The role of medial temporal lobe in item recognition and source recollection of emotional stimuli

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Recent neuroimaging results suggest that distinct regions within the medial temporal lobe (MTL) may differentially support the episodic encoding of item and relational information for nonemotional stimuli (for a review, see Davachi, 2006). The present study was designed to assess whether these findings generalize to emotional stimuli. Behaviorally, we found that emotion reduced item recognition accuracy but did not reliably affect relational memory. fMRI analyses revealed that neutral and emotional words elicited distinct activation patterns within MTL regions predictive of subsequent memory. Consistent with previous findings for neutral words, hippocampal activation predicted later relational memory, whereas activation in the perirhinal cortex predicted successful item recognition. However, for emotional words, activation in the amygdala, hippocampus, and posterior parahippocampal cortex predicted item recognition only. These data suggest that MTL regions differentially support encoding of neutral and emotional stimuli.

It has long been known that structures in the medial temporal lobe (MTL), including the hippocampus, perirhinal, entorhinal, and parahippocampal cortices, are instrumental for episodic memory formation (Scoville & Milner, 1957). Research in both animals and humans has focused on characterizing the contributions that different MTL regions make to episodic memory formation (Cansino, Maquet, Dolan, & Rugg, 2002; Davachi, Mitchell, & Wagner, 2003; Jackson & Schacter, 2004; Kirwan & Stark, 2004; Ranganath et al., 2004; Sperling et al., 2003; see Brown & Aggleton, 2001, for a review). Although there is evidence for distinct contributions of MTL subregions in episodic memory formation for neutral stimuli (Davachi et al., 2003; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Ranganath et al., 2004; Uncapher & Rugg, 2005; for a review, see Davachi, 2006), the precise contribution of these structures to episodic memory formation for emotional stimuli remains relatively unexplored. The goal of the present research is to directly compare the contribution of distinct MTL subregions to the formation of episodic memories for neutral and emotional stimuli.

Evidence from animal studies suggests that encoding of the individual items encountered within an episode may be supported by mechanisms distinct from those involved in the encoding of the relationship among those items (Brown & Aggleton, 2001; Cohen & Eichenbaum, 1993). One widely used method for determining in humans which episodic memories contain item and relational information is to objectively measure the ability to recover a specific detail engendered within the encoding episode, commonly referred to as *source memory*. Accurate recollection of a specific contextual detail associated with an item is indicative of relational memory, whereas recognition of the item itself without accurate recollection of contextual details indicates item memory only. Neuroimaging studies have shown that encoding-related activity in the hippocampus and posterior parahippocampal cortex correlates with later relational memory, whereas encoding activity in the perirhinal cortex correlates with later item recognition, irrespective of recollection of episodic details (Davachi et al., 2003; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Ranganath et al., 2004; Uncapher & Rugg, 2005). Furthermore, patients with lesions limited to the hippocampus have been reported to be selectively impaired on recognition judgments that depend on recollection of episodic details, leaving item recognition proportionally intact (Holdstock et al., 2002; Mayes, Holdstock, Isaac, Hunkin, & Roberts, 2002; Mayes et al., 2004; Yonelinas et al., 2002; but see Manns, Hopkins, Reed, Kitchener, & Squire, 2003).

Many behavioral studies have asked whether item and relational memory are enhanced for emotional stimuli, relative to neutral ones. However, a review of the studies that measured memory for contextual details surrounding emotional stimuli indicates that there is little consensus as to whether emotion actually enhances relational memory. Whereas there have been some reports that emotion enhances the accuracy of memory for the font color of words or the cognitive operations performed during encoding (Doerksen & Shimamura, 2001; Kensinger & Corkin,

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2003; Kensinger & Schacter, 2005), other studies either have failed to replicate these findings or have reported a reduction in the accuracy of memory for other types of contextual details, such as the screen location of the test item (Cook, Hicks, & Marsh, 2007; D'Argembeau & Van der Linden, 2004; Mather et al., 2006). Thus, whether emotion enhances relational memory as determined by recollection of contextual details is, at present, unclear on the basis of the existing literature. Indeed, it is possible that emotion may enhance memory for some aspects of an event but not for others (Burke, Heuer, & Reisberg, 1992).

