

Retrieving accurate and distorted memories: Neuroimaging evidence for effects of emotion

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While limbic activity is known to be associated with successful encoding of emotional information, it is less clear whether it is related to successful retrieval. The present fMRI study assessed the effects of emotion on the neural processes engaged during retrieval of accurate compared to distorted memories. Prior to the scan, participants (16 young adults) viewed names of neutral (e.g., frog) and emotional (e.g., snake) objects and formed a mental image of the object named. They were shown photos of half of the objects. During the fMRI scan, participants saw object names and indicated whether or not they had seen the corresponding photo. Memory distortions (misattributions) occurred when participants incorrectly indicated whether or not a photo had been studied. Activity in some regions (e.g., L anterior hippocampus) was related to accurate retrieval (correct attribution->misattributions) for emotional and neutral items. However, activity in other regions corresponded with accurate retrieval specifically for emotional items (e.g., in R amygdala/periamygdaloid cortex and L orbitofrontal cortex) or for neutral items (e.g., in lateral inferior prefrontal cortex and R posterior hippocampus). Results indicate that emotional salience modulates the processes engaged during accurate retrieval and that activity in limbic regions corresponds with accurate memory assignment for emotional items. To our knowledge, this study is the first to demonstrate a link between limbic engagement at retrieval and accurate memory attribution.

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Memory retrieval often involves the reconstruction of a prior experience rather than its verbatim replaying. Abundant evidence has shown that this reconstruction process can be flawed, leading to memory errors, illusions, and distortions (reviewed by Roediger and McDermott, 2000; Schacter, 1999; Schacter et al., 1998). A relatively common form of memory distortion arises when individuals must distinguish whether an item was previously

imagined or perceived (often referred to as *reality monitoring*; Johnson and Raye, 1981). Individuals sometimes incorrectly attribute the source of an item's familiarity; for example, a person may believe an item was externally presented when it actually was imagined.

Memory misattributions can occur less often for items that contain emotional relevance than for those void of emotional content (Kensinger and Corkin, 2004a; Kensinger and Schacter, in press(b); Pesta et al., 2001), plausibly because emotional information is more likely to be remembered with contextual details than nonemotional information (D'Argembeau and Van der Linden, 2004; Doerksen and Shimamura, 2001; Kensinger and Corkin, 2003). Neuroimaging studies have suggested that encoding processes play a critical role in this memory enhancement for emotional memory. In particular, amygdalar engagement appears to be critical for increasing the likelihood that verbal (e.g., Kensinger and Corkin, 2004b) and nonverbal (e.g., Cahill et al., 1996; Canli et al., 2000) emotional information is remembered. Further, limbic activity (in the amygdala and orbitofrontal cortex) during encoding is related to subsequent correct memory attributions for emotional items (Kensinger and Schacter, in press(a)). These effects of emotion occur even when individuals study information without the intention to remember it (i.e., under incidental encoding conditions; Kensinger and Schacter, in press(a,b)), suggesting that the neural processes recruited to process emotional information increase the probability of successful and detailed encoding. This increased encoding efficacy likely emerges in part through interactions between the amygdala and the hippocampal formation during encoding and consolidation (reviewed by Phelps, 2004). Consistent with this hypothesis, neuroimaging studies have demonstrated correlations between amygdalar and hippocampal activity (e.g., Dolcos et al., 2004; Kensinger and Corkin, 2004b; Kensinger and Schacter, in press(a); Richardson et al., 2004) and increases in functional connectivity of the two regions (Kilpatrick and Cahill, 2003) during encoding of emotional information.

In contrast to the rich neuroimaging literature examining the processes relating to encoding of emotional information, relatively few studies have examined retrieval processes. Two studies have suggested that retrieval processes are modulated by emotional content, with activity in visual cortex (Taylor et al., 1998) and

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limbic regions (amygdala and anterior temporal lobe; Dolan et al., 2000) showing greater activity during retrieval of emotional information than during retrieval of neutral information. Because these studies utilized blocked designs, however, they cannot distinguish state effects from item effects (e.g., Otten et al., 2002), nor can they pinpoint the neural activity that is related specifically to successful retrieval.

A few other event-related potential (Maratos and Rugg, 2001; Smith et al., 2004a) and fMRI studies (Maratos et al., 2001; Smith et al., 2004b) have examined how retrieval of neutral information is affected by the emotional context in which it was presented. These studies again have suggested that limbic regions (e.g., amygdala and orbitofrontal cortex) play a role during retrieval of information studied in emotional compared to neutral contexts. The critical comparison in these studies was between items correctly recognized from an emotional context and from a neutral context (i.e., a comparison of activity for “hits”) and thus these data do not speak to whether limbic activity is related to accurate retrieval more so for emotional than for neutral items.

To address this issue (i.e., whether activity in limbic regions shows an interaction between memory accuracy and an item’s emotional content), a more informative comparison is between successful and unsuccessful retrieval of emotional and neutral items. This comparison is especially appropriate for two reasons. First, this contrast mirrors that used during subsequent-memory paradigms which, as outlined above, have been the primary focus of neuroimaging studies of emotional memory. Second, this comparison also holds constant the emotional content of the items being retrieved, reducing the concern that differences in limbic engagement during retrieval arise from emotional processing of the retrieval cue.

