividness of their memories, they could not directly relate emotion's modulation of visual activity to the retrieval of visual detail.

In the present study, participants distinguished "same" items (identical to previously seen objects) from "similar" (same verbal label as previously seen objects, but different visual details) and "new" (unrelated) items. This design allowed assessment of three questions relating to the link between visual activity at retrieval and the visual specificity of memories. The first question was whether amygdala engagement during retrieval would correspond with the retrieval of visual detail. It is unclear whether retrieval-related amygdala activity biases a person to believe information is remembered vividly (Sharot et al., 2004) or corresponds with retrieval of episodic detail (Kensinger & Schacter, 2005b; Smith, Stephan, Rugg, & Dolan, 2006). The most direct way to examine this issue is to compare veridical recognition with false recognition. The present study examined whether amygdala activity would correspond with accurate retrieval of detail (i.e., would be greatest when *same* items were correctly labeled "same," of intermediate strength when *same* items were labeled "similar," and lowest when *same* items were labeled "new") but not with false endorsements (i.e., "same" or

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"similar" responses to *new* items) or whether limbic engagement would be equally high whenever a person believed they recognized an item, regardless of the accuracy of that belief.

Two additional questions were whether there would be greater activity in visual-processing regions when items were retrieved with accurate visual detail rather than only with non-specific information, and whether the emotional content of the items would influence the magnitude of this retrieval-related visual processing. Although items remembered with visual specificity are associated with greater activity in the right fusiform gyrus during *encoding* (Garoff, Slotnick, & Schacter, 2005), and negative items show enhanced *encoding*-related recruitment of right fusiform regions (Kensinger, Garoff-Eaton, & Schacter, in press), as mentioned above, it was not clear whether these findings would extend to retrieval. Although recapitulation within the same sensory regions engaged during encoding often serves to enhance the perceptual specificity of a memory (Wheeler, Petersen, & Buckner, 2000), it is possible that visually specific memories could occur in the absence of the re-engagement of the fusiform processes known to be recruited during the encoding of visual details.

2. Method

2.1. Participants

Participants comprised 19 adults (10 women, 9 men), ages 18–30 (mean age of 22.2 years). All participants had normal or corrected to normal vision, and all were screened to exclude those with any contra-indicators for MRI scanning, or with any history of neurological trauma or psychiatric disorder. No participant reported taking any medications that affected the central nervous system. Informed consent was obtained from all participants in a method approved by the Harvard University and Massachusetts General Hospital Institutional Review Boards.

2.2. Materials and methods

Materials comprised 386 pairs of colored, nameable photo objects (Hemera Technologies Inc., 2002, Canada), taken from those used in Kensinger et al.

(2006). The photo objects were sized to 300 pixels in their largest dimension. Pairs of objects were selected so that the two items of a pair shared the same verbal label (e.g., both tomatoes) but differed in other perceptual features such as color, shape, size or orientation. Object pairs were selected so that half were negative and arousing, and half were neutral and non-arousing. Pairs also were selected to assure that the negative and neutral item pairs were matched for the overall similarity of the two items, the dimensions (color, size, shape and orientation) that differed between the two items, and the familiarity of the items (see Kensinger et al., 2006 for more details on the valence and arousal ratings procedures, and on the procedures for judging pair similarity).

2.2.1. Study procedure

About 1 h prior to the fMRI scan, participants were presented with 304 nameable, colored objects (half negative arousing, half neutral). Each item was presented for 1 s. Participants made a size decision about whether each object, in the real world, would fit inside of a filing cabinet drawer. Participants were asked to make their decision as quickly as possible. There were no reaction time differences in the time it took participants to make the decision for the negative and neutral objects.

2.2.2. Test procedure

Participants were scanned during a surprise recognition test. Debriefing indicated that no participant was aware that his or her memory would be tested while inside of the scanner. Participants had been instructed during the study phase that they would be asked to perform a "related task" during the fMRI scan, and most participants assumed that the task would require similar ratings about the objects.

On the recognition task, participants were presented with 456 objects: 152 objects (76 negative, 76 neutral) were identical to those that had been studied (*same* objects), 152 objects (76 negative, 76 neutral) shared the same verbal label as a studied item but differed in color, size, shape or orientation (*similar* objects) and 152 objects were *new* (76 negative, 76 neutral). These items were divided across four different lists, with each list associated with a separate functional scan. Items were presented for 3 s, with a jittered interstimulus interval ranging from 3 to 12 s. A fixation cross (+) was shown during this interval (Fig. 1).

For each object presented on the recognition memory task, participants were asked to indicate whether the item was "new" (never studied), was "similar" to a studied item (i.e., was an object that shared the same verbal label but that differed in visual features from the studied object), or was the "same" as a studied item (i.e., was the identical photo of the object). The member of the object pair that was included on the recognition task was held constant for all participants. The condition of each object (i.e., whether it was *same*, *similar* or *new*) was manipulated by counterbalancing between participants the items presented at study.
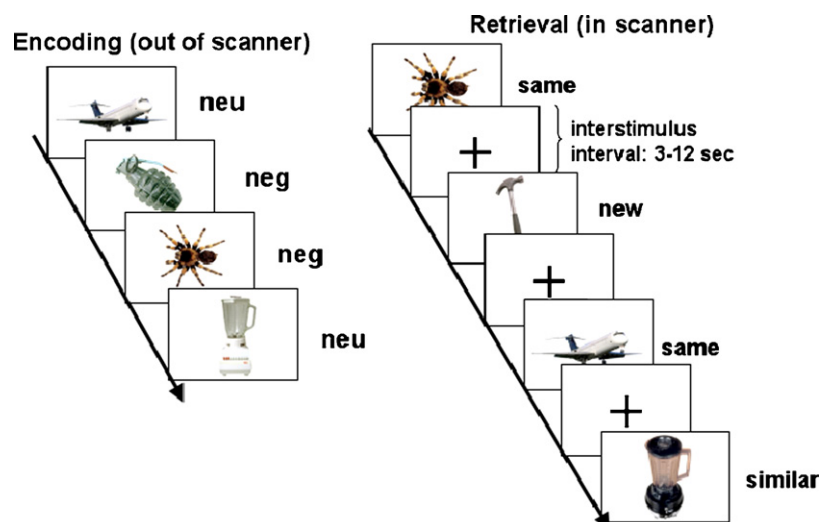

Fig. 1. *Task methods*: During encoding, participants viewed negative and neutral objects and decided whether each would fit inside of a drawer. During retrieval, participants decided whether objects were the same as a studied object, were similar to a studied object, or were new.

