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The effects of valence and arousal on the neural activity leading to subsequent memory

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Abstract

This study examined how valence and arousal affect the processes linked to subsequent memory for emotional information. While undergoing an fMRI scan, participants viewed neutral pictures and emotional pictures varying by valence and arousal. After the scan, participants performed a recognition test. Subsequent memory for negative or high arousal information was associated with occipital and temporal activity, while memory for positive or low arousal information was associated with frontal activity. Regression analyses confirmed that for negative or high arousal items, temporal lobe activity was the strongest predictor of later memory whereas for positive or low arousal items, frontal activity corresponded most strongly with later memory. These results suggest that the types of encoding processes relating to memory (e.g., sensory vs. elaborative processing) can differ based on the affective qualities of emotional information.

Research has consistently shown that emotional information is remembered better than nonemotional information. The enhancement in memory for emotional information exists for positive as well as for negative stimuli, and for nonarousing as well as arousing stimuli. However, the processes supporting the memory enhancement are likely to differ depending on the valence (how positive/pleasant or negative/unpleasant) and arousal (how exciting/agitating or calming/subduing) of the emotion elicited by the stimuli (see Kensinger, 2004; LaBar, 2007 for discussion).

The vast majority of studies that have examined the neural processes that support memory enhancement for emotional information have focused on the influence of the arousal dimension in relation to the “memory modulation hypothesis” of emotional memory (Cahill, 2000; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Canli, Desmond, Zhao, & Gabrieli, 2002; McGaugh, 2004). This hypothesis proposes that interactions between the amygdala and the hippocampus guide successful encoding and consolidation of emotionally arousing information. In support of this hypothesis, a number of studies have revealed that activity in the amygdala and the hippocampus corresponds with the likelihood that emotionally arousing information is later remembered (reviewed by Phelps, 2004; LaBar & Cabeza, 2006). These interactions between the amygdala and the hippocampus appear to modulate memory for both positive and negative information, so long as it is arousing (e.g., Dolcos, LaBar, & Cabeza, 2004a; Kensinger & Schacter, 2006; Sharot, Delgado, & Phelps, 2004). By contrast, interactions between these regions seem not to play a critical role in influencing memory for emotional experiences that are of insufficient arousal to trigger autonomic responses (e.g., Kensinger & Corkin, 2004; Anderson, Yamaguchi, Grabski, & Lacka, 2006).

Though the majority of research on emotional memory has focused on these amygdala-hippocampal interactions, there are mechanisms aside from these interactions that are proposed to guide successful encoding of emotional information. Recently, increasing emphasis has been placed on emotion's ability to influence encoding via interactions with elaborative, attentional, and sensory processes supported by regions of the prefrontal cortex, parietal cortex, and fusiform/parahippocampal gyri (e.g., Dolcos et al., 2004b; Kensinger, Garoff-Eaton, & Schacter, 2007; Sommer et al., 2008; Talmi et al., 2008; see Dolcos & Denkova, 2008 for a review). For example, memory for emotional items appears to be enhanced due to the item's distinctiveness (Schmidt & Saari 2007; Talmi, Schimmack, Paterson, & Moscovitch, 2007) and semantic relation to other items (Buchanan, Etzel, Adolphs, & Tranel, 2006; Dewhurst & Parry, 2000; Manning and Julian, 1975; Talmi, et al., 2007; Talmi & Moscovitch, 2004), due to selective attention devoted to the item (e.g., Kensinger & Corkin, 2004; Kern, Libkuman, Hajime, & Holmes, 2005), and due to enhanced sensory processing of the item (e.g., Kensinger, Garoff-Eaton, & Schacter, 2007; Talmi et al., 2008).

Though there has been increasing evidence for the role of these processes in guiding emotional memory, it has been unclear whether the strength of influence of these processes differs based on the arousal or the valence of the emotional information. Some research has suggested that cognitive benefits from elaboration or semantic relatedness may primarily be important for boosting memory for nonarousing information and may play less of a role in guiding memory when stimuli are arousing (e.g., Buchanan et al., 2006; Kensinger & Corkin, 2004; LaBar, 2007). Thus, when information is nonarousing, divided attention has a large impact on memory (Kensinger & Corkin, 2004; Kern et al., 2005), and controlling for factors such as semantic relatedness or elaborative processing tends to eliminate the advantage in memory for the nonarousing emotional items (e.g., Buchanan et al., 2006; Talmi & Moscovitch, 2004). By contrast, for arousing information, memory may be supported primarily by amygdala-hippocampal interactions (e.g., Sommer et al., 2008; Kensinger & Corkin, 2004) or by enhanced sensory processing (Kensinger et al., 2008; Talmi et al., 2008). Thus, memory for arousing items may include more sensory detail (Mather & Nesmith, 2008; MacKay et al., 2004) and may do so even in the face of limited attentional resources (e.g., Bush & Geer, 2001; Kern et al., 2005).