In neuroimaging investigations, such comparisons often are made between items confidently or vividly remembered and those forgotten (e.g., Eldridge et al., 2000; Henson et al., 2000; Otten et al., 2001; Wheeler and Buckner, 2004). While these contrasts are useful for neutral items, they introduce a potential difficulty when comparing memory for emotional and neutral items: emotion can enhance subjective ratings of a memory’s vividness without increasing the objective accuracy of the memory (e.g., Neisser and Harsch, 1992; Talarico and Rubin, 2003; Winograd and Neisser, 1992). While emotion does not always have this paradoxical effect on memory (e.g., Doerksen and Shimamura, 2001; Kensinger and Corkin, 2003), this possible dissociation between subjective confidence and objective accuracy of an emotional memory makes it important to assess the accuracy of a memory directly, rather than relying only on subjective self-reports of a memory’s vividness or an individual’s confidence in their memory. When only subjective report is obtained, amygdala activity during vivid retrieval could be interpreted either as modulating retrieval of rich, detailed memories or as enhancing the subjective feeling that a memory is associated with contextual detail without affecting the amount of detail retrieved (discussed by Sharot et al., 2004).

To assess memory accuracy for emotional and neutral items, the present study employed a reality-monitoring paradigm previously used with neutral items (Gonsalves and Paller, 2000; Okado and Stark, 2003). Outside of the scanner, participants performed a task that required them to form mental images of objects. In the present study, half of the stimuli contained negative emotional content and half were of neutral content. Participants were shown the corresponding photo for half of those objects. The retrieval task,

performed during the fMRI scan, required participants to indicate whether objects had been externally presented. Thus, activity could be compared for correct memory attributions and memory misattributions. Two central questions were addressed: (1) what neural processes support accurate retrieval of both emotional and neutral information? and (2) How does the emotional content of the items influence the neural processes that are associated with accurate retrieval?

With regard to the first question, we were particularly interested in the relation between hippocampal activity and memory accuracy. Based on prior research implicating the hippocampal formation in retrieval of contextual details associated with a study episode (e.g., Dobbins et al., 2003; Wheeler and Buckner, 2003), we hypothesized that hippocampal activity would correspond with correct memory attributions at retrieval. However, the few studies that examined retrieval of illusory memories found either no hippocampal activity (Okado and Stark, 2003) or that hippocampal activity did not discriminate true from false memories (Cabeza et al., 2001; Slotnick and Schacter, 2004). The tasks used by Cabeza et al. (2001) and Slotnick and Schacter (2004) were quite different from the present study: False recognition responses in those studies indicated acceptance of an item that was semantically (Cabeza et al., 2001) or visually (Slotnick and Schacter, 2004) associated with studied items. Thus, it is not clear whether their findings generalize across recognition tasks or whether they are specific to tasks on which retrieval of gist information can support false recognition. While the methods of Okado and Stark (2003) were similar to those used here, their null finding (i.e., of no hippocampal activity) must be interpreted cautiously and does not provide compelling evidence regarding whether the hippocampus contributes to accurate memory attribution. In summary, the data have been mixed with regard to the role of the hippocampus in accurate retrieval, making it difficult to confidently predict the relation between hippocampal activity and accurate retrieval.

In regard to the second question, we were most interested in whether activity in regions known to be important for the processing of emotional information (e.g., amygdala and orbitofrontal cortex) would show a relation to accurate retrieval for emotional items. As outlined above, these regions have been implicated in subsequent-memory paradigms (reviewed by Hamann, 2001; Phelps, 2004) and in retrieval of neutral items presented in an emotional context (Smith et al., 2004b). However, it is not clear whether activity in these regions is related specifically to accurate retrieval. This issue is of central importance in understanding the memory phases during which amygdala response modulates memory accuracy. While it is clear that the amygdala plays a role during early memory phases (encoding and consolidation), its role during retrieval is debated (e.g., Nader, 2003; LeDoux, 2000).

Method

Participants

Participants comprised 17 native English speaking Harvard undergraduate or graduate students. The data from one participant were excluded due to scanner malfunction. The remaining 16 young adults (8 women, 8 men) were ages 18–30. All were right-handed, native English speakers screened to exclude those with contra-indicators for MRI scanning, or with a history of

depression. No participant was taking centrally-active medications. Informed consent was obtained from all participants in a manner approved by the Institutional Review Boards of Harvard University and the Massachusetts General Hospital.

Materials and procedure

Materials comprised 450 concrete words and 450 photo objects depicting a single object on a white background (e.g., a baseball, a tarantula; taken from Hemera Technologies Inc, 2002, Canada). Words and photo objects were selected as pairs, such that each word named a photo object (e.g., “tarantula” and a picture of a tarantula).