In the literature, there have been two neuroimaging studies in which an attempt has been made to identify the MTL encoding correlates of relational memory for emotional stimuli by testing memory for the cognitive operations performed during the encoding task. Kensinger and Schacter (2005) found that reality monitoring (e.g., the ability to correctly indicate whether an image was internally generated or actually seen) was more accurate for emotional than for neutral stimuli, and accurate, as compared with inaccurate, reality monitoring of emotional stimuli was associated with activity in the amygdala, posterior hippocampus, and posterior parahippocampal cortex. However, the memory test used by Kensinger and Schacter (2005) assessed accurate, as compared with inaccurate, recollection of the episodic details without the conditions necessary to determine whether these MTL regions also predicted item recognition independently of source. More recently, Kensinger and Schacter (2006) directly compared item recognition and relational memory for items that were encoded in one of two cognitive tasks; judgments of animacy or frequency. Using this paradigm, they found no behavioral difference in the source recollection accuracy for neutral and emotional stimuli, and they again reported that episodic encoding of emotional stimuli was dependent on the same MTL regions that were previously determined to support encoding of item and relational information for neutral stimuli. These data (1) demonstrate that emotion may not always enhance relational binding and (2) provide support for similar engagement of MTL regions during the encoding of neutral and emotional events.

In the present study, we also ask whether the same MTL regions support encoding processes that give rise to subsequent item and relational memory. However, our approach differs from previous studies in two potentially important ways. First, like several previous behavioral studies investigating memory for contextual details of emotional stimuli, we assessed relational memory for the font color of the encoding items, rather than memory for the encoding task. Studies of the contribution of MTL regions that support subsequent item and relational memory for emotional stimuli have not yet examined memory for an episodic detail intrinsic to the item itself. Second, we controlled for features of the stimuli that may have confounded the results of previous studies of memory for emotional stimuli. In particular, we matched the semantic relatedness of the neutral and emotional words (in addition to their word frequency) to prevent one class of items from being more distinctive than the other (e.g., Phelps et al., 1998).

The primary goal of this study was to determine whether the same or different MTL structures support item and relational memory for neutral and emotional stimuli. On the basis of previous findings, we expected that activation in the amygdala would be predictive of subsequent recognition memory for the emotional, but not the neutral, words (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000). If the same MTL structures support subsequent item recognition and relational memory for episodic details related to the item itself, as well as the encoding task, we would expect that activation in the perirhinal cortex would correlate with item recognition for both neutral and emotional stimuli and that activation in the posterior parahippocampal cortex and hippocampus would correlate with relational memory for neutral and emotional stimuli (e.g., Davachi et al., 2003; Kensinger & Schacter, 2006). Another possibility, however, was that the font color of emotional and neutral words might be processed differently, leading to distinct patterns of encoding activation in the MTL for neutral and emotional stimuli.

METHOD

Subjects

Data from 14 subjects (9 of them female, mean age = 24 years) were included in the analysis. The subjects were right-handed and native English speakers. They responded to a posted advertisement, and all gave informed consent. Data from an additional 15 subjects (9 of them female, mean age = 23) were excluded from the analyses due to chance-level source memory accuracy ($n = 4$), scanner malfunction ($n = 2$), or an inadequate number of observations (fewer than 9) for each predictor in the general linear model (GLM; $n = 9$).

Stimuli

Stimuli were selected from the Affective Norms for English Words (ANEW) pool of words (Bradley & Lang, 1999), for which normative valence and arousal scores were obtained. From the ANEW pool, 96 positive and arousing words (mean valence = 7.79; mean arousal = 6.48), 96 negative and arousing words (mean valence = 2.24; mean arousal = 6.63), and 192 neutral and nonarousing words (mean valence = 5.16; mean arousal = 4.15) were selected. Francis and Kučera (1982) word frequencies were equated for the groups in order to control for effects of item familiarity. Latent semantic analysis (Landauer, Foltz, & Laham, 1998) was used to control for semantic interrelatedness within each valence category of words (mean similarity: neutral = .12, negative = .14, positive = .13). This ensured that memorial differences between the emotional and the neutral words were not due to increased semantic relatedness among the emotional words (Phelps et al., 1998; Windmann & Kutas, 2001). Assignment of words to conditions was completely randomized.