Though these studies emphasize the importance of paying attention to a stimulus' arousal level, the valence of the item may also critically impact the influence of cognitive factors (see discussion in Dolcos & Denkova, 2008). Less research has been conducted in this vein. However, there is some evidence to suggest that frontal-mediated elaborative processes may be disproportionately tied to the encoding of positive information while temporo-occipital mediated sensory processes may be disproportionately involved in the encoding of negative information (Dolcos et al., 2004b; Mickley & Kensinger, 2008).

Based on the evidence outlined above, it seems plausible that frontal regions are most important when information is either positive or nonarousing, and that temporo-occipital processes become more important when information is either negative or arousing. However, no study has simultaneously examined the effects of arousal and valence on subsequent memory for emotional stimuli, nor has any study examined whether some regions are *stronger* predictors of subsequent memory performance than others. Thus, it remains an open question how valence and arousal impact the array of processes recruited in the service of episodic encoding.

The goal of this study was to examine the encoding processes beyond amygdala-hippocampal interactions that correspond with later memory for items with a range of valence and arousal characteristics. Based on the extant data, we hypothesized that items

that were negative, and items that were arousing, would be more likely to be associated with engagement of sensory regions (e.g., regions of the temporo-occipital cortex such as the fusiform and parahippocampal gyri) during encoding. This hypothesis was based upon prior evidence suggesting that negative arousing items are particularly likely to be remembered with visual detail (reviewed by Kensinger, in press) and that negative items that are later remembered vividly elicit more visual activity at encoding than do positive items that are later remembered vividly (Mickley & Kensinger, 2008). We also hypothesized that items that were positive, and items that were low in arousal, would be associated with additional memory-related recruitment of regions tied to conceptual and semantic processing, including regions of the prefrontal cortex. This hypothesis arose from prior findings that positive and low arousal items are more likely to be remembered without episodic details than are negative or high arousal items (Ochsner, 2000; LaBar et al., 1998), suggesting that these items may be processed in a more schematic or conceptual fashion, and with less attention to detail (see reviews by Anderson, 2005; Gasper, 2004; Gasper & Clore, 2002). Because regions of the ventrolateral prefrontal cortex have frequently been tied to elaborative processing (e.g., Bookheimer, 2002; Raposo et al., 2008), and regions within the dorsolateral prefrontal cortex have been linked to the ability to manipulate and monitor information held in mind (e.g., Mottaghy, 2006; Naghavi & Nyberg, 2005), we hypothesized that these lateral frontal regions might play a particularly important role in supporting the successful encoding of positive or nonarousing information. With regard to valence effects within the prefrontal cortex, it has been proposed that the processing and expression of positive affect may be guided disproportionately by *dorsolateral* (rather than ventrolateral) prefrontal regions (e.g., Dolcos et al., 2004a; Kensinger & Schacter, 2006) and by left-lateralized prefrontal regions (reviewed by Davidson & Irwin, 1999; Dolcos & Denkova, 2008 for discussion). Based on these data, it seemed plausible that the link between prefrontal engagement and memory for positive information could be particularly strong within left dorsolateral prefrontal regions; however, because these prior studies had not directly examined the dorsal/ventral or left/right distinctions in relation to subsequent memory, it was also possible that lateral prefrontal engagement would more generally correspond with memory for positive information, without following those same anatomical subdivisions.

These hypotheses were examined by showing participants positive arousing, positive nonarousing, negative arousing, negative nonarousing, and neutral photographs while they underwent an fMRI scan. Neural activity during encoding was sorted based upon whether the photographs were later recognized or later forgotten, to allow us to distinguish how valence and arousal influences the processes corresponding with subsequent memory. Regression analyses were then conducted to examine whether the neural processes that were the strongest predictors of subsequent memory differed as a function of valence or arousal.

Method

Participants

There were twenty-one participants (12 men) who took part in this study. Two participants were excluded: one was trying to remember the pictures during the encoding task, and one reported an anxiety disorder. Thus, the reported analyses included nineteen participants (11 men). All participants were right-handed native English-speakers, aged 18 – 35, with no history of psychiatric or neurological disorders. All participants had normal or corrected to normal vision. Depressed participants and participants taking medication that would affect the central nervous system were excluded from the study. Informed consent was obtained in a method approved by the institutional review boards from Massachusetts General Hospital and Boston College.

Materials

The stimuli were 350 pictures: 70 negative arousing (M (SD) valence = 2.9 (0.76), M (SD) arousal = 5.9 (0.48)), 70 negative nonarousing (M (SD) valence = 2.9 (0.71), M (SD) arousal = 4.2 (0.66)), 70 positive arousing (M (SD) valence = 7.2 (0.54), M arousal = 5.9 (0.57)), 70 positive nonarousing (M (SD) valence = 7.1 (0.54), M (SD) arousal = 5.9 (0.43)) and 70 neutral pictures (M (SD) valence = 5.1 (0.38), M arousal = 3.3 (0.84)) taken from the International Affective Picture System database (Lang, Bradley & Cuthbert, 1999). Positive, negative and neutral pictures were matched on visual complexity, brightness [as indicated in Adobe Photoshop (Adobe Systems, San Jose, CA)], and number of pictures that included people, animals and buildings/landscapes (normative data from Kensinger & Schacter, 2006). Care was taken to assure that positive and negative images were equated on arousal level (i.e., positive arousing images were just as arousing as negative arousing images, and positive nonarousing and negative nonarousing images were of similarly low arousal levels; $p > .2$). Valence also was equated across arousal levels (e.g., positive arousing images and positive nonarousing images were rated as similarly positive in valence, $p > .2$) as were absolute valence differences between the positive and negative stimuli (e.g., the negative and positive images were given valence ratings that were equivalently far away from neutral valence; $p > .2$).