Half of the words and objects were high in arousal (scores >2.5 on a scale of -5 to $+5$, with negative values indicating that an item was calming or soothing, and positive values indicating that an item caused excitement or agitation). The other half of the words and objects were neutral, having received arousal ratings lower than $+1$. These items had been judged by a separate group of 20 young adults (10 males) prior to the present study (Kensinger and Schacter, *in press(a,b)*). They also were rated by the participants in this study, and the ratings agreed with those from the separate group of participants. Neutral and emotional objects did not differ in the numbers that included animals, people, or objects, nor did the neutral and emotional words differ in word length, word frequency, or word familiarity (Coltheart, 1981).

One or two days before the scanning session, each participant viewed a study list with 150 emotional words and 150 neutral words presented for 2 s each (randomly intermixed). Participants were instructed to make a button press to indicate whether each word named an object that was bigger or smaller than a shoebox. They were told that the study was examining mental imagery performance and thus that they should use mental imagery to perform the size-judgment task. Half of the words were followed by the corresponding photo object, presented for 2 s, and the remaining words were followed by a blank square shown for 2 s (design adapted from Gonsalves and Paller, 2000). Participants were instructed to simply view the square or the photo object that occurred after the word and were told that no response was required to these items.

After a delay of 1–2 days, participants returned for the fMRI scan. During the functional scans, participants performed a surprise recognition task (Debriefing indicated that no participants realized that their memory would be tested for the items studied in the laboratory). The recognition task was divided across three functional scans. In each scan, participants viewed 150 words. 50 of the words corresponded to items that had been studied in the word-only condition; 50 to items studied in the word–picture condition; and 50 to items that had not been studied. Emotional and neutral words from the three conditions (items from word-only trials, items from word–picture trials, and novel items) were pseudorandomly intermixed with one another and with fixation crosses (+) to provide jitter (Dale, 1999). Stimuli were back-projected onto a screen in the scanner bore, and participants viewed the words through an angled mirror attached to the head coil. For each word, participants indicated whether or not the corresponding photo object had been presented at study. Thus, a “no” response was required both for novel words that had not been studied and for words that had been presented without their corresponding photo object at study.

Image acquisition and data analysis

Images were acquired on a 1.5-T Siemens Sonata 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 = 40 ms, FOV = 200 mm; flip angle = 90°). Twenty-one axial-oblique slices (5 mm thickness, 1 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 SPM99 (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 (resampling 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 first conducted in which 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 event type. Effects for each event type were estimated using a subject-specific, fixed-effects model. These data were then entered into a second-order, random-effects analysis. Analyses contrasted activation as a function of memory performance (comparing correct memory attributions and memory misattributions) separately for each emotion type (emotional or neutral) and item history (from a word-only trial or a word–picture trial). Analyses were conducted at the level of $P < 0.001$. Conjunction analyses (using the masking function in SPM99) then examined what regions showed activation that varied as a function of memory accuracy (a) regardless of emotion type or item history, and (b) for a particular emotion type, regardless of item history. The threshold for each contrast entered into a conjunction analysis was set at $P < 0.05$.

All activations are presented in neurological coordinates (i.e. activity on the right hemisphere is presented on the right side of the brain images). Voxel coordinates are reported in Talairach coordinates (Talairach and Tournoux, 1998). We report coordinates of the most significant voxel within the cluster of activation (peak voxel) and the voxel located at the geographical center of the cluster (center voxel). Event-related time-courses were extracted from active clusters by creating regions-of-interest (ROI) as 8 mm spheres using the ROI toolbox implemented in SPM99. Analysis of variance (ANOVA) was performed on these extracted time-courses to examine whether the ROIs showed an interaction between memory accuracy and emotion type (i.e., activity relating to memory accuracy for emotional but not neutral items, or vice-versa).

Results

Behavioral data

ANOVA with response type (picture, no picture), item history (word-only, word–picture, new), and emotion type (emotional, neutral) as within-subject factors revealed a main effect of response type ($F(1,15) = 21.1$, $P < 0.001$, partial eta-squared = 0.59) as well as interactions between response type and item history ($F(1,14) = 393.$, $P < 0.001$, partial eta-squared = 0.85) and among response

Table 1

Regions in which activity was related to accurate retrieval of emotional word–picture items ($P < 0.001$)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area
Middle frontal gyrus	L	–44, 48, –13	–41, 46, –11	BA 10/11/47
Precentral gyrus	L	–35, –26, 59	–35, –25, 58	BA 4
Postcentral gyrus	L	–53, –20, 18	–51, –22, 17	BA 2
Inferior parietal lobe	L	–36, –65, 42	–37, –63, 44	BA 7
		–39, –41, 57	–40, –37, 53	BA 40
Amygdala/ periamygdaloid cortex	R	18, –3, –17	17, –2, –18	
Cerebellum				

type, item history, and emotion type ($F(1,14) = 13.0$, $P < 0.001$, partial eta-squared = 0.65). This three-way interaction resulted because while the proportion of correct (“no picture”) responses did not differ for new emotional and neutral items (0.85 and 0.84, respectively), participants were significantly more likely to make correct memory attributions for emotional items than for neutral items from word–picture trials (0.67 versus 0.57) and from word-only trials (0.69 versus 0.65 for emotional and neutral, respectively). Thus, memory was more accurate (i.e., included more correct attributions) for the emotional items than for the neutral items.