Behavioral Task

Across two fMRI scans, subjects encoded 96 emotional (48 negative arousing and 48 positive arousing) and 96 neutral words presented in either red or blue font. On each encoding trial, subjects were instructed to generate a mental image of a spatial scene that integrated the study word and font color of the word. For example, subjects may have seen the word *terrorist* presented in blue font and would be instructed to imagine a scene incorporating *terrorist* with the color blue. Encoding trials consisted of the following events: presentation of a word in red or blue font for 500 msec, presentation of a fixation cross (+) for 4,000 msec, during which time subjects performed the imagery task, and finally presentation of a fixation cross in green font for 750 msec, indicating that subjects should rate their level of task success via a button box response. Subjects were

Table 1
Mean Image Ratings (and Standard Errors of the Means)
During Encoding as a Function of Emotion and
Source Recollection Accuracy

Source	Neutral		Negative		Positive	
	M	SEM	M	SEM	M	SEM
Accurate	3.83	0.04	3.75	0.04	3.81	0.04
Inaccurate	3.73	0.06	3.66	0.05	3.73	0.05

instructed to press "1" if they could not come up with an image at all, "2" if they came up with a faint nonspecific image, "3" if they came up with a rich image incorporating the font color but it was difficult to do so, and "4" if they came up with a rich image incorporating the font color with ease. The total duration of each encoding trial was 5,400 msec. Each encoding scan was 11.2 min in duration, and the two scans were separated in time by a brief delay. Subsequent memory analyses were limited to trials on which subjects indicated that they successfully formed a rich mental image that incorporated the font color (i.e., a 3 or 4 response).

An unscanned surprise two-step recognition memory test was given the next day (~21–26 h) following the encoding session. During each recognition trial, subjects first made an *old/new* recognition judgment; if an *old* response was made, subjects were then instructed to indicate whether the word had appeared in red or blue font. All 192 emotional and neutral studied items were presented for recognition, along with 192 emotional and neutral distractor items. This recognition test allowed us to divide encoding trials on the basis of whether subjects (1) later recognized the word and were able to recollect the color of the font (item + source), (2) later recognized the word but were not able to recollect the color of the font (item only), and (3) later forgot the word (forgotten).

fMRI Image Acquisition and Analysis

Functional imaging was performed on a 3 Tesla Siemens Allegra head-only scanner with a standard Siemens head coil located at the Center for Brain Imaging at New York University. Head motion was reduced by using a head-immobilizing pillow. Prior to functional imaging, high-resolution T1-weighted structural images were obtained for anatomical visualization of each subject. Functional slices were prescribed perpendicular to the axial plane of the hippocampus. Functional data were acquired with a fast gradient-echo echo-planar sequence (TR = 1,750 msec; TE = 30 msec; FOV = 114.6 mm; flip angle = 80°; bandwidth = 4,340), resulting in the acquisition of 32 3-mm-thick slices with a 0.6-mm gap between each slice, allowing whole-brain coverage. The experimental design was fast-event related; null trials were presented for a variable amount of time to introduce jitter among the experimental trials. Trials were presented in an optimized sequence to maximize power in each imaging run (Dale & Buckner, 1997).

fMRI data were analyzed with BrainVoyager software (Maastricht, Netherlands). Image preprocessing involved motion correction, spatial smoothing with a 3-D Gaussian filter (6-mm FWHM), temporal processing to remove scanner drift, and transformation into Talairach space to allow for group analyses. A random-effects GLM was used to construct group maps. Statistical contrast maps were created using a threshold of $p < .001$ uncorrected. We performed contrasts that were unbiased with respect to subsequent memory outcome and identified functional regions of interest (ROIs) from the resulting maps on the basis of a priori hypotheses. To ensure that regions involved in memory were not overlooked, we also performed direct memory contrasts separately for the neutral and the emotional items. The ROIs were further investigated by conducting random effects ANOVAs on the beta weight estimates of the time course of the hemodynamic response functions, and direct statistical contrasts were performed on the beta values representing the peak activation in percent signal change (7 sec post-stimulus-onset).

RESULTS

Behavioral Effects

We removed all encoding trials that received an image quality rating of 1 or 2, indicating the inability to perform the encoding task. This resulted in exclusion of 11% of the encoding trials. The remaining image ratings (3 and 4) are shown in Table 1 as a function of emotion and accuracy of subsequent source recollection. The image ratings were higher for items that were subsequently recognized with the correct source ($M = 3.8$) than for those with the incorrect source ($M = 3.7$) [$F(1,13) = 14.49$, $MS_e = 0.01$, $p < .01$]. Image ratings were also higher for the neutral items than for the negative items [$F(2,26) = 4.8$, $MS_e = 0.01$, $p < .05$], although the negative and the positive items did not differ from each other ($p > .20$).

