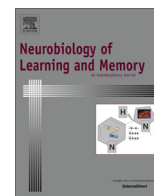




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Review

Prior perceptual processing enhances the effect of emotional arousal on the neural correlates of memory retrieval

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ABSTRACT

A fundamental idea in memory research is that items are more likely to be remembered if encoded with a semantic, rather than perceptual, processing strategy. Interestingly, this effect has been shown to reverse for emotionally arousing materials, such that perceptual processing enhances memory for emotional information or events. The current fMRI study investigated the neural mechanisms of this effect by testing how neural activations during emotional memory retrieval are influenced by the prior encoding strategy. Participants incidentally encoded emotional and neutral pictures under instructions to attend to either semantic or perceptual properties of each picture. Recognition memory was tested 2 days later. fMRI analyses yielded three main findings. First, right amygdalar activity associated with emotional memory strength was enhanced by prior perceptual processing. Second, prior perceptual processing of emotional pictures produced a stronger effect on recollection- than familiarity-related activations in the right amygdala and left hippocampus. Finally, prior perceptual processing enhanced amygdalar connectivity with regions strongly associated with retrieval success, including hippocampal/parahippocampal regions, visual cortex, and ventral parietal cortex. Taken together, the results specify how encoding orientations yield alterations in brain systems that retrieve emotional memories.

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1. Introduction

It is well known that emotionally arousing events are better remembered than neutral events. This effect is modulated by the release of stress hormones that affect noradrenergic transmission in the basolateral amygdala and its interactions with the anterior medial temporal lobes, which are important for memory formation, consolidation, and/or retrieval operations (Dolcos, LaBar, & Cabeza, 2004; Kensinger, 2009; LaBar & Cabeza, 2006; McGaugh, 2004; Wolf, 2008). However, very little is known about the neural bases of cognitive factors known to modulate emotional memory, such as encoding orientations that determine how emotional information is processed.

One variable that may modulate the effect of emotional arousal on memory is the degree to which perceptual properties of stimuli or events are attended or processed. A fundamental idea in memory research is that semantic processing leads to better memory than perceptual processing (the levels-of-processing effect, or LOP) (Craik & Lockhart, 1972). However, the vast majority of the studies showing the LOP effect have used affectively neutral information (Craik, 2002), and it is unclear if the effect generalizes

to emotional information. In fact, studies have shown that attending to and processing perceptual, rather than semantic, aspects of incoming information tends to boost emotional memory (Jay, Caldwell-Harris, & King, 2008; Reber, Perrig, Flammer, & Walther, 1994; Ritchey, LaBar, & Cabeza, 2011). For instance, Reber et al. (1994) found that whereas recall of neutral words showed the standard LOP effect, such that performance was higher for semantic than perceptual processing, recall of emotional words showed a “reverse LOP effect,” wherein performance was higher for perceptual than semantic processing. More generally, mounting evidence from different literatures and methodological techniques suggests a strong link between emotional memory and perceptual processing, particularly for negative emotions. For example, vivid visual imagery of negative events is frequently reported by patients with post-traumatic stress disorder (Hackmann & Holmes, 2004). In addition, emotional memories are often subjectively rated as more vivid (e.g., Kensinger & Corkin, 2003; Ochsner, 2000) and may contain sensory details absent in neutral memories (Doerksen & Shimamura, 2001). In the domain of implicit memory, emotion has been shown to enhance perceptual (LaBar et al., 2005) but not conceptual (Ramponi, Handelsman, & Barnard, 2010) priming effects. Finally, research on affect labeling (e.g., Lieberman et al., 2007) has shown that activity in emotion-related limbic regions is reduced when people attend to or label the semantic category or emotional pictures, suggesting that semantic encoding orientations may actually dampen emotional experience.

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The neural mechanisms whereby perceptual processing enhances emotional memory are unclear. There is evidence that emotion enhances visual cortex activity (Bradley et al., 2003; Lang et al., 1998; Sabatinelli, Lang, Keil, & Bradley, 2007; Simpson et al., 2000), most likely via feedback projections from the amygdala to visual cortex (Amaral, Behnia, & Kelly, 2003; Anderson & Phelps, 2001). However, neural evidence of the link between perceptual processing and emotional memory is scarce and available only for encoding. One recent fMRI study (Todd, Talmi, Schmitz, Susskind, & Anderson, 2012) found that visual noise overlaid on scenes was rated as less noisy when the scenes were emotional, an effect that was linked to activations in the amygdala and occipital cortex. Importantly, these activations also predicted memory vividness ratings on a recognition test 1 week later (see also Todd, Schmitz, Susskind, & Anderson, 2013). In another study (Kensinger, Garoff-Eaton, & Schacter, 2007), right amygdalar activity during object encoding predicted the ability to distinguish between identical and visually similar objects during retrieval. Finally, Ritchey et al. (2011) found that right amygdala activity predicted subsequent emotional memory to a greater extent when pictures were perceptually- rather than semantically-encoded.

Although the foregoing studies established preliminary links between perceptual processing and emotional memory encoding, it is an open question whether prior perceptual processing enhances the neural mechanisms of emotional memory during retrieval. Because perceptual processing occurs during encoding, any effect on retrieval mechanisms would have to be mediated by the nature of memory representations. That is, a difference in amygdalar activity as a function of *prior* processing strategy cannot be explained by processes elicited by the retrieval cue, but rather has to be mediated by the nature of the memory representations stored during perceptual processing and recovered during retrieval. It is currently uncertain how perceptual processing applied during memory formation will affect neural activations that occur during later emotional retrieval.

A second open question is whether prior perceptual processing enhances the quality of emotional memories. In addition to quantitative differences in memory strength, episodic memory researchers distinguish two qualitatively different forms of memory: recollection and familiarity (for review, see Yonelinas, 2002). Recollection refers to remembering a past event together with its associated contextual details, whereas familiarity refers to knowing that the event occurred in the past in the absence of contextual details. Several studies have shown that emotion tends to enhance recollection rather than familiarity (Douglass, Phelps, & Davachi, 2007; Ochsner, 2000; Sharot, Verfaellie, & Yonelinas, 2007). Dolcos, LaBar, and Cabeza (2005) found that, during retrieval, the emotion-induced enhancement of recollection was mediated by increased activity in the amygdala and the hippocampus. It is unknown, however, how the mechanisms of emotional recollection are modulated by prior perceptual processing.

Finally, a third open question is whether the enhancing effects of prior perceptual processing on emotional memory are mediated by localized changes in the amygdala or whether they also involve changes in the interactions between the amygdala and the regions mediating successful memory operations. In fMRI studies of recognition memory, successful retrieval has been associated with increased activations in hippocampus (e.g., Buckner & Wheeler, 2001; Dobbins, Rice, Wagner, & Schacter, 2003), and the enhancing effects of emotion on memory have been linked to increases in amygdalar activity with the hippocampus (Dolcos et al., 2005). In non-memory studies, as noted above, emotional effects on visual processing have been linked with feedback projections from the amygdala to visual cortex (Amaral et al., 2003; Anderson & Phelps, 2001). However, it is currently uncertain how prior perceptual processing enhances amygdalar interactions with medial temporal and other cortical regions associated with memory success. One possibility is that