Neuroimaging data

Random-effects analyses contrasted activation as a function of memory performance (comparing correct memory attributions and memory misattributions) separately for each emotion type (emotional or neutral) and item history type (from a word-only or word–picture trial; Tables 1–4). Because the goal of this study was to examine how the emotional content of the stimuli (regardless of their item histories) affected the neural processes that were associated with accurate memory assignment, conjunction analyses were performed to examine the regions in which activity was related to accurate retrieval both for word-only and word–picture items. The results of these conjunctions are discussed below.

Accurate retrieval for both emotional and neutral items

A conjunction analysis was conducted to examine the regions in which activity was related to memory accuracy for all items (i.e., a conjunction of the four contrasts corresponding to correct attributions > misattributions for neutral word-only items, emotional word-only items, neutral word–picture items, and emotional word–picture items¹). The regions that showed this pattern of activation are in accord with those implicated in prior studies of episodic retrieval (Table 5). We had been particularly interested in whether the hippocampus would show this pattern of response and, indeed, activity in a region centered in the left anterior hippocampus² was related to accurate retrieval for emotional and neutral items (Fig. 1).

¹ The contrasts entered into the conjunction were analyzed at a threshold of $P < 0.05$. Because the P value of each individual contrast was lower than the standard threshold of $P < 0.001$, some regions that were not detected in the initial analyses (reported in Tables 1–4) were revealed by the conjunction analyses.

² Although the activity did extend anteriorly to the border with the amygdala, the cluster of activity was centered in the hippocampus.

Accurate retrieval for emotional but not neutral items

We were additionally interested in activity that was associated with accurate retrieval for the emotional items. To isolate these regions, we conducted a conjunction analysis of emotional word-only correct attributions > misattributions and emotional word–picture correct attributions > misattributions. Table 6 presents the regions that resulted in that conjunction, but not in the conjunction described above for both emotional and neutral items. Our a priori regions of interest had been the amygdala and orbitofrontal cortex, as activity in these regions has been shown to correspond with successful encoding of emotional items (Hamann, 2001; Phelps, 2004) and with retrieval-related processes for emotional information (Dolan et al., 2000; Sharot et al., 2004; Smith et al., 2004b). Activity in these regions was related to accurate retrieval specifically for the emotional items (Fig. 2), with ANOVA indicating a significant interaction between response type (correct attribution, misattribution) and emotion (emotional, neutral).

Accurate retrieval for neutral but not emotional items

To examine the regions that were associated with accurate retrieval for the neutral items, but not the emotional items, we performed a conjunction of neutral word-only correct attributions > misattributions and neutral word–picture correct attributions > misattributions. Table 7 presents the regions resulting from that analysis that were not included in the conjunction for both emotional and neutral items. Of most interest, activity in the inferior prefrontal cortex bilaterally and in the right posterior hippocampus was related to memory accuracy specifically for the neutral items and not for the emotional items [with ANOVA indicating a significant interaction between response type (correct attribution, misattribution) and emotion (emotional, neutral); Fig. 3].

Discussion

The central aim of this study was to examine the processes that were related to accurate memory assignment for emotional and neutral items. The results suggest three principal conclusions. First, activity in regions implicated in prior studies of episodic retrieval (including a region of activity centered in the anterior hippocampus) corresponded with accurate retrieval regardless of the item’s emotional content. Second, despite these commonalities, emotional content modulates the neural processes recruited during successful retrieval. Third, activity in the amygdala/periamygdala-

Table 2
Regions in which activity was related to accurate retrieval of neutral word–picture items ($P < 0.001$)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area
Middle frontal gyrus	L	–30, –9, 61 –27, 37, –7	–30, –8, 60 –28, 42, –5	BA 6
Medial frontal gyrus	L	–9, –6, 50	–14, –5, 50	BA 6
Precentral gyrus	L	–35, –20, 62	–34, –16, 56	BA 4
Postcentral gyrus	L	–48, –23, 51	–51, –21, 50	BA 1
Inferior parietal lobe	L	–33, –36, 43	–34, –35, 45	BA 7
Inferior temporal gyrus	L	–35, –64, –2	–37, –60, –4	BA 19/37
Cuneus	R	18, –97, –1	15, –91, –1	BA 18
Posterior cingulate gyrus	L	–3, –31, 24	–1, –31, 24	BA 23/31
Anterior hippocampus	L	–27, –6, –15	–28, –12, –12	
Putamen	R	24, 9, 9	27, 10, 7	
Thalamus				
Cerebellum				

loid cortex and orbitofrontal cortex does not merely inflate the confidence or vividness with which individuals believe that they remember information, but it also corresponds with accurate memory attributions for emotional information. We elaborate on each of these conclusions below.

Accurate retrieval for all items

A question posed by the present study regarded the neural processes that were related to accurate retrieval for all items, regardless of their emotional content. We were particularly interested in whether the hippocampus would show this pattern of results. As discussed in Introduction, hippocampal activity does not discriminate true and false recognition responses when false recognition signifies endorsement of an item semantically or visually associated with studied items (Cabeza et al., 2001; Slotnick and Schacter, 2004). The present study allowed examination of whether this finding would generalize to a paradigm in which false recognition was not driven by retrieval of gist-based (i.e., global semantic or visual) information present in many items from the encoding episode.