There was a main effect of emotion on item recognition; subjects were more likely to respond *old* to both studied (mean: negative = .74, positive = .69, neutral = .62) and new (mean: negative = .33, positive = .25, neutral = .13) emotional words [$F(2,26) = 15.89$, $MS_e = 0.01$, $p < .01$]. In addition, recognition accuracy, as measured by d', was lower for negative ($d' = 1.15$) and positive ($d' = 1.26$) words than for neutral words ($d' = 1.53$) [$F(2,26) = 3.98$, $MS_e = 0.13$, $p < .05$].
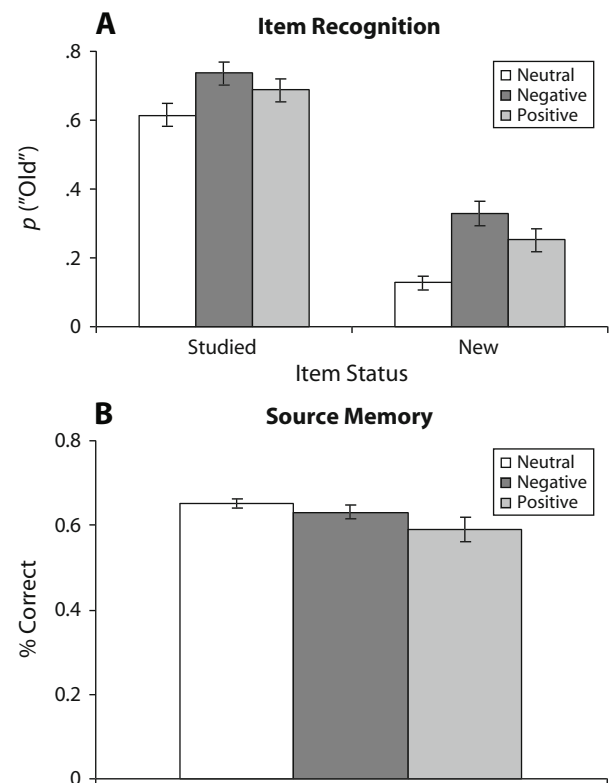

Figure 1. Item recognition and source memory accuracy. (A) Proportion of *old* judgments to emotional and neutral words as a function of item status and emotion. (B) Percentage of correct source judgments as a function of emotion.

Figure 2. The direct contrast between emotional and neutral encoding trials revealed that the left amygdala ($-24, -10, -11$) was more active during encoding of emotional words and the bilateral posterior parahippocampal cortex ($-26, -33, -10$ and $30, -34, -10$) was more active during encoding of neutral words. Amygdala activation is shown in red; posterior parahippocampal cortex activation is shown in blue.

Similarly, there was a nonsignificant trend for recollection of the font color to be more accurate for neutral words ($M = .65$) than for negative ($M = .63$) or positive ($M = .59$) words [$F(2,26) = 2.39$, $MS_e = 0.006$, $p = .11$]. Importantly, relational memory accuracy was significantly greater than chance for both neutral and emotional words (chance $= .50$, $p < .01$). The behavioral results are depicted in Figure 1.

fMRI Main Effects of Emotion

fMRI analyses revealed both overlapping and distinct regions of activation within the MTL during encoding of neutral and emotional words. Both neutral and emotional encoding trials, independently compared with baseline fixation, resulted in significant activation in the bilateral hippocampus (peak Talairach coordinates: neutral, -17, $-12, -10$ and $33, -19, -13$; emotional, $-31, -12, -12$ and $34, -18, -13$) and the left perirhinal cortex (neutral, $-33, -8, -24$; emotional, $-31, -4, -29$). Although the right hippocampal regions involved in encoding neutral and emotional items overlapped, we observed distinct regions of the left hippocampus involved in encoding neutral and emotional items. In addition, the comparison of neutral trials with baseline fixation revealed additional activation in the left parahippocampal cortex ($-32, -31$, -17), whereas the comparison of emotional items with fixation resulted in bilateral amygdala activation (17, $-12, -10$ and $-18, -10, -7$).