The neuroimaging analyses focus on participants' responses to *same* or *new* item exemplars. A "same" response to a *same* item signifies memory for the visual details of a studied item (referred to here as *visually specific recognition*); a "similar" response indicates memory for the general type of item but not for its exact visual details (referred to here as *non-specific recognition*); and a "new" response reflects complete forgetting of the item's presentation. Taken together, a "same" or a "similar" response to a *same* item indicates memory for at least the general features of an item (referred to here as *overall recognition*). A "same" or "similar" response to a *new* item signifies false retrieval of either specific visual details (in the case of a "same" response) or of non-specific information (in the case of a "similar" response), whereas a "new" response to a *new* item signifies a correct rejection of a *new* exemplar.

Responses to items tested as *similar* exemplars are more difficult to interpret. For example, a "similar" response to a *similar* exemplar could reflect memory for specific visual details (e.g., a participant could remember the details of the studied tomato and thus know that the tested exemplar was similar rather than same); however, a "similar" response also could reflect memory for only the general item type (e.g., a participant could remember that a tomato was studied but, having no memory for its visual details, indicate that the tested tomato was "similar" to the studied one). A "new" response is also ambiguous: it could signify that the studied item was forgotten, but it also is possible that a "new" response could be given despite memory for the studied item, if the participant did not apply the same verbal label to the two objects. Because of these ambiguities, responses to *similar* exemplars will not be considered further; *similar* exemplars were included on the recognition task with equal frequency to the *same* and *new* items in order to avoid biasing participants' responses to the other exemplar types.

2.2.3. Image acquisition and data analysis

Images were acquired on a 3 T Siemens Allegra MRI scanner. Detailed anatomic data were acquired using a multiplanar rapidly acquired gradient echo (MP-RAGE) sequence. Functional images were acquired using a $T2^*$-weighted echo planar imaging (EPI) sequence (TR = 3000 ms, TE = 30 ms, FOV = 200 mm; flip angle = 90°). Twenty-eight axial-oblique slices (3.2 mm thickness, .6 mm skip between slices), aligned along the anterior commissure/posterior commissure line, were acquired in an interleaved fashion.

All pre-processing and data analysis were conducted within SPM2 (Wellcome Department of Cognitive Neurology). Standard pre-processing was performed on the functional data, including slice-timing correction, rigid body motion correction, normalization to the Montreal Neurological Institute template (re-sampling at 3 mm cubic voxels), and spatial smoothing (using an 8-mm full-width half maximum isotropic Gaussian kernel).

For each participant, and on a voxel-by-voxel basis, an event-related analysis was conducted; all instances of a particular event type were modeled through convolution with a canonical hemodynamic response function. All participants had at least 10 instances of every modeled event type.[1] These data were then entered into second-order, random-effects analyses, contrasting activation as a function of retrieval response (e.g., "same," "similar," "new"), emotion type (negative arousing or neutral), and type of exemplar (*same* or *new*).

Conjunction analyses (using the masking function in SPM2) were then used to examine what regions showed activation across two or more contrasts (e.g., for "same" > "similar" responses to *same* negative items and also for "same" > "similar" responses to *same* neutral items), with both contrasts thresholded with a *p*-value of .01 (leading to a joint probability of .001, using Fisher's estimate; Fisher, 1950) and a five-voxel extent. For these conjunction analyses, coordinates refer to clusters localized in the contrast listed first (e.g., for "same" > "similar" responses to *same* negative items). Interaction analyses were performed to reveal the regions that showed a correspondence to retrieval for one emotion type but not for the other (e.g., corresponded with visually specific recognition of negative items but not of neutral items). All regions revealed in these interaction analyses showed a significant (*p* < .005, five-voxel extent)

relation to retrieval of one emotion type and a non-significant (*p* > .05) relation to retrieval of the other emotion type. All activations are presented in neurological coordinates (i.e., activity on the right-hemisphere is presented on the right side of the brain images) and are shown on the SPM canonical brain. Voxel coordinates were converted to Talairach space (Talairach & Tournoux, 1998) using the Talairach Daemon Client version 2.0 (The Research Imaging Center, UTHSCSA). Reported coordinates identify the voxel with peak activity within the cluster of activation.

Event-related time-courses were extracted from active clusters by creating regions-of-interest (ROI), including all significant voxels within an 8 mm radius of each chosen maximum voxel, using the Marsbar toolbox implemented in SPM (Brett, Anton, Valabregue, & Poline, 2002). Within each of these ROIs, a hemodynamic response function was calculated for each individual subject and for each condition type (relative to fixation baseline) as a function of peristimulus time (0–21 s). Statistics were performed on the peak of the signal change within peristimulus times 3–9 s. These signal change values are displayed in the figures. Analysis of variance (ANOVA) was performed on these extracted signal change values with response type ("same", "similar," "new"), exemplar type (*same*, *new*) and emotion type (negative, neutral) as factors.

3. Results

Below, we report the results of participants' behavioral performance on the task, and the results of the neuroimaging analyses. Behavioral and neuroimaging data were analyzed with participants' sex as a factor. The qualitative nature of the results were not influenced by participants' sex, and so all reported results combine data from men and women.

3.1. Behavioral results

Consistent with a prior behavioral study (Kensinger et al., 2006), visually specific recognition (saying "same" to a *same* item) was significantly higher for negative items (60%) than for neutral items (51%, *p* < .01; see Table 1). Thus, negative items were more likely to be remembered with specific visual detail than were neutral items. Emotion did not influence the distribution of responses given to *similar* or *new* items (*p* > .25).