In contrast to those prior studies, activity in a region centered in the left anterior hippocampus was greater for correct attributions

than for misattributions regardless of the emotion type. These data suggest that this region plays a role in retrieval of particular contextual details required for accurate memory attribution (in this case, whether an item was externally presented). This finding aligns well with prior data implicating the anterior hippocampus in successful retrieval of contextual details associated with an encoding episode (e.g., Dobbins et al., 2003; Eldridge et al., 2000; Wheeler and Buckner, 2003) and in the ability to recognize items paired together at encoding (e.g., Giovanello et al., 2004). The present data further suggest that emotional content does not alter the relation of this region to accurate memory attribution: the anterior hippocampus appears important for accurate retrieval of emotional and neutral items.

More broadly, the network of regions that was related to accurate retrieval for all items, regardless of their emotional content, was consistent with that implicated in many prior studies of episodic retrieval. For example, activity in the left anterior prefrontal cortex has been found to be related to retrieval of perceptual details (Ranganath et al., 2000), and activity in the left parietal cortex also has been found to track the amount of contextual information retrieved (Cabeza et al., 2001; Henson et al., 1999a,b; Wheeler and Buckner, 2004). In fact, Cabeza et al. (2001) found that parietal activity distinguished true from false

Table 3
Regions in which activity was associated with accurate retrieval of emotional word-only items ($P < 0.001$)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area
Orbitofrontal gyrus	L	–12, 34, –7	–7, 34, –11	BA 11
Middle frontal gyrus	L	–30, 37, 42	–27, 36, 41	BA 8
Precentral gyrus	R	45, –9, 53	52, –5, 44	BA 4
Postcentral gyrus	R	54, –18, 51	42, –12, 37	BA 1
Precuneus	L	–9, –50, 44	–10, –48, 46	BA 7
Superior temporal gyrus	R	62, –43, 10	61, –42, 10	BA 22
Middle temporal gyrus	R	47, –49, 0	50, –50, 0	BA 21
		62, 0, –10	58, –1, –15	BA 21
		45, 12, –33	44, 12, –33	BA 38
		50, –1, –22	51, 0, –21	BA 20/21
	L	–56, –6, –22	–56, –6, –21	BA 20
Amygdala/peri-amygdaloid cortex	R	20, 0, –18	24, 0, –12	
Hippocampus	L	–27, –9, –22	–27, –12, –22	
Hippocampus/parahippocampal gyrus	R	21, –12, –22	22, –14, –24	
Cerebellum				

Table 4

Regions in which activity was associated with accurate retrieval of neutral word-only items ($P < 0.001$)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area
Middle frontal gyrus	R	29, 33, 29	23, 34, 28	BA 9
Inferior parietal lobe	R	47, -51, 22	50, -52, 22	BA 40
Postcentral gyrus	R	48, -22, 29	44, -24, 27	BA 2
Superior temporal gyrus	L	-41, 2, -10	-43, 3, -11	BA 22
Inferior temporal gyrus	L	-56, -21, -20	-55, -21, -22	BA 20
Putamen	R	27, -5, 8	25, -5, 8	

recognition, consistent with the findings of the present study. Activity in the posterior cingulate and inferior temporal gyrus also may be related to retrieval of contextual information: given the role of these regions in mental imagery and visual processing (D'Esposito et al., 1997; Ehrsson et al., 2003; Malouin et al., 2003; Mummery et al., 1999; Simons et al., 2001), it is plausible that activity in these regions is related to retrieval of visual information encountered during the study episode (either from mental imagery or photo presentation; see Kahn et al., 2004; Wheeler and Buckner, 2004; Wheeler et al., 2000).

In summary, the network of regions found to correspond with accurate memory attribution for emotional and neutral items fits well with prior studies of episodic retrieval. There appears to be broad overlap in the processes used to remember emotional and neutral events accurately, with activity in many regions, including the anterior hippocampus, relating to memory accuracy for emotional and neutral items.

Emotion modulates activity associated with retrieval accuracy

Despite these regions of overlap, emotional content did affect the neural processes that were associated with accurate memory assignment. Of note, activity in the amygdala/periamygdaloid cortex and orbitofrontal cortex was related to accurate retrieval only for the emotional items. These results confirm and extend the results from prior neuroimaging investigations of episodic retrieval of emotional information. The finding is consistent with prior evidence implicating limbic structures in retrieval of emotional information (Dolan et al., 2000; Sharot et al., 2004; Smith et al., 2004b) and further suggests that this activity is related not to

general emotional processing during retrieval but to accurate memory assignment.