To statistically test for differences in MTL activation for neutral and emotional encoding trials, we performed a direct contrast of all neutral encoding trials to all emotional encoding trials. This confirmed the distinctions resulting from the individual contrasts, with significantly greater activation seen in the left amygdala ($-24, -9, -11$) during encoding of emotional words, as compared with neutral words, and greater activation in the bilateral posterior parahippocampal cortex ($-26, -33, -10$, and $30, -35$, -10) during encoding of neutral words, as compared with emotional words (Figure 2).

fMRI Subsequent Memory Effects

Performance on the two-step recognition memory test was used to classify each encoding trial according to whether the item was subsequently recognized and memory for the font color was accurate (item + source) or inaccurate (item only) or whether the item was missed on the recognition test (forgotten). If the same MTL regions support encoding of emotional and neutral stimuli, we would expect to find regions that were correlated with subsequent memory for both neutral and emotional stimuli. However, if distinct MTL regions support memory for neutral and emotional stimuli, we would expect to find regions that were correlated with memory for neutral or emotional stimuli, but not both. To this end, our fMRI data analysis involved identifying MTL regions that were engaged during the encoding task for neutral and emotional items and further investigating these ROIs to determine whether they predicted memory for the neutral words, the emotional words, or both.

All encoding trials versus fixation. In order to reveal the MTL regions that were engaged during encoding that were unbiased with respect to emotionality or subsequent memory, a direct contrast of all encoding trials (neutral and emotional) versus fixation was conducted

Figure 3. Medial temporal lobe regions that were predictive of subsequent memory for neutral stimuli. (A) Left hippocampus. (B) Left perirhinal cortex. Mean beta weights are shown in blue for neutral stimuli and in red for emotional stimuli.

and revealed several foci of activation in the MTL including the left amygdala (-16, -10, -7), the left perirhinal cortex (-34, -11, -16 and -34, -4, -30), and the left hippocampus (-29, -11, -10). Of these regions, activation within the left hippocampus (-29, -11, -10; see Figure 3A) and the left perirhinal cortex (-34, -11, -16; see Figure 3B) was predictive of subsequent memory for neutral words. ANOVAs conducted on the time course data extracted from these regions revealed that activity in the left hippocampus correlated with later source memory for neutral items. Specifically, significantly greater activation was observed in this region for item + source trials than for both item-only and forgotten trials [item only, $t(13) = 4.11$, $p < .01$; forgotten, $t(13) = 2.33$, $p < .05$]. Importantly, activation in this region did not correlate with later item recognition, since item-only trials did not differ from those that were later forgotten [$t(13) = -1.61$, $p > .10$]. Thus, encoding activation in the left hippocampus correlated with later source recollection, and not with item recognition. These findings replicate previous results implicating the hippocampus in episodic relational binding (Davachi et al., 2003; Ranganath et al., 2004) and, importantly, extend them by demonstrating that hippocampal encoding activation also correlates with binding of detailed features of the item itself, such as the font color (see also Staresina & Davachi, 2006; Uncapher & Rugg, 2005).

In contrast, the ROI analysis in the perirhinal cortex revealed a pattern consistent with a role in item encoding. Specifically, activation was significantly greater for

item + source and item-only trials than for forgotten trials [item + source, $t(13) = 2.50$, $p < .05$; item only, $t(13) = 2.44$, $p < .05$; see Figure 3B]. Critically, activation in this region did not differ for item + source trials and item-only trials ($p > .20$). Thus, encoding activation in the left perirhinal cortex correlated with subsequent item recognition for neutral items but did not differentially predict source recollection. This finding is also consistent with those of previous neuroimaging studies (Davachi et al., 2003; Ranganath et al., 2004) and adds support to the evidence from patient studies (e.g., Aggleton et al., 2005) identifying the perirhinal cortex as a putative MTL locus supporting episodic encoding of item information. The other MTL regions (left amygdala and an additional left perirhinal region) identified from the contrast of neutral and emotional trials, as compared with baseline fixation, were not predictive of subsequent memory for neutral words.

We next examined activation for emotional word trials within each ROI described above that was predictive of memory for the neutral stimuli in order to determine whether the same MTL regions predicted memory for neutral and emotional words. As can be seen in Figure 3 (panels A and B), the MTL ROIs that predicted memory for the neutral words were not predictive of memory for the emotional words. Thus, we next asked which MTL regions did support encoding of the emotional stimuli.

Further analysis of the ROIs identified from the direct contrast of all encoding trials (neutral and emotional) versus fixation revealed that the region of activation in the

Figure 4. Medial temporal lobe regions that were predictive of subsequent memory for emotional stimuli. (A) Right hippocampus. (B) Right parahippocampal cortex. (C) Left amygdala. Mean beta weights are shown in red for emotional stimuli and in blue for neutral stimuli.

right hippocampus shown in Figure 4A (34, −18, −13) was predictive of subsequent item recognition, but not of source recollection, for the emotional items. Activation was greater for emotional item + source trials and item-only trials than for forgotten trials [item + source > forgotten, $t(13) = 2.19$, $p < .05$; item only > forgotten, $t(13) = 2.25$, $p < .05$], with no difference seen between item + source and item-only trials ($p > .30$). The finding that encoding activation in the hippocampus correlated with item recognition, and not with accurate source recollection, is surprising and inconsistent with previous neuroimaging results for neutral stimuli (Davachi et al., 2003; Kirwan & Stark, 2004; Ranganath et al., 2004; but see Gold et al., 2006) and will be considered further in the Discussion section.