Procedure

Participants underwent a functional magnetic resonance imaging (fMRI) scan as they viewed 175 pictures (35 from each emotion category). The stimuli were presented for 2000 ms. During this time, participants were asked to rate the quality of the picture, with high ratings signifying “high enough quality to be found in a magazine such as National Geographic or The Smithsonian” and low ratings signifying that the picture was not of high enough quality to be found in such a magazine. A task was included to assure that participants were attending to each of the stimuli, and this particular task was chosen because it did not force participants to process the affective content of the pictures. Interstimulus intervals were jittered, ranging from 2 to 14 s, in order to optimize the ability to isolate the hemodynamic response associated with each picture’s presentation (Dale, 1999)

About 1.5 hours later, outside the scanner (after completing an hour long attention task), participants underwent a surprise recognition test. Participants were shown a series of pictures on a computer for 2 s each and were asked to indicate if each item was one that they had seen in the scanner. If the participant indicated that it was an item that they had seen before, the participant was then asked to complete a modified version of the Memory Characteristics Questionnaire (MCQ, Johnson, Foley, Suengas, & Raye, 1988), though responses to these questions will not be discussed here.

There were 350 total pictures at test, one fifth from each emotion category (positive arousing, positive nonarousing, negative arousing, negative nonarousing, and neutral). Half of the items from each emotion category were old and half were new. Items from each emotion category, and items that were old and new, were intermixed randomly. The recognition test remained the same for all participants; the study lists viewed while participants were inside the fMRI scanner were counterbalanced to determine which of the tested items were old and which were new. Pictures that served as studied items versus as nonstudied foils were balanced for their valence and arousal ratings as well as for brightness and for the number of pictures that included people, animals and buildings/landscapes.

Image Acquisition and Preprocessing—Data was acquired on a 1.5 Tesla Siemens whole body Avanto MRI scanner (Erlangen, Germany) using a standard birdcage head coil.

The stimuli were projected from a Macintosh iBook G4 to a Sharp200 color LCD projector through a collimating lens (Buhl Optical) that projected onto a screen mounted in the magnet bore. Participants viewed the screen through mirrors located on the head coil.

Anatomic data were acquired with a multiplanar rapidly acquired gradient echo (MP-RAGE) sequence (TR = 2,730 ms, TE = 3.31 ms, flip angle = 40°, Field of view = 256 × 256 mm, acquisition matrix 256 × 256, slice thickness = 128, slice thickness = 1.33 mm, no gap, 1×1×1.33 mm resolution). Co-planar and high-resolution T1 weighted localizer images were acquired. In addition, a T1 weighted inversion recovery echo planar image was acquired for auto alignment.

Functional images were acquired via a T2* weighted echo planar imaging sequence sensitive to the blood oxygenation level dependant (BOLD) signal, with a repetition time (TR) of 3000 ms, an echo time (TE) of 40 ms, and a flip angle of 90°. Twenty-nine interleaved axial-oblique slices (parallel to the line between the anterior and posterior commissures) were collected in a 3.125 mm × 3.125 mm × 3.72 mm matrix with a 3.12 thickness and a 0.6 mm skip between slices.

Preprocessing and data analysis were completed using SPM2 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, London, UK). Slice time correction was completed and motion correction was run, using a six parameter, rigid body transformation algorithm by SPM2. The images were normalized to the Montreal Neurological Institute template (resampling at 3mm isotropic resolution), and spatial smoothing was completed at a 7.6 mm isotropic Gaussian kernel.

Event-Related fMRI Data Analysis—Events were divided based upon the emotion category of the pictures. Items from each emotion category were further divided into subsequent hits (remembered items) and subsequent misses (forgotten items). Event-related analyses were completed using the general linear model approach: for each participant, on a voxel by voxel basis, event types were modeled through convolution with a canonical hemodynamic response function. This yielded beta-weights for each voxel. For each statistical contrast, voxels were considered active when the difference between beta-weights was statistically positive as determined by a one-tailed paired t-test with variance estimated using random-effect analysis. The results of these contrast analyses were restricted to regions that consisted of at least five contiguous voxels, all active at $p < .001$, unless otherwise specified. All activations are presented in neurological coordinates while voxel coordinates are reported in Talairach coordinates at the most significant voxel in each cluster (Talairach & Tournoux, 1988). The data are displayed on canonical images provided within SPM2.