In contrast to the pattern of activity in the amygdala/periamygdaloid cortex and orbitofrontal cortex, activity in the inferior prefrontal cortex bilaterally and in the right posterior hippocampus was associated with retrieval accuracy specifically for the neutral items. These regions often have been implicated in episodic retrieval (Cabeza et al., 2002; Greicius et al., 2003; Kensinger et al., 2003; Lepage et al., 1998; Pihlajamaki et al., 2003); however, it is not clear why this activity would be related specifically to accurate retrieval of neutral, and not of emotional, information. The dissociation may reflect differences in the types of information retrieved, or in the processes required to guide successful retrieval.

This ambiguity is related to an open question regarding whether the activity found to correspond with correct attributions vs. misattributions is the cause or effect of retrieval success. For example, the increased limbic activation for correctly attributed items could underlie successful recovery of information (e.g., modulation of recollective search processes) or, alternately, it could reflect the outcome of such recovery (i.e., the recapitulation of information from encoding). The present results cannot distinguish these possibilities. The fact that these same limbic regions have been found to be associated with successful encoding (Kensinger and Schacter, in press(a)) and with the retrieval of information encoded in an emotional context (Smith et al., 2004b) may suggest recapitulation processes. Prior studies have found that auditory cortex can become active when individuals retrieve items that had been paired with a sound, and that regions implicated in visual processing can become active when individuals retrieve items that

Table 5

Regions in which activity was related to accurate retrieval for emotional and neutral items (emotional correct attributions > emotional misattributions AND neutral correct attributions > neutral misattributions)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area
Superior frontal gyrus	L	-15, 48, 36	-15, 48, 36	BA 9/10
Middle frontal gyrus	R	39, 36, 18	39, 36, 14	BA 45/46
		36, 39, 21	35, 39, 17	BA 9/46
Insula	R	35, 6, 11	37, 8, 8	BA 13
Inferior parietal lobe	L	-32, -42, 26	-27, -45, 25	BA 7/40
	R	45, -39, 32	44, -38, 32	BA 40
Cingulate gyrus	R	18, -24, 37	18, -24, 38	BA 23/31
Inferior temporal gyrus	L	-59, -21, -16	-60, -21, -17	BA 20
	R	50, -50, -5	50, -50, -6	BA 37
Anterior hippocampus (see Fig. 1)	L	-21, -6, -18	-20, -13, -17	
Putamen	R	24, 9, 13	23, 6, 10	
Hypothalamus	R	5, -3, -9	4, -6, -12	

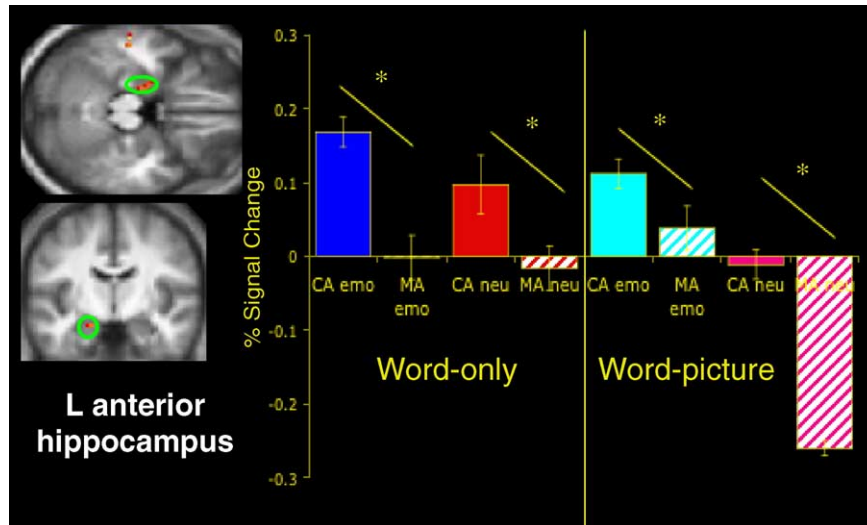


Fig. 1. Activity in a region centered in the anterior hippocampus was greater during retrieval of correctly-attributed (CA) as compared to misattributed (MA) emotional (emo) and neutral (neu) items. (*Indicates significant difference at $P < 0.05$).

were paired with a visual image (Kahn et al., 2004; Nyberg et al., 2000; Wheeler and Buckner, 2004; Wheeler et al., 2000; Vaidya et al., 2002). Thus, retrieval-related activity in limbic regions may reflect the repetition or bringing on-line of emotion-relevant information that was present during encoding. It also could reflect the reinstatement of the emotion evoked during encoding. However, it is also plausible that limbic activity enhances the processes that guide episodic retrieval. Perhaps, the amygdala influences medial temporal-lobe regions during retrieval, as well as during encoding and consolidation, increasing not only the likelihood that a memory is encoded and stored, but also the likelihood that the memory trace is reactivated at retrieval.

Similar logic can be used to contemplate the role of the prefrontal and posterior hippocampal regions that were implicated in accurate retrieval of the neutral, but not the emotional, items. These regions have been associated with successful encoding (reviewed by Paller and Wagner, 2002), and thus activity in these regions may represent recapitulation processes. However, it is equally plausible that these regions may be recruited in the service of information retrieval. Future studies will be required to disentangle the extent to which emotional content modulates processes that lead to, versus result from, recovery of information at retrieval.