It is important to note that participants' memory performance was well above chance, even for the neutral items. If performing at chance, participants would have been equally likely to give "same," "similar" or "new" responses to *same* items and to *new* items, and they would have given each type of response one-third of the time. Instead, participants gave "same" responses to *same* items and "new" responses to *new* items more than half of the time. Moreover, they were least likely to call a *same* item "new,"

Table 1
Proportion (mean, S.E.) of items given a "same," "similar" or "new" response as a function of item type (*same*, *similar* or *new*) and emotion type (neutral or negative arousing)

Response	Same	Similar	New
Neutral			
"same"	.51 (.03)	.26 (.03)	.18 (.03)
"similar"	.32 (.03)	.45 (.03)	.29 (.03)
"new"	.17 (.03)	.28 (.03)	.53 (.03)
Negative arousing			
"same"	.60 (.03)	.28 (.03)	.19 (.03)
"similar"	.25 (.03)	.44 (.03)	.28 (.03)
"new"	.15 (.03)	.28 (.03)	.54 (.03)

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[1] The instances for each event type ranged from 10 to 45 for "new" responses to *same* items, from 11 to 51 for "similar" responses to *same* items, from 25 to 54 for "same" responses to *same* items, from 10 to 31 for false alarms to *new* items and from 26 to 66 for correct rejections of *new* items.

were somewhat more likely to call a *same* item "similar," and were most likely to call a *same* item "same." In contrast, they were least likely to call a *new* item "same," were more likely to call a *new* item "similar," and were most likely to call a *new* item "new." Thus, the large number of items included on the recognition memory task allowed us to analyze all responses to *same* items and to *new* items (i.e., resulted in a sufficient number of "new," "similar" and "same" responses to these items), but did not lead to memory performance that approached chance.

3.2. Neuroimaging results

3.2.1. Overall recognition memory

If we consider "same" and "similar" responses to *same* items to reflect at least general memory for the studied items, and "new" responses to *same* items to reflect forgetting of the studied item, then comparing ("same" + "similar") > "new" responses to *same* items gives us a way to examine the standard recognition-memory effect (i.e., remembered > forgotten) for the negative and the neutral items. A conjunction analysis identified regions that showed this correspondence to overall recognition for the negative items and also the neutral items (i.e., ["same" or "similar" response to *same* negative items > "new" response to *same* negative items] and ["same" or "similar" response to *same* neutral items > "new" response to *same* neutral items]). This analyses revealed a fronto-parietal network of regions consistent with those demonstrated in many studies of episodic retrieval (e.g., Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Ranganath, Johnson, & D'Esposito, 2000; Wheeler & Buckner, 2004; regions reported in upper portion of Table 2).

We then performed an interaction analysis to identify regions that showed a correspondence to overall recognition for the negative items but not for the neutral items. This analysis revealed a network of regions including the left fusiform gyrus, the amygdala and the parahippocampal gyrus (see middle portion of Table 2). Regions showing the opposite pattern of response (i.e., a correspondence to overall recognition for the neutral items but not for the negative items) included regions throughout the prefrontal cortex, as well as a cluster within the left fusiform gyrus posterior to the cluster that corresponded with overall recognition of the negative items only (see lower portion of Table 2).

These results are broadly consistent with those of prior neuroimaging investigations of emotion's modulation of retrieval processes: there often is extensive overlap in the processes corresponding with retrieval of negative and neutral items, but also modulation within the amygdala and the hippocampal formation during retrieval of emotional items (e.g., Dolcos et al., 2005; Fenker et al., 2005; Kensinger & Schacter, 2005b).

3.2.2. Relation of limbic engagement to retrieval accuracy

Although these results implicate limbic regions in retrieval, as noted earlier, there have been extensive debates about whether amygdala engagement during retrieval corresponds with inflated confidence in a memory or with enhanced memory for detail (see Phelps, 2004; Sharot et al., 2004; Smith et al., 2006). One

of the most direct ways to address this issue is to examine whether amygdala engagement is equally strong when individuals falsely endorse an item and when they correctly endorse an item, or whether amygdala engagement is disproportionately greater when individuals are correct in their recognition of an item.

To address this question, we compared the neural processes leading to successful recognition of at least some information about a negative item (i.e., a "same" or "similar" response to a *same* item compared to a "new" response to a *same* item) and those leading to false recognition of a negative item (i.e., a "same" or "similar" response to a *new* item compared to a "new" response to a *new* item). A conjunction analysis revealed that there were no regions that corresponded both with successful recognition and also with false recognition of negative items.[2] In contrast, an interaction analysis revealed that there was a large network of regions that corresponded with successful recognition but not with false recognition of negative items (see Table 3 for listing of all regions). Critically, the left amygdala[3] and orbitofrontal cortex (BA 11/47) were among those regions that showed this correspondence to successful recognition and not to false recognition (see Fig. 2). Moreover, these regions showed a greater response during true recognition than during false recognition. These results suggest that amygdala and orbitofrontal engagement during retrieval can correspond with the accurate retrieval of information rather than with a person's belief that information about an item's prior presentation has been retrieved. The only region to show the reverse correspondence (i.e., to false recognition but not to successful recognition of negative items) was the medial prefrontal cortex (Talairach coordinates: 4, 31, −10, Brodmann areas 10, 11 and 32). We also examined the regions that were related to false recognition and successful recognition for the neutral items (see Table 4 for all regions); the amygdala showed a relation to neither (as expected based on prior evidence that amygdala activity relates only to retrieval of emotional items; e.g., Dolcos et al., 2005; Kensinger & Schacter, 2005b). Interestingly, just as for the negative items, the medial prefrontal cortex (Talairach coordinates: 2, 34, −13; Brodmann areas 11 and 32) showed a relation to false recognition but not to successful recognition of the neutral items.

3.2.3. Visually specific recognition

Two related questions of interest concern the neural processes that corresponded with visually specific recognition. One question was whether there would be visual-processing regions

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[2] When the threshold of each contrast entered into the conjunction analysis was dropped to $p < .05$, the conjunction analysis did reveal shared activity in the left middle frontal gyrus and bilateral inferior temporal gyrus. The fact that these regions did not overlap when the contrasts were analyzed at more stringent thresholds suggests that, for negative items, there are regions that are weakly associated with all item endorsements (true or false) but not that are strongly associated with both true and false endorsements.