To depict the pattern of activity within regions of interest (ROI), 8mm spheres were created around regions identified within contrast analyses, and signal change within these spheres was estimated using the MarsBar toolbox implemented within SPM2 (Brett et al., 2002). For each region and for each item type, the magnitude of the subsequent memory effect was calculated (i.e., activity to subsequently forgotten items was subtracted from activity to subsequently remembered items), and the centered (z-scored) subsequent-memory effects are depicted in the bar graphs accompanying the figures.

Multiple Regression Analyses—Multiple regression analyses were conducted to examine which regions were the strongest predictors of subsequent memory performance. Separate regression analyses were conducted for each type of emotional item. Participants' ability to recognize that type of item (i.e., their corrected recognition score) was the dependent variable and the independent variables were the peak levels of activity reached

within five regions of interest. These regions of interest were defined functionally, from a whole-brain analysis that revealed the regions that corresponded with subsequent recognition, collapsing across all encoded items. This analysis revealed regions that showed a tie to subsequent memory, but importantly, the analysis was unbiased with regard to whether those regions corresponded with subsequent memory for all item types or for only a subset of them. The five regions that emerged from this analysis and that were included in the regression analyses were: the left middle frontal gyrus (spanning Brodmann Area (BA) 9 and 46; Talairach coordinates: $-38, 18, 28$), the left middle occipital gyrus (BA 18; Talairach coordinates: $-26, -86, -1$), the left anterior hippocampus (Talairach coordinates: $-34, -9, -21$), the left temporal lobe (spanning BA 37 and 39; Talairach coordinates: $-38, -60, 6$) and the bilateral amygdala (taken as the signal change averaged across clusters centered at Talairach coordinates: $-24, -1, -18$ and $22, -2, -16$). Signal change was extracted from 8mm spheres centered on each of these regions using the Marsbar toolbox implemented within SPM2 (Brett et al., 2002). The peak percentage of signal change reached between 4–6 sec post-stimulus onset was computed separately for each item type, for each person, and for each region, and these were the values that were entered into the regression analysis.

Results

Behavioral Results

Corrected recognition scores were calculated by subtracting the false alarm rate from the hit rate, and these corrected recognition scores were computed separately for each emotional item type (e.g. “old” responses to new negative arousing items were subtracted from “old” responses to old negative arousing items). In addition, difference scores were computed for each emotion category by subtracting the corrected recognition rate for neutral items from the corrected recognition rate for a particular emotion type (e.g., negative arousing rate – neutral rate). These difference scores were computed in order to allow us to examine the effects of valence and arousal on emotional memory. An ANOVA with valence (positive, negative) and arousal (high, low) as within-subject factors was conducted on the corrected recognition difference scores, revealing only a significant effect of arousal, $F(1, 18) = 14.596$, $p < .01$, Partial Eta Squared = .448, with arousing items remembered better than nonarousing items (see Table 1). Items from each emotion subtype were remembered with greater recognition accuracy than neutral items (all $t > 3.2$, $p < .01$) with a single exception; positive nonarousing items were not remembered significantly more often than neutral items ($t(18) = 1.38$, $p > .10$).

Functional MRI Results

Though our principle interest was in examining neural activity as a function of valence and arousal, we first wanted to make sure that our results generally replicated those from previous studies of emotional memory. We therefore performed an analysis to reveal the regions that corresponded more strongly with subsequent memory for all emotional items (regardless of valence or arousal) than for neutral items (i.e., [emotional remembered items > emotional forgotten items] > [neutral remembered items > neutral forgotten items]). As would be expected based upon the results of prior experiments, this analysis revealed activity in the amygdala and the hippocampus as well as a number of regions within the frontal lobe and temporo-occipital cortex (see Table 2).

As outlined in the introduction, our main interest was in examining how arousal and valence influence the relation between encoding processes and subsequent memory. Therefore, for the remainder of analyses, we focused on the comparison between the different types of emotional items (i.e., excluded neutral items) and examined how valence and arousal

affected the neural processes that corresponded with subsequent memory for emotional items (see Table 3 and Table 4).¹

Effects of Arousal on Subsequent Memory Processes—An interaction contrast analysis was conducted to determine the regions that were more active in the successful encoding of arousing items than in the successful encoding of nonarousing items, i.e., (arousing remembered items – arousing forgotten items) > (nonarousing remembered items – nonarousing forgotten items) (See Figure 1 and upper portion of Table 3). By definition, these regions' activity corresponded not just to the arousal level of the stimuli, or just to subsequent memory performance, but to the interaction between arousal and subsequent memory. Because the analysis revealed no areas in which five contiguous voxels were all significant at $p < .001$, we lowered the threshold to require the five contiguous voxels to each be significant at $p < .005$. This analysis revealed a network of regions in the frontal, parietal and occipital lobes. When the threshold was lowered to $p < .01$, activity in the bilateral amygdala also was revealed (Talairach coordinates $-24, -4, -21$ and $20, -4, -18$). A separate interaction analysis was conducted to determine the regions that were more active in the successful encoding of nonarousing items than in the successful encoding of arousing items, i.e., (nonarousing remembered items – nonarousing forgotten items) > (arousing remembered items – arousing forgotten items). Of most interest, this analysis revealed a number of regions within the frontal lobe as well as the cuneus (See Figure 1 and lower portion of Table 3). To further elucidate whether a different pattern of correspondence to subsequent memory existed in the frontal lobe versus the temporo-occipital lobe, an ANOVA was conducted on the strength of the subsequent memory effect shown in the regions included Table 3 with arousal (low, high) and brain region (frontal, temporo-occipital) as factors. This ANOVA revealed an interaction between arousal and brain region ($F(1, 150) = 10.68, p < .01$), with a greater subsequent memory effect in the frontal lobe when items were low in arousal, but a greater subsequent memory effect in the temporo-occipital lobe when items were high in arousal (see Figure 1).