Neutral versus emotional encoding trials. In order to further consider that the encoding correlates for emotional and neutral stimuli may differ as a function of which regions were differentially engaged during encoding, we explored regions identified in the direct contrast between the neutral and the emotional encoding trials (left amygdala and bilateral posterior parahippocampal cortex). The results of the ROI analysis showed that greater activation in the right posterior parahippocampal cortex (30, −35, −10) correlated with *forgetting* for the emotional words (Figure 4B); there was more encoding activation in this region for emotional items that were subsequently forgotten, as compared with those that were recognized and accompanied by both accurate and inaccurate source recollection [item + source, $t(13) = 3.50$, $p > .01$; item only, $t(13) = 2.17$, $p < .05$]. Thus, not only does activity in this region show reduced activation during encoding of

emotional, as compared with neutral, items, but also this activation is inversely correlated with item recognition for emotional words. Activation in the amygdala and left parahippocampal ROIs identified in the contrast between neutral and emotional trials did not show subsequent memory effects for either emotional or neutral words.

Direct memory contrasts for emotional items. For completeness, additional direct memory contrasts were performed to reveal regions that were predictive of subsequent memory for emotional words at the statistical map level. The direct contrast of emotional items that were subsequently recognized (item + source and item only) with forgotten items revealed activation in the left amygdala (−18, −7, −7) that was spatially distinct from the ROI revealed from the contrast of emotional and neutral trials. Examination of the time courses revealed that, indeed, activation in this region correlated with subsequent item recognition only (item only and item + source > forgotten) for the emotional, but not the neutral, items (Figure 4C), in line with previous results implicating a role of the amygdala in item recognition, but not in source recollection (Kensinger & Schacter, 2006). A right posterior parahippocampal cortical region (39, −46, −4) was also revealed from this contrast. Like the left parahippocampal ROI identified from the emotion versus neutral contrast, greater encoding activation in this ROI also correlated with forgetting for the emotional words.

Finally, in order to reveal regions correlating with source recollection for emotional words, a direct statistical contrast of emotional item + source trials with item-only and forgotten trials revealed one region in the left precentral gyrus (−47, −7, 23). The time courses con-

firmed that this region was predictive of accurate source recollection (item + source > item only and forgotten) for the emotional words. This finding was not predicted but was interesting, given that other recent studies have reported encoding-related activity in the precentral gyrus for subsequent recollection of episodic details of neutral (Ranganath et al., 2004) and emotional (Mather et al., 2006) stimuli. Surprisingly, we did not find any MTL regions that correlated with source memory for emotional words.

DISCUSSION

The results of this study inform two questions about episodic recognition memory of emotional stimuli. First, do the same MTL structures support memory encoding for neutral *and* emotional stimuli? And second, does relational memory for a contextual detail of an item (e.g., the font color) result in the same pattern of MTL encoding activation as relational memory for a component of the general encoding context (e.g., the encoding task itself)? Our neuroimaging findings extend previous results for neutral stimuli by demonstrating that distinct MTL subregions (the perirhinal cortex and the hippocampus) support later item and relational memory, respectively, even when relational memory depends on recovery of a feature of the encoding item (but see Gold et al., 2006). On the other hand, we found that MTL encoding activation in the amygdala, hippocampus, and parahippocampal cortex correlates exclusively with item recognition of emotional stimuli and does not respond differentially to relational memory for a feature of the encoding task. These findings suggest that nonoverlapping MTL regions predict memory for neutral and emotional stimuli. Furthermore, these data suggest that the emotionality of an experience may impact upon what elements are bound into a memory trace.