[3] The right amygdala did not show a correspondence to successful recognition, even when the threshold of the analyses was reduced substantially ($p < .05$). Left-lateralized amygdala activity was present in both men and women.

Table 2
Regions that showed a correspondence to *overall recognition* (i.e., "same" or "similar" response to *same* item > "new" response to *same* item)

Lobe	Region	Hemisphere	Talairach coordinates (x, y, z)	Approximate Brodmann area
Negative and neutral items				
Frontal	Middle frontal gyrus	L	−46, 31, 28	9
		L	−42, 22, 21	46
		L	−38, 58, 3	10
		L	−24, 6, 46	6
		R	38, 30, 19	46
		R	50, 38, 22	46
	Medial frontal gyrus	L	−8, 20, 45	10
		L	−4, 35, 37	10
	Inferior frontal gyrus	L	−42, 21, −1	47
		R	34, 29, −3	47
Parietal	Superior parietal lobule	L	−32, −54, 47	7
		R	36, −63, 53	7
	Precuneus	L	−8, −71, 51	7
		L	−6, −58, 49	7
		R	12, −60, 47	7
	Inferior parietal lobule	L	−42, −40, 48	40
		L	−34, −43, 41	40
		R	34, −62, 42	39
		R	38, −52, 45	40
		R	38, −35, 46	40
Temporal	Middle temporal gyrus	L	−51, −56, −2	37
Occipital	Middle occipital gyrus	L	−46, −64, −7	37
Other	Putamen	L	−18, 5, 13	
Negative but not neutral items				
Frontal	Middle frontal gyrus	L	−51, 19, 36	9
		L	−44, 36, 20	46
		R	48, 15, 34	9
	Inferior frontal gyrus	R	46, 35, 9	46
		R	46, 15, 23	9
Parietal	Superior parietal lobe	L	−34, −62, 44	7
		R	28, −60, 51	7
	Precuneus	Bilateral	0, −62, 36	7
		L	−24, −50, 47	7
		R	34, −62, 34	39
	Inferior parietal lobe	R	38, −58, 40	40
Temporal	Fusiform gyrus	L	−42, −38, −13	20
	Parahippocampal gyrus	R	30, −56, 8	30
	Middle temporal gyrus	R	57, −56, 3	21
	Inferior temporal gyrus	L	−44, −51, −1	37
Other	Cingulate gyrus	Bilateral	0, −3, 22	24
		R	16, −55, 27	31
	Insula	L	−36, 22, 4	13
	Amygdala	L	−18, −5, −15	
Neutral but not negative items				
Frontal	Superior frontal gyrus	L	−12, 31, 46	8
		R	44, 40, 31	9
	Middle frontal gyrus	L	−49, 44, −6	47
		L	−44, 18, 19	46
		L	−42, 46, −14	11
		L	−34, 16, 45	8
		L	−28, 8, 38	6
		R	44, 48, 22	46
	Medial frontal gyrus	L	−18, 4, 48	6
	Inferior frontal gyrus	L	−42, 1, 22	9

Table 2 (*Continued*)

Lobe	Region	Hemisphere	Talairach coordinates (x, y, z)	Approximate Brodmann area
		L	−32, 29, −1	47
		R	32, 32, 13	46
Parietal	Inferior parietal lobe	L	−57, −31, 48	40
Temporal	Inferior temporal gyrus	L	−55, −56, −2	37
		L	−51, −55, −12	20
		R	55, −51, −1	37
	Middle temporal gyrus	L	−59, −43, −5	21
		L	−57, −45, −6	37
Occipital	Middle occipital gyrus	L	−49, −63, −9	37
	Fusiform gyrus	L	−38, −64, −7	19
	Lingual gyrus	R	12, −82, −6	18
Other	Cingulate gyrus	Bilateral	0, −22, 27	23
		L	−12, 20, 43	32
	Caudate	L	−8, 14, 1	
		L	−6, 4, 11	

that related to visually specific recognition for the negative items and also for the neutral items. To address this question, we conducted a conjunction analysis to reveal regions whose activity was greater when a "same" response was given to a *same* item than when a "similar" response was given to a *same* item, regardless of whether that item was negative or neutral (i.e., ["same" > "similar" response to *same* negative item] and ["same" > "similar" response to *same* neutral item]). This conjunction analysis revealed that activity in the left fusiform gyrus showed this correspondence to visually specific recognition for both the negative items and also for the neutral items (see Fig. 3). This left-hemisphere lateralization is interesting because at encoding, activity in the *right* fusiform gyrus tends to show a relation to memory specificity (Garoff et al., 2005; Kensinger,

Garoff-Eaton, & Schacter, in press). Thus, although we did find visual activity that corresponded with visually specific recognition, it does not appear that this activity reflects a recapitulation of the same processes engaged during the encoding of visually specific detail.

An interaction analysis revealed that there were a number of regions that showed a correspondence to visually specific recognition for the negative items but not for the neutral items. These regions included the orbitofrontal cortex, the amygdala and the parahippocampal gyrus (see Table 5 for full listing of regions). Notably absent were visual-processing regions; there was no evidence for differential engagement of the fusiform gyrus, or of other visual-processing regions, during the specific recognition of negative items compared to neutral ones.
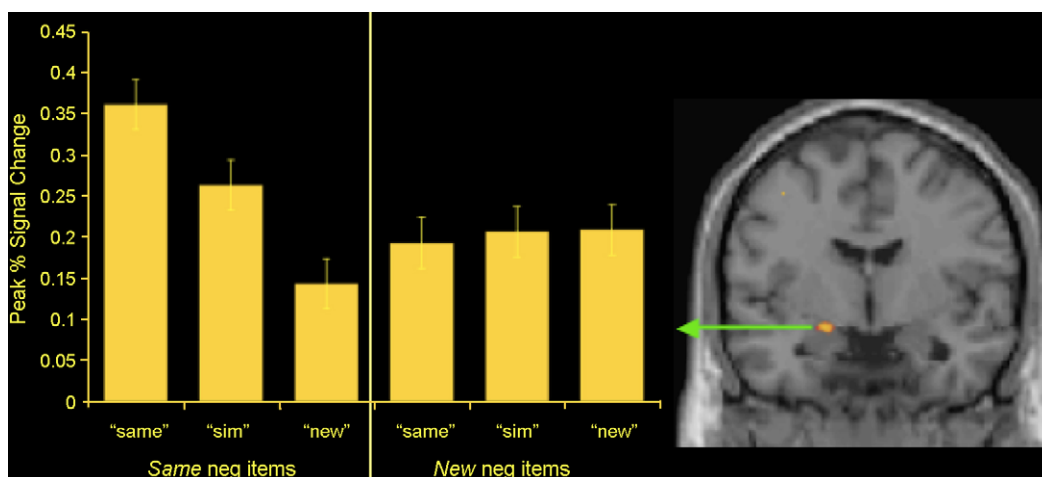