Effects of Valence on Subsequent Memory Processes—Interaction analyses were conducted to determine the regions that were more active in the successful encoding of positive items (collapsed across both arousal levels) than in the successful encoding of negative items (collapsed across both arousal levels; i.e., [negative remembered items – negative forgotten items] > [positive remembered items – positive forgotten items]) and vice versa (see Figure 2 and Table 4). Successfully encoded negative items were associated with more activity than successfully encoded positive items in a network that included the parahippocampal gyrus, the thalamus, and other occipital and temporal regions. Successfully encoded positive items yielded more activity than successfully encoded negative items in the frontal and parietal lobes, including the middle and superior frontal gyrus and the inferior parietal lobule. Thus, the successful encoding of positive items was disproportionately associated with engagement of a fronto-parietal network whereas the successful encoding of negative items was associated with increased activity within a temporo-occipital network.

Regression Analysis

The analyses described so far suggested that different regions correspond with subsequent memory for items that are negative or arousing (temporo-occipital regions) versus for items that are positive or nonarousing (frontal regions). To more specifically assess whether there were differences in the regions that were the strongest predictors of later memory performance, we conducted separate regression analyses for each type of emotional item

¹As depicted in the bar graphs accompanying the figures, arousal effects generalized to both valences, and valence effects were apparent at both arousal levels.

with the ability to recognize that type of item (corrected recognition score) as the dependent variable. The independent variables were activity within regions of interest in the middle frontal gyrus, the left middle occipital gyrus, the hippocampus, the left temporal lobe, and the bilateral amygdala (see the Methods section for details on the selection of these regions). The results showed that the activity that most strongly predicted subsequent memory performance differed based upon the valence and arousal of the emotional item. For arousing items, only increased activation of the temporal lobe predicted subsequent recognition scores ($\beta = .905$, $t = 2.42$, $p < .05$). Similarly, for negative items, only increased activation in the temporal lobe predicted corrected recognition scores ($\beta = .682$, $t = 2.133$, $p < .055$). For nonarousing items, increased activation of the frontal lobe predicted corrected recognition scores ($\beta = .925$, $t = 3.34$, $p < .01$), and there was a negative relationship with the middle occipital gyrus such that more activity in the middle occipital gyrus predicted lower corrected recognition scores ($\beta = -0.741$, $t = -2.127$, $p < .055$). For positive items, no region reached significance, though there was a marginal effect indicating that activation of the frontal lobe was related to corrected recognition scores ($\beta = 0.591$, $t = 1.87$, $p < 0.1$). For neutral items, only increased activity in the hippocampus corresponded with later memory ($\beta = .705$, $t = 2.76$, $p < .05$).

Discussion

The present results emphasize the importance of looking beyond amygdala-hippocampal interactions to understand the effects of valence and arousal on subsequent-memory processes. Activity in the amygdala and hippocampus did relate disproportionately to later memory for emotional compared to neutral information, and activity in the amygdala was particularly related to subsequent memory for arousing information (see also Kensinger & Corkin, 2004; Anderson et al., 2006). However, activity in a number of frontal, parietal, and occipital regions also corresponded with subsequent memory for emotional items, and the link between these regions' engagement and subsequent memory performance differed depending upon the valence and arousal of the emotional stimuli. The successful encoding of arousing and negative information was associated with occipito-temporal regions, whereas the successful encoding of nonarousing and positive information involved more frontal activation. The importance of each of these findings will be elaborated upon below.

Effects of Arousal on Subsequent Memory

As noted above, subsequent memory for arousing information was associated with more activity than subsequent memory for nonarousing information in regions such as the inferior parietal lobule, the middle occipital gyrus and the parahippocampal gyrus. Because these regions have been previously associated with sensory processing and with visual attention and visual memory, we believe that the link between activity in these posterior cortices and subsequent memory for arousing items may represent the tie between successful encoding of arousing information and the implementation of enhanced attentional and sensory processing. For example, regions in the middle occipital gyrus have been associated with visual attention and sensory processing (Clower, West, Lynch, & Strick, 2001; Mangun, Buonocore, Girelli, & Jha, 1998), while the parahippocampus has been associated with visiospatial memory (Cabeza et al., 2004; Davachi, Mitchell, & Wagner, 2003; Squire, Stark, & Clark, 2004). The inferior parietal lobule is important in the guidance of attention, and it has robust connections with the parahippocampal gyrus (Clower, et al., 2001), making it well suited to serve as an interface between attentional and mnemonic processes. Given the role of these regions, it seems likely that these structures together may focus attention and sensory processing resources on the arousing pictures, enhancing memory for those images.