Many previous studies of item and relational memory for neutral stimuli have operationalized relational memory as the recovery of the cognitive operation performed during the encoding task (Davachi et al., 2003; Dobbins, Rice, Wagner, & Schacter, 2003; Gonsalves et al., 2004; Kahn, Davachi, & Wagner, 2004; Ranganath et al., 2004). In contrast, in our study, relational memory was dependent upon recovery of the font color of the encoding item. Specifically, the encoding task in our study required subjects, first, to form a rich mental image of a scene corresponding with each word and then, additionally, to incorporate the color of the font (red or blue) into the scene. Attention to the font color of the words was required in order to incorporate the color into the scenes, but it can be considered a detail of the encoding event and secondary to the primary goal of imagining a scene. Nonetheless, using this paradigm, we replicated previous results for neutral stimuli in showing that activation in the hippocampus correlates with subsequent relational memory accuracy, whereas activation in the perirhinal cortex was predictive of item recognition only (Davachi et al., 2003; Kensinger & Schacter, 2006; Kirwan & Stark, 2004; Ranganath et al., 2004; Uncapher & Rugg, 2005; but see Gold et al., 2006). These data are consistent with the notion that hippocampal

encoding mechanisms support the relational binding of various episodic details, irrespective of their domain or salience to the event (Cohen & Eichenbaum, 1993).

In contrast to the subsequent memory results for neutral stimuli, we found that activation in the left amygdala, right hippocampus, and right parahippocampal gyrus predicted later item recognition for emotional stimuli. Indeed, a region in the precentral gyrus was the only brain region where activation correlated with accurate source memory for emotional stimuli. Consistent with previous research (e.g., Canli et al., 2000; Kensinger & Corkin, 2004), we find that encoding activation in the amygdala and hippocampus correlates with recognition memory for emotional stimuli. Interestingly, however, we did not reveal any MTL region—most notably, the hippocampus—where activation differentially correlated with later source recollection for emotional stimuli. Furthermore, we also did not see any evidence that the same MTL regions predicted memory for both neutral and emotional stimuli. Indeed, an exhaustive analysis of encoding activation in the MTL revealed that no one ROI predicted memory for both neutral and emotional stimuli.

These data suggest that even though the encoding task was identical for neutral and emotional items, the underlying encoding mechanisms supporting later memory for neutral and emotional stimuli differ. There are two possibilities that remain to be examined. First is the possibility that the emotionality of a stimulus leads to differential allocation of attention to various aspects of the event. In our task, arousal associated with the emotional words may have reduced processing of the item-level information, as well as the processes involved in binding of the font color with the scene. This notion is consistent with Easterbrook's (1959) hypothesis that emotional stimuli produce a narrowing of attention that affects subsequent memory performance and may explain both the effects of emotion that we observed behaviorally and the differential subsequent memory effects in the MTL. Specifically, if the neutral and emotional encoding trials elicit distinct cognitive processing because subjects are attending differentially to the details of the items and the event, regions that correlate with subsequent memory should also differ, since these regions are a subset of the regions engaged during encoding (Paller & Wagner, 2002). If this is the case, our differential MTL effects may reflect the differing content of the representations that result from the arousal of the emotional stimuli. Another possibility, however, is that the differential activation seen here fundamentally reflects differences in the anatomical and functional connections from the amygdala to the rest of the MTL (Phelps, 2004; Stefanacci, Suzuki, & Amaral, 1996). From this perspective, the observed effects of emotion are a consequence of arousal's leading to amygdala activation, which, in turn, leads to the activation of pathways within the MTL distinct from those engaged for neutral stimuli.

The behavioral analysis revealed that the emotional arousal of the words increased the likelihood of classifying them as *old* regardless of whether they had actually been encountered previously. In relational memory performance, there was a trend for recollection of the font color

to be greater for neutral than for emotional words. Indeed, the finding that, overall, subjects tended to report greater success (3.8, as compared with 3.7) during encoding in incorporating the font color into the scenes for neutral than for emotional items may help explain why we observed a difference in source memory. This finding is in contrast to some previous reports in the literature of enhanced source memory for the font color of emotional words (Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; but see D'Argembeau & Van der Linden, 2004), although other studies have shown no difference in source memory accuracy for neutral and emotional stimuli (e.g., Cook et al., 2007; Kensinger & Schacter, 2006; Mather et al., 2006). It is noteworthy that none of these prior studies have controlled for all the other factors that influence memory independently of emotional arousal, such as semantic relatedness. A consequence of this is that both memory performance and functional activation in these prior studies may not have been driven entirely by emotion per se but, rather, by other factors that make emotional stimuli either more distinctive or interrelated (Phelps et al., 1998; Phelps, LaBar, & Spencer, 1997).