Fig. 2. *Activity in the left amygdala was related to the accuracy of visual detail retrieved about negative items*: An ANOVA computed on the signal change values extracted from the amygdalar region revealed an interaction between valence (neg, neu), response type ("same", "similar", "new") and exemplar type (same, new; $p < .01$). Amygdala activity was greatest when visual detail was accurately recognized ("same" response to *same* negative item), was significantly reduced when visual detail was not accurately recognized, but non-specific information was retrieved ("similar" response to *same* negative item), and was lowest when no information was accurately retrieved ("new" response to *same* negative item). When negative items had not been studied previously (*new* items), amygdala activity was not modulated by participants' beliefs about whether visual details had been recognized (i.e., amygdala activity was equivalent for *new* negative items given a "same," "similar" or "new" response). There was no correspondence between amygdala activity and recognition of neutral items (data not shown). "sim" = "similar" response, neg = negative.

Table 3
Regions corresponding with successful recognition (i.e., a "same" or "similar" response to a *same* item compared to a "new" response to a *same* item), but not false recognition (i.e., a "same" or "similar" response to a *new* item compared to a "new" response to a *new* item), of negative items (top portion of table) and with false, but not successful, recognition of negative items (bottom portion of table)

Lobe	Region	Hemisphere	Talairach coordinates (x, y, z)	Approximate Brodmann area
Successful but not false recognition of negative items				
Frontal	Middle frontal gyrus	L	−48, 30, 24	46
		L	−44, 44, 16	46
		R	46, 34, 22	46
		R	48, 15, 34	9
	Medial frontal gyrus	Bilateral	−6, 18, 47	8
		Bilateral	−4, 29, 35	6
	Inferior frontal gyrus	L	−53, 25, 1	45
		L	−44, 9, 27	9
		R	34, 25, −1	11/47
		R	46, 9, 24	9
		R	46, 35, 9	46
Parietal	Superior parietal lobule	L	−34, −58, 49	7
		R	32, −62, 51	7
	Angular gyrus	R	32, −62, 36	39
	Precuneus	Bilateral	0, −62, 36	7
		L	−30, −50, 47	7
	Inferior parietal lobule	L	−40, −33, 42	40
		R	36, −31, 38	40
Temporal	Fusiform gyrus	L	−40, −36, −13	20
	Parahippocampal gyrus	L	−18, −24, −19	35
		R	30, −56, 8	30
	Middle temporal gyrus	R	57, −56, 3	21
	Inferior temporal gyrus	L	−49, −60, −2	19
Occipital	Middle occipital gyrus	L	−46, −57, −7	19
		R	28, −79, 11	19
Other	Cingulate gyrus	Bilateral	6, −3, 22	24
		L	−8, −28, 29	23
		R	16, −55, 27	31
	Insula	L	−32, 20, 5	13
	Amygdala	L	−18, −5, −17	
False but not successful recognition of negative items				
Frontal	Medial frontal gyrus	Bilateral	4, 31, −10	10, 11, 32

No regions related to successful and also to false recognition of negative items.

The only region to show the opposite pattern of response (i.e., a correspondence with visually specific recognition for the neutral items but not for the negative items) was a region within the middle occipital gyrus (BA 19). Thus, these results indicate that, even in instances in which negative items are more likely to be remembered with visual detail than neutral items, there is not always an emotion-related enhancement in visual processing during retrieval. In fact, if anything, there is more visual activity associated with the recognition of a neutral item's visual details than of a negative item's visual details.

4. Discussion

To briefly summarize the results, we found that activity within the amygdala and orbitofrontal cortex corresponded specifically with the accurate recovery of detail, and not more generally with a person's belief that visual detail was retrieved. Thus, activity in the amygdala and orbitofrontal cortex showed a strong relation to successful recognition of *same* exemplars, but no correspondence to false recognition of *new* exemplars. We also found that activity in a region of the left fusiform gyrus corresponded with retrieval of visually specific information for negative items and also neutral items. There was no evidence that emotion enhanced processing within this fusiform region nor within other visual regions: despite the fact that negative items were more likely to be remembered with visual detail than neutral items, interaction analyses revealed no visual regions whose activity was disproportionately related to the visually specific recognition of negative items as compared to neutral ones. Rather, the enhanced visual specificity associated with memory for negative items corresponded with additional engagement of regions including the amygdala, the orbitofrontal cortex and the parahippocampal gyrus. Each of these findings will be elaborated on below.