The correspondence of these processes to the successful encoding of arousing items would be consistent with extensive evidence that arousal can enhance perceptual processing (see Lang et al., 1998; Lane, Chua, & Dolan, 1999) and that visual attention can be captured by and focused on arousing stimuli to a much greater extent than on nonarousing stimuli (Anderson, 2005; Keil & Ihssen, 2004; Reisburg & Hertel, 2004). Indeed, previous behavioral studies have implicated the attentional focusing on arousing information as an important influencer of subsequent memory (Talmi, Anderson, Riggs, Caplan & Moscovitch, 2008; Keil & Ihssen, 2004; Reisburg & Hertel, 2004; Kensinger, Garoff-Eaton & Schacter, 2007); although further research will be required to confirm the importance of the link between visual attention, sensory processing, and memory for arousing information, it seems likely that the network revealed here influences later memory through the guidance of attention toward arousing information.

Regression analyses revealed that out of all of the regions included within the model, it was posterior temporal activity that showed the strongest correspondence to later memory for arousing items. This area of the temporal lobe has also been associated with visual processing and object recognition (e.g., Nakamura et al., 2000; Tanaka, 1997), and so the link between this region and subsequent memory for the arousal items is in keeping with our proposal that high-arousal information may be retained well because of the enhanced sensory processing engaged during encoding. It is interesting to note that this posterior temporal activity was an even stronger predictor of subsequent memory than amygdala activity, plausibly because we tested memory after a fairly short (1.5 hr) delay. It is possible that the role of the amygdala may become exaggerated after longer delays, due to its influence on consolidation processes (e.g., McGaugh, 2004; Talmi et al., 2008), while after shorter delays, sensory or attentional processes may play a more dominant role. This finding emphasizes the importance of examining activity beyond that of the amygdala when investigating the mechanisms by which emotion enhances memory, particularly when short delay intervals are used.

In contrast to the pattern of results revealed for the arousing items, subsequent memory for nonarousing information was associated with more activation in bilateral frontal areas, and frontal activity was the strongest predictor of performance on the recognition memory test (again, an even stronger predictor than the amygdala, perhaps because of the short delay after which memory was assessed).

The regions of the frontal lobe such as the middle frontal gyrus have been implicated in a range of tasks that rely on conceptual processing. For example, middle frontal gyrus activity has been revealed when participants process the meaning of cartoons (Gallagher et al., 2000) or engage in self-referential processing of trauma-related autobiographical information (Reinders et al., 2003). Although theory of mind processing may be most commonly connected to activity within the medial frontal gyrus (Fletcher et al., 1995; Gallagher et al., 2000; Stone, Baron-Cohen & Knight, 1998), studies also have revealed enhanced activity in regions of the lateral middle frontal gyrus as well (Gallagher et al., 2000; Marjoram et al., 2006; Vollm et al., 2005), suggesting that these lateral regions may also play a role in working with information relevant to understanding others' minds or social interactions. More generally, the middle frontal gyrus has been linked to verbal elaboration and to semantic processing (e.g., Kirchhoff, Shapiro, & Buckner, 2005; Logan, Sanders, Snyder, Morris & Buckner, 2002), thus it is plausible that this activity influences memory through the engagement of self-referential and elaborative processing.

The link between activity in these prefrontal regions and subsequent memory for nonarousing information is consistent with the proposal that nonarousing information may be remembered well because of people's enhanced conceptual and elaborative processing of

this information (see Kensinger, 2004; LaBar, 2007). These findings are generally consistent with those of Kensinger & Corkin (2004), who found that memory for nonarousing items was associated with enhanced prefrontal engagement during encoding. They also are consistent with the proposal that attention focusing on emotional information may be particularly likely to occur when information is arousing, whereas nonarousing information may be less prone to automatic attention capture (e.g., Anderson, 2005; MacKay et al., 2004; Mather, 2007) and may benefit more from effects of emotion on elaborative or organizational encoding processes (e.g., Talmi et al., 2004).

Effects of Valence on Subsequent Memory

There were also differences in the encoding of subsequently remembered pictures based on valence. Specifically, negative items that were later remembered engaged more activity in areas such as the lingual gyrus and the middle temporal gyrus than did positive items that were later remembered, and activity within these temporo-occipital regions was the strongest predictor of later memory for the negative items. Interestingly, very similar regions were shown in a prior study to be disproportionately engaged during the encoding of negative high-arousal items as compared to positive high-arousal items (Mickley & Kensinger, 2008), particularly when the negative items were later vividly recollected. Thus, it appears to be a consistent finding that the encoding of negative items recruits more temporo-occipital activity than does the encoding of positive items. These regions of the temporo-occipital cortex have been associated with visual processing in a number of studies (Macaluso, Frith & Driver, 2000; Tanaka, 1997), and these regions are particularly likely to be engaged during the processing of negative items (reviewed by Dolan & Vuilleumier, 2007). Based on the extant data, it seems plausible that these temporo-occipital regions may show a particularly strong tie to subsequent memory for negative information because of the more focused attention and analytical processing associated with negative items (Gasper, 2004; Gasper & Clore, 2002).