There are also methodological differences across the studies that do and do not report enhanced source memory for emotional events. For example, in studies reporting source memory enhancement for emotional words, memory encoding was intentional because subjects were explicitly alerted to the fact that memory for the font color would be tested later (e.g., Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003). Thus, emotionality may enhance source memory for information that is made more salient, and attention may have been better oriented to the font color under intentional encoding instructions in these studies. When encoding occurs under incidental conditions, the emotionality of a stimulus may be less likely to orient attention to the font color, which is not intrinsically emotional, but, instead, may modulate attention to other aspects of the encoding event (but see D'Argembeau & Van der Linden, 2004, for an exception).

The idea that the neutral and the emotional encoding trials elicited different attentional demands may also explain why no relational encoding effects were observed in the hippocampus for emotional items, as have been reported in previous studies (Kensinger & Schacter, 2005, 2006). Arousal during emotional trials may have led to less binding of the font color to the emotional imagined scenes, consistent with the trend for poorer source memory performance that we observed for emotional stimuli. However, there is always the possibility with source memory paradigms that other contextual details of the encoding experience will be bound into memory, although subjects do not recollect the criterial piece of information (e.g., font color). Thus, it is possible that recollection contributed to subsequent memory for emotional items in our study, just not criterial recollection of the font color. If this was the case, it is not surprising that the hippocampus showed equivalent levels of activation for item-only and item + source trials. This possibility underscores the importance of cautious interpretation of a null effect when using such paradigms. Of course, a second possibility,

related to the first, is that we did not have enough power in our paradigm to detect a source memory effect in the MTL, and this remains to be further examined. Thus, we interpret our lack of a hippocampal source memory effect for emotional words not as representing a distinction in the role of the hippocampus in relational binding per se but rather, perhaps, as being a consequence of the limitations of using source memory paradigms in which one piece of criterial information distinguishes between memory conditions.

One particularly striking aspect of the fMRI data is that we observed a main effect of emotion in an MTL region not commonly associated with emotional processing, the posterior parahippocampal cortex. Specifically, this region was *less responsive* during emotional than during neutral encoding trials (similar to the results in Dolcos, LaBar, & Cabeza, 2004; see also Sharot, Delgado, & Phelps, 2004, and Sharot, Martorella, Delgado, & Phelps, 2007, for similar findings during retrieval). The posterior parahippocampal cortex has been previously implicated in scene processing (Epstein & Kanwisher, 1998), scene imagery (Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001), and the successful encoding of scene stimuli (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Kirchhoff, Wagner, Maril, & Stern, 2000; Stern et al., 1996). The role of this region in encoding appears to not be specific to scene stimuli per se, but encoding activation in the posterior parahippocampal cortex has also been implicated in successful relational encoding of episodic details (Davachi et al., 2003; Ranganath et al., 2004). To our knowledge, this is the first time that encoding activation in the posterior parahippocampus has been shown to correlate with subsequent memory for emotional stimuli. A critical point, however, is that activity was greater in the posterior parahippocampal cortex for emotional items that were subsequently *forgotten*. Taken together, to the extent that the operations supported by the posterior parahippocampal region are important in the representing and encoding of episodic details, including spatial layout, the present findings suggest that when a subject successfully encodes the emotional item, attention to the surrounding details of the episode (in this case, the imagined image and the font color) may suffer. On the other hand, it is also possible that during unsuccessful encoding of the emotional item (i.e., forgotten trials), subjects may have been engaging in enhanced episodic relational processing for a noncriterial detail of the encoding event, at the expense of memory for the item. Future work should focus on specifying the consequences of enhanced item processing, as may occur with emotion, compared with encoding of different types of contextual details that may suffer.

In conclusion, we find that different regions of the MTL predict memory for neutral and emotional words. Whereas our fMRI data are consistent with previous findings for neutral stimuli, they suggest that emotion may fundamentally change the pattern of activation in the MTL during encoding and, thus, alter the correlation of activation in these regions with subsequent item and relational memory. Behaviorally, emotion reduced item

discriminability and tended to reduce detailed source encoding. Our MTL imaging results revealed that activation in many MTL regions, including the amygdala and hippocampus, correlated with subsequent item memory for emotional stimuli. Interestingly, reduced activation in the posterior parahippocampal cortex was correlated with memory formation only for emotional stimuli. This raises the possibility, although speculative, that emotion may reduce attention to certain types of contextual details. The role of future research in understanding the differences in memory-encoding tasks as they relate to memory for episodic details will be critical to understanding how emotion influences memory.

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