Table 4

Regions associated with both successful recognition (i.e., a "same" or "similar" response to a *same* item compared to a "new" response to a *same* item) and false recognition (i.e., a "same" or "similar" response to a *new* item compared to a "new" response to a *new* item) of neutral items (top portion of table), with successful but not false recognition of neutral items (middle portion of table), or with false but not successful recognition of neutral items (bottom portion of table)

| Lobe	Region	Hemisphere	Talairach coordinates (x, y, z)	Approximate Brodmann area
Successful and false recognition of neutral items				
Frontal	Superior frontal gyrus	L	−18, 16, 40	8
	Middle frontal gyrus	L	−28, 21, 34	9
Parietal	Postcentral gyrus	L	−61, −25, 42	1
		R	61, −27, 49	2
	Inferior parietal lobule	R	61, −38, 46	40
Temporal	Fusiform gyrus	L	−42, −63, −12	37
	Middle temporal gyrus	L	−26, −57, 23	39
	Inferior temporal gyrus	R	48, −57, −4	19
Occipital	Middle occipital gyrus	L	−30, −78, −8	18
	Inferior occipital gyrus	L	−38, −74, 0	19
Other	Caudate	L	−16, −5, 22	
		L	−14, 11, 22	
		R	12, 18, 12	
		R	20, −9, 23	
	Thalamus	R	16, −25, 14	
	Cingulate gyrus	R	30, −67, 11	30
Successful but not false recognition of neutral items				
Frontal	Superior frontal gyrus	R	44, 40, 31	9
	Middle frontal gyrus	L	−49, 44, −6	11
		L	−46, 31, 28	9
		L	−42, 22, 21	46
		L	−24, 6, 46	6
		R	50, 38, 22	46
	Medial frontal gyrus	Bilateral	−8, 20, 45	8
	Inferior frontal gyrus	R	32, 32, 13	46
Parietal	Superior parietal lobule	L	−32, −54, 47	7
		R	36, −63, 53	7
	Inferior parietal lobule	L	−34, −43, 41	40
Temporal	Middle temporal gyrus	L	−59, −43, −5	21
	Inferior temporal gyrus	L	−53, −56, −2	37
		R	55, −51, −1	37
Occipital	Lingual gyrus	R	12, −82, −6	18
Other	Caudate	L	−6, 4, 11	
False but not successful recognition of neutral items				
Frontal	Middle frontal gyrus	L	−20, 29, 35	8
	Medial frontal gyrus	Bilateral	2, 34, −13	11, 32
			6, 54, −11	11
			6, 57, 16	10
Parietal	Precuneus	R	30, −71, 16	31
	Inferior parietal lobule	R	53, −35, 33	40
Temporal	Middle temporal gyrus	R	34, −60, 12	19
			50, 2, −32	21
Occipital	Cuneus	R	28, −84, 28	19
	Middle occipital gyrus	L	−42, −73, 7	19
	Inferior occipital gyrus	L	−30, −82, −3	18
Other	Cingulate gyrus	Bilateral	2, 44, −7	32
		L	−28, −70, 7	30
		R	12, −34, 20	23
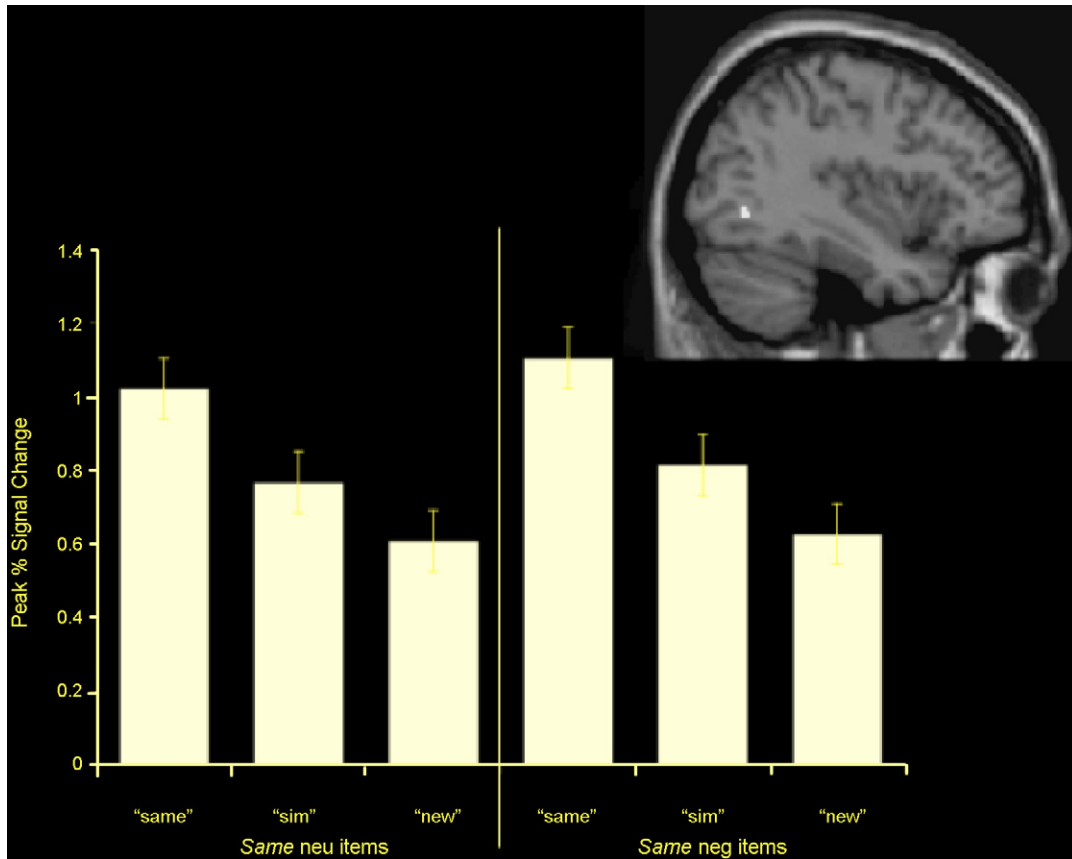
Fig. 3. Activity in the left fusiform gyrus, and in no other regions, corresponded with visually specific recognition for the neutral items and also the negative items: Activity in this region was greatest when visual detail was accurately recognized ("same" response to same item), was significantly reduced when visual detail was not recognized but non-specific information was retrieved ("similar" response to same item), and was lowest when no information was recognized ("new" response to same item). An ANOVA revealed that the activity in this left fusiform region was influenced by the visual specificity of a memory (p < .01) but not by the emotional nature of the item. "sim" = "similar" response; neu = neutral; neg = negative.