Amygdalar activity is related to retrieval success

The results of the present study are important in indicating that activity in limbic regions (particularly the amygdala/periamygdaloid cortex and orbitofrontal cortex) can correspond with accurate retrieval. As outlined in Introduction, it has been unclear whether limbic engagement during memory retrieval would increase only the subjective richness associated with a memory (Dolcos et al., 2005; Sharot et al., 2004), or also its objective accuracy. Behavioral demonstrations of “flashbulb memories” have suggested that perhaps limbic engagement enhances primarily the former, as individuals often report high confidence in their memories of emotional events even when they are not remembered accurately (Talarico and Rubin, 2003; Winograd and Neisser, 1992; Neisser and Harsch, 1992). In contrast, demonstrations of enhanced source memory for emotional stimuli have suggested that limbic engagement may increase memory accuracy (e.g., Davidson and Glisky, 2002; Doerksen and Shimamura, 2001). The present study sheds light on this issue, indicating that limbic activity does not act solely on confidence assessments while leaving memory accuracy unchanged. Rather, amygdala/periamygdaloid activity during retrieval does correspond with increased memory accuracy. While the mechanisms underlying this relation require clarification, this

Table 6

Regions in which activity corresponded with accurate retrieval of emotional items (emotional correct attributions > emotional misattributions)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area
Inferior frontal/ orbitofrontal gyrus	L	-35, 43, -17	-35, 43, -17	BA 10/11/47
Superior temporal gyrus	L	-35, 13, -21	-35, 13, -21	BA 38
Middle temporal gyrus	R	48, -50, 0	50, -49, -4	BA 21
Temporo-parietal junction	L	-56, -54, 25	-45, -48, 18	BA 22/39/40
Fusiform gyrus	L	-41, -61, -14	-40, -62, -15	BA 37
	R	41, -70, -12	42, -68, -13	BA 37
Precuneus	L	-41, -71, 40	-40, -69, 40	BA 19
Amygdala/periamygdaloid cortex (see Fig. 2)	R	15, -2, -20	12, -1, -16	
Cerebellum				

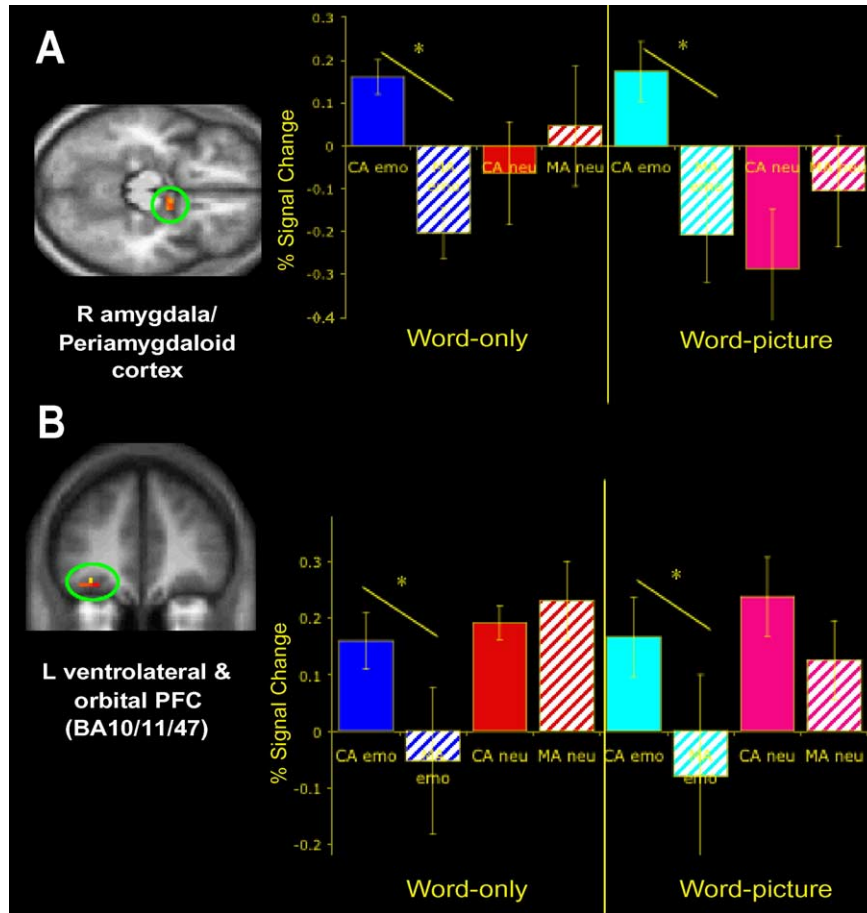


Fig. 2. Activity in the amygdala (A) and orbitofrontal cortex (B) was related to accurate retrieval for the emotional items, but not for the neutral items. CA = correct attribution; MA = misattribution.

study highlights the fact that amygdala engagement at retrieval, as well as during encoding (Kensinger and Schacter, in press(a)) can reduce the probability of memory misattributions.