The successful encoding of positive pictures was associated with more activity in areas in the superior and middle frontal gyrus than was the successful encoding of negative pictures. Once again, these prefrontal regions overlapped with those that had been revealed in a previous study to correspond with successful encoding of positive items more than negative items, particularly when those positive items were later judged to be familiar rather than vividly recollected (Mickley & Kensinger, 2008). These regions are thought to be associated with conceptual and elaborative processing (Gallagher et al., 2000; Reinders et. al., 2003), so we believe that these regions' correspondence to the encoding of positive items reflects the fact that these positive items are processed in a more conceptual and heuristic fashion than negative items (Fredrickson & Branigan, 2005; Rowe, Hirsh & Anderson, 2007). There was not evidence of a dorsal/ventral or left/right distinction with regard to the prefrontal regions that corresponded with memory for positive items: Activity in both superior and inferior frontal regions corresponded with subsequent memory for positive items, as did activity in both the left and right hemisphere. Given the dearth of data that speak to the link between prefrontal recruitment and valence-specific modulation of memory, it remains to be clarified whether there are prefrontal specializations with regard to the link between subsequent memory and valence-specific processing, and if so, how best to characterize those specializations.

Though continued research will be required to test the validity of the hypothesis that memory for negative items is tied to more sensory processes whereas memory for positive items is tied to more conceptual processing, the present results are consistent with that hypothesis. More generally, the present results emphasize that the influence of valence on the neural processes supporting subsequent memory is a factor that will need to be more closely examined in future research. The vast majority of theories regarding emotion's

effects on memory have only considered the arousal level of the stimuli, and have not simultaneously considered the item's valence. However, as outlined in the introduction, there are an increasing number of studies suggesting that valence can also influence the behavioral effects of emotion on memory, and the present study adds to a small but growing literature emphasizing that the neural processes that support memory may also differ based upon stimulus valence (reviewed by Dolcos & Denkova, 2008; Kensinger, in press). The current results emphasize the need to consider the effects of both arousal and valence on emotional memory, particularly when examining processes beyond those implemented via amygdala-hippocampal interactions.

General Conclusions

Although previous studies have focused primarily on interactions between the amygdala and other regions of the medial temporal lobe during the encoding of emotional items, the present results emphasize that there are other regions that are important in the encoding of emotional memories. Emotional information can be better remembered than nonemotional information not only because of amygdala-hippocampal interactions but also because of widespread changes in activity within the frontal lobes as well as the temporal and occipital cortices. The present study also emphasizes that the particular way in which emotion influences memory is critically impacted by the valence and arousal of an emotional experience. The temporo-occipital regions are more strongly associated with subsequent memory for arousing information and for negative information, while regions in the frontal lobes, including the lateral middle frontal gyrus, are associated with the subsequent memory of nonarousing information and of positive information. Focusing on the array of mechanisms through which emotion can influence memory will be likely to provide important insights (e.g., Sommer et al., 2008; Talmi et al., 2008), and the present results emphasize the need to consider both item valence and item arousal when examining the myriad processes that can influence the formation of emotional memories.

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Figure 1. Effects of arousal on subsequent memory

The red regions were disproportionately related to subsequent memory for the arousing items compared to the nonarousing items, i.e., (arousing remembered items – arousing forgotten items) > (nonarousing remembered items – nonarousing forgotten items). The green regions were disproportionately tied to subsequent memory for the nonarousing items, i.e., (nonarousing remembered items – nonarousing forgotten items) > (arousing remembered items – arousing forgotten items). Bar graphs indicate the magnitude of the z-scored subsequent memory effect for each valence and arousal type, with higher values indicating a greater difference between the amount of activity to subsequently remembered versus subsequently forgotten items.

Figure 2. Effects of valence on subsequent memory

The red regions were disproportionately related to subsequent memory for negative items compared to positive ones, i.e., (negative remembered items – negative forgotten items) > (positive remembered items – positive forgotten items). The green regions showed the opposite correspondence, i.e., (positive remembered items – positive forgotten items) > (negative remembered items – negative forgotten items). Bar graphs indicate the magnitude of the z-scored subsequent memory effect for each valence and arousal type, with higher values indicating a greater difference between the amount of activity to subsequently remembered versus subsequently forgotten items.

Table 1

Mean (SE) hit, false alarm, and corrected recognition (hit – false alarm) rates as a function of emotion type.