Table 5
Regions that showed a correspondence to *visually specific recognition* (i.e., "same" response to *same* item > "similar" response to *same* item)

Lobe	Region	Hemisphere	Talairach coordinates (*x, y, z*)	Approximate Brodmann area
Negative and neutral items				
Temporal	Fusiform gyrus	L	−38, −64, 2	37
Negative but not neutral items				
Frontal	Medial frontal gyrus	R	10, 37, −7	10
	Inferior frontal gyrus	L	−28, 29, −12	11/47
Parietal	Superior parietal lobule	L	−34, −71, 50	7
	Inferior parietal lobule	R	40, −33, 31	40
Temporal	Superior temporal gyrus	L	−61, −17, 3	22
		L	−40, −49, 21	22
		R	59, −23, 10	42
		R	67, −33, 7	22
	Parahippocampal gyrus	L	−22, −26, −12	35
Other	Cingulate gyrus	Bilateral	−2, 33, −10	32
	Caudate	R	18, −32, 18	
	Amygdala	L	−16, −1, −17	
Neutral but not negative items				
Occipital	Middle occipital gyrus	L	−30, −78, 13	19

4.1. Amygdala engagement corresponds with accurate retrieval of detail

Although amygdala activity tracked the amount of accurate detail retrieved about *same* negative items, its activity was equally strong when participants gave a "same," "similar" or "new" response to a *new* negative item. Thus, amygdala activity was related to successful recognition, but not to false recognition. This result provides strong evidence that amygdala activity does not correspond with a person's belief that visual detail is recognized: had this been true, amygdala activity would have been equally high whenever a "same" response was given, regardless of the accuracy of that response. Rather, amygdala activity appears to be related to the amount of accurate detail recognized; thus, its activity is equally low whenever information about an item's prior presentation is not recognized (i.e., when a "new" response is given to a *same* item, thereby indicating no memory for that item, or when any response is given to a *new* item—by definition, a class of items whose prior presentation cannot be remembered).

It is potentially important that the link between amygdala activity and accurate retrieval was revealed within a region of the left amygdala. It has been proposed previously (e.g., Smith et al., 2006) that the left amygdala may relate to explicit retrieval of information, whereas the right amygdala may be involved in implicit memory processes. More broadly, the left amygdala may be related to the conscious processing of arousal whereas the right amygdala may guide automatic, autonomic responses to emotional information (e.g., Gläscher & Adolphs, 2003). Thus, it is plausible that the left-lateralized amygdala activity emerged because the left amygdala plays a more direct role in the explicit retrieval of episodic detail – including affective arousal – than the right amygdala. For example, the left amygdala engagement during retrieval could reflect the recapitulation, or successful recovery, of information present during encoding. The left amygdala often is associated with successful encoding (Kensinger et al., 2007; Kensinger & Schacter, 2005a, 2006) and with the retrieval of information encoded in an emotional context (Fenker et al., 2005; Smith, Henson, Dolan, & Rugg, 2004; Smith et al., 2006). Thus, it is possible that, just as auditory or visual cortices can become reactivated when individuals retrieve items that had been paired with a sound or a visual image (Kahn, Davachi, & Wagner, 2004; Nyberg, Habib, McIntosh, & Tulving, 2000; Vaidya, Zhao, Desmond, & Gabrieli, 2002; Wheeler & Buckner, 2004; Wheeler et al., 2000), so might retrieval-related activity in limbic regions reflect the reactivation of emotion-relevant information present during an encoding episode. The pattern of results within the left amygdala (i.e., tracking successful recovery of detail) would be consistent with this interpretation.

Although we have focused upon the amygdala's relation to successful recognition, the results revealed a broader relation between limbic activity (not only in the amygdala but also in the orbitofrontal cortex and along the cingulate gyrus) and successful recognition. Importantly, these limbic regions showed no correspondence with false recognition. This focal association between limbic engagement and true recognition is likely to explain why negatively emotional information can be less

prone to memory distortion than non-emotional information (see Kensinger, in press, for review). When comparing the regions that are related to successful but not false recognition for negative items (i.e., the top panel of Table 3) and for neutral items (i.e., the middle panel of Table 4), it is clear that there is extensive overlap in the cortical regions that show this correspondence for the two types of items. However, for the negative items, there are additional limbic regions whose activity relates to true but not false recognition. Thus, for negative items, there is a broader network of activity that distinguishes true from false recognition. Moreover, negative items have less overlap in the neural processes that are recruited during both true and false recognition, whereas there is extensive overlap in those processes recruited for true and false recognition of neutral items. It makes sense that the more distinction there is between the processes that underlie true recognition and false recognition, the lesser the likelihood of memory errors.

4.2. Relation between visual processing at retrieval and the visual specificity of a memory

We found that enhanced processing within a visual-processing region (particularly, the left fusiform gyrus) can relate to enhanced visual specificity of a memory. This result is important in demonstrating that there can be links between visual processing at retrieval and the visual specificity of a memory. It is interesting, however, that there was strong left lateralization within the fusiform region. Prior studies have demonstrated that there is a link between *right* fusiform activity and the processing of the specific details of an item's presentation (Koutstaal et al., 2001; Marsolek, 1999; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003), and neuroimaging studies have revealed a correspondence between engagement of the right (but not left) fusiform during encoding and subsequent memory for an item's visual details (Garoff et al., 2005; Kensinger et al., in press). Yet, we found no evidence for right fusiform involvement in retrieval of the specific visual details of an item's presentation. Thus, there does not appear to be strong overlap between the types of visual processes that lead to the *encoding* of visual details and those that lead to the *retrieval* of visual details. Although recapitulation within the same sensory regions engaged during encoding often leads to a more perceptually specific memory (e.g., Nyberg et al., 2000; Wheeler et al., 2000), in the present study, this recapitulation within the right fusiform gyrus does not appear to be required in order for successful retrieval of visual details to occur. Further studies will be needed to clarify whether the right fusiform gyrus plays any role in the retrieval of visual specifics, or whether its role is confined to the processing of visual detail—a type of processing that might occur regardless of whether an item has been presented previously.