Summary

By adopting a reality-monitoring paradigm that required participants to indicate which memories were attributable to external presentation, the present study could examine the processes engaged during correct memory attributions versus

misattributions of emotional and neutral items. The results indicated that many of the regions found to correspond with retrieval of contextual details for neutral items (e.g., Dobbins et al., 2003; Giovanello et al., 2004; Wheeler and Buckner, 2003) also were associated with accurate memory attribution for emotional items. Despite the overlaps in the neural networks, however, the emotional content of items affected the regions in which activity corresponded with accurate retrieval. Engagement of limbic regions was related to accurate retrieval of emotional items specifically, while engagement of additional prefrontal and medial temporal-lobe regions corresponded with accurate retrieval of

Table 7
Regions with activity was associated with accurate retrieval of neutral items (neutral correct attributions > neutral misattributions)

Region	Hemisphere	Talairach coordinates of peak voxel (x, y, z)	Talairach coordinates of center voxel (x, y, z)	Approximate Brodmann area (BA)
Inferior frontal gyrus	R	53, 20, 7	55, 21, 7	BA 45/47
	R	60, 15, 24	59, 15, 21	BA 9/44
	L	-51, 7, 19	-50, 7, 18	BA 9/44
Anterior cingulate gyrus	L	-11, 20, -4	-11, 19, -4	BA 24/32
Insula	L	-35, 11, -5	36, 13, 9	BA 13
Fusiform gyrus/ middle occipital gyrus	R	38, -70, -6	35, -61, 1	BA 19
Lingual gyrus	L	-24, -84, -6	-24, -84, -7	BA 18
Hippocampus (see Fig. 3)	R	18, -24, -4	18, -24, -7	

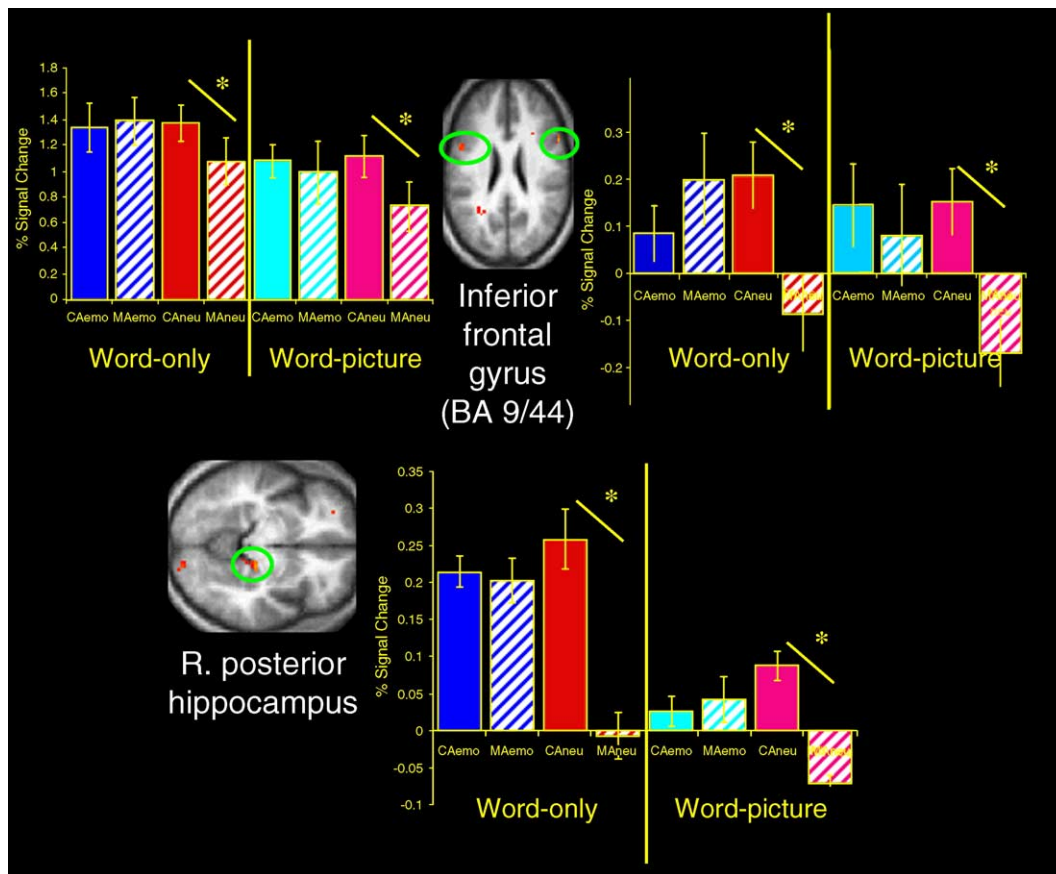


Fig. 3. Activity in the inferior prefrontal cortex bilaterally (A) and in the right posterior hippocampus (B) was associated with accurate memory retrieval for the neutral, but not the emotional, items. CA = correct attribution; MA = misattribution.

neutral items. Although the role of limbic structures during successful encoding of emotional information has been well established (e.g., Hamann, 2001; Phelps, 2004), to our knowledge, this study is the first to demonstrate a link between limbic engagement and accurate memory attribution at retrieval.

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