	Positive Arousing	Positive Nonarousing	Negative Arousing	Negative Nonarousing	Neutral
Hits	0.70 (0.03)	0.62 (0.03)	0.72 (0.03)	0.66 (0.04)	0.62 (0.04)
False Alarms	0.03 (0.01)	0.04 (0.02)	0.04 (0.02)	0.02 (0.01)	0.09 (0.01)
Corrected Recognition	0.66 (0.03)	0.58 (0.04)	0.68 (0.04)	0.63 (0.04)	0.53 (0.04)

Table 2

Regions disproportionately associated with the successful encoding of emotional items compared to the successful encoding of neutral items. All effects were significant at $T > 3.20$, $p < .001$ and a five voxel extent.

Hemisphere	Lobe	Region	Talairach Coordinates (x, y, z)	Approx. Brodmann Area
Right	Frontal	Inferior Frontal Gyrus	55, 29, 6	45
Left	Frontal	Medial Frontal Gyrus	-4, 63, 17	10
Right	Frontal	Medial Frontal Gyrus	8, 59, 19	10
Right	Occipital	Superior Occipital Gyrus	40, -82, 23	19
Left	Occipital	Middle Occipital Gyrus	-36, -91, 14	19
Left	Occipital	Middle Occipital Gyrus	-53, -70, 7	19
Left	Occipital	Middle Occipital Gyrus	-22, -91, 16	18
Left	Occipital	Middle Occipital Gyrus	-22, -99, 9	18
Left	Occipital	Middle Occipital Gyrus	-38, -91, 3	18
Right	Occipital	Middle Occipital Gyrus	28, -93, 8	18
Right	Occipital	Middle Occipital Gyrus	22, -99, 3	18
Right	Occipital	Inferior Occipital Gyrus	44, -70, -5	19
Right	Occipital	Cuneus	30, -90, 23	19
Right	Temporal	Superior Temporal Gyrus	36, -42, 11	41
Right	Temporal	Middle Temporal Gyrus	40, -60, -4	37
Right	Temporal	Middle Temporal Gyrus	46, -49, -4	37
Right	Temporal	Middle Temporal Gyrus	40, -73, 24	39
Right	Temporal	Inferior Temporal Gyrus	48, -64, 0	37
Left	Temporal	Inferior Temporal Gyrus	-55, -68, 0	
Right	Temporal	Fusiform Gyrus	36, -34, -17	20
Right	Temporal	Fusiform Gyrus	48, -45, -11	37
Right	Limbic	Insula	42, -40, 17	13
Left	Limbic	Amygdala	-22, -5, -15	
Right	Limbic	Hippocampus	32, -13, -18	
Right		Striatum	34, -8, -10	
Right		Striatum - Caudate	36, -16, -8	
Left		Striatum - Caudate	-8, 8, -4	
Left		Cerebellum	-30, -44, -16	
Left		Cerebellum	-28, -34, -18	

Table 3

Effect of Arousal. Regions that were disproportionately active during the successful encoding of arousing items (top portion of table) or nonarousing items (bottom portion of table). All effects were significant at $T > 3.10$, $p < .005$ and a five voxel extent.

Hemisphere	Region	Talairach Coordinates (x, y, z)	Approx. Brodmann Area
(arousing remembered items – arousing forgotten items) > (nonarousing remembered items – nonarousing forgotten items)			
Left	Inferior Parietal Lobule	–55, –35, 39	40
Left	Middle Occipital Gyrus	–26, –71, 9	30
Right	Precentral Gyrus	36, –3, 26	6
Left	Parahippocampal Gyrus	–16, –22, –19	28
Right	Inferior frontal gyrus	48, 5, 26	9
(nonarousing remembered items – nonarousing forgotten items) > (arousing remembered items – arousing forgotten items)			
Right	Superior Frontal Gyrus	2, –32, 59	6
Right	Middle Frontal Gyrus	44, 2, 44	6
Left	Inferior Frontal Gyrus	–36, 22, 21	9
Left	Cuneus	–26, –88, 34	19

Table 4

Effect of Valence. Regions that were disproportionately active for the successful encoding of negative items (top portion of table) or of positive items (bottom portion of table). All effects were significant at $T > 3.35$ $p < .001$ and a five voxel extent.

Hemisphere	Region	Talairach Coordinates (x, y, z)	Approx. Brodmann Area
(negative remembered items –negative forgotten items) > (positive remembered items – positive forgotten items)			
Right	Precentral Gyrus	32, –28, 59	4
Right	Middle Temporal Gyrus	55, –31, –3	21
Left	Parahippocampal Gyrus	–28, –51, –3	19
Left	Lingual Gyrus	–24, –58, 1	19
Left	Thalamus	–14, –33, 7	
(positive remembered items –positive forgotten items)> (negative remembered items – negative forgotten items)			
Left	Superior Frontal Gyrus	–26, 56, –11	11
Left	Middle Frontal Gyrus	–40, 11, 31	9
Right	Middle Frontal Gyrus	24, 9, 27	8
Right	Middle Frontal Gyrus	38, 47, 11	10
Right	Middle Frontal Gyrus	34, 53, 7	10
Right	Inferior Parietal Lobule	50, –52, 52	40
Left	Thalamus	–24, –21, 5	