4.3. Processes that correspond with the enhanced visual specificity of emotional memories

In the present paradigm, negative items were more likely to be remembered with visual detail than neutral items (see also Kensinger et al., 2006, in press). This advantage in memory

for visual detail did not appear to stem from disproportionate engagement of visual-processing regions during the retrieval of the negative items. There were no visual regions that showed a stronger correspondence to visually specific recognition of negative items compared with neutral items. In fact, if anything, visually specific recognition of neutral items was associated with more visual engagement; there was a region of the middle occipital gyrus whose activity was related to visually specific recognition of neutral, but not negative, items.

The finding that visually specific recognition of negative items is not associated with enhanced visual processing is consistent with at least a couple of prior neuroimaging experiments demonstrating that visual activity is not enhanced, and in fact often can be reduced, when participants claim that they vividly "remember" emotional items compared to non-emotional ones (Dolcos et al., 2005; Sharot et al., 2004). This lack of visual recruitment during retrieval of emotional memories occasionally has been used as evidence that emotional memories are associated with a reduction in memory for visual detail (see Sharot et al., 2004). However, the results of the present study emphasize that this lack of enhancement in visual activity does not always correspond with a lack of visual detail in the emotional memory. In the present study, memory for the visual details of an item was *better* for the negative items than for the neutral items, despite the fact that there was not an enhancement in visual processing activity for the negative items. Further research will be needed to clarify the reasons for this disconnect between visual processing activity and the amount of visual detail remembered about an item.

4.4. Concluding remarks

The role of limbic engagement during retrieval has been actively debated. Although, it has been argued that limbic engagement during retrieval may bias people to believe that they remember an emotional item (e.g., Sharot et al., 2004), the present results do not support that conclusion. Rather, these data build upon prior research (Fenker et al., 2005; Kensinger & Schacter, 2005b; Smith et al., 2006) to suggest that limbic engagement during retrieval can correspond with the ability to accurately remember item details. Although there are retrieval-related processes that lead people to falsely believe that they have seen a negative item previously, limbic activation is not always one of those processes.

Acknowledgments

References

Adolphs, R., Denburg, N. L., & Tranel, D. (2001). The amygdala's role in long-term declarative memory for gist and detail. *Behavioral Neuroscience*, *115*, 983–992.

Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. (2002). Region of interest analysis using an SPM toolbox [abstract]. In *Presented at the 8th International Conference on Functional Mapping of the Human Brain* (Available on CD-ROM in NeuroImage 16).

Cabeza, R., Rao, S. M., Wagner, A. D., Mayer, A. R., & Schacter, D. L. (2001). Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 4805–4810.

Dolcos, F., LaBar, K. S., & Cabeza, R. (2005). Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 2626–2631.

Fenker, D. B., Schott, B. H., Richardson-Klavehn, A., Heinze, H. J., & Duzel, E. (2005). Recapitulating emotional context: Activity of amygdala hippocampus and fusiform cortex during recollection and familiarity. *European Journal of Neuroscience*, *21*, 1993–1999.

Fisher, R. A. (1950). *Statistical methods for research workers*. London: Oliver and Boyd.

Garoff, R. J., Slotnick, S. D., & Schacter, D. L. (2005). The neural origins of specific and general memory: The role of the fusiform cortex. *Neuropsychologia*, *43*, 847–859.

Gläscher, J., & Adolphs, R. (2003). Processing of the arousal of subliminal and supraliminal emotional stimuli by the human amygdala. *Journal of Neuroscience*, *12*, 10274–10282.

Henson, R. N., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, *19*, 3962–3972.

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *Journal of Neuroscience*, *24*, 4172–4180.

Kensinger, E. A. (in press). How negative emotion affects memory accuracy: Behavioral and neuroimaging evidence. *Current Directions in Psychological Science*.

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (in press). How negative emotion enhances the visual specificity of a memory. *Journal of Cognitive Neuroscience*.

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2006). Memory for specific visual details can be enhanced by negative arousing content. *Journal of Memory and Language*, *54*, 99–112.

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, *56*, 575–591.

Kensinger, E. A., & Schacter, D. L. (2005a). Emotional content and reality-monitoring ability: fMRI evidence for the influences of encoding processes. *Neuropsychologia*, *43*, 1429–1443.

Kensinger, E. A., & Schacter, D. L. (2005b). Retrieving accurate and distorted memories: Neuroimaging evidence for effects of emotion. *NeuroImage*, *27*, 167–177.

Kensinger, E. A., & Schacter, D. L. (2006). Amygdala activity is associated with the successful encoding of item but not source information for positive and negative stimuli. *Journal of Neuroscience*, *26*, 2564–2570.

Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: fMRI evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, *39*, 184–199.

Marsolek, C. J. (1999). Dissociable neural subsystems underlie abstract and specific object recognition. *Psychological Science*, *10*, 111–118.

Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 11120–11124.

Phelps, E. A. (2004). Human emotion and memory: Interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology*, *14*, 198–202.

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2000). Left anterior prefrontal activation increases with demands to recall specific perceptual information. *Journal of Neuroscience*, *20*, RC1081–RC1085.

Sharot, T., Delgado, M. R., & Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nature Neuroscience*, *7*, 1376–1380.

Simons, J. S., Koutstaal, W., Prince, S., Wagner, A. D., & Schacter, D. L. (2003). Neural mechanisms of visual object priming: Evidence for perceptual and semantic distinctions in fusiform cortex. *NeuroImage*, *19*, 613–626.

Smith, A. P., Henson, R. N., Dolan, R. J., & Rugg, M. D. (2004). fMRI correlates of the episodic retrieval of emotional contexts. *Neuroimage*, *22*, 868–878.

Smith, A. P., Stephan, K. E., Rugg, M. D., & Dolan, R. J. (2006). Task and content modulate amygdala-hippocampal connectivity in emotional retrieval. *Neuron*, *49*, 631–638.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme Medical.

Vaidya, C. J., Zhao, M., Desmond, J. E., & Gabrieli, J. D. (2002). Evidence for cortical encoding specificity in episodic memory: Memory-induced re-activation of picture processing areas. *Neuropsychologia*, *40*, 2136–2143.

Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage*, *21*, 1337–1349.

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 11125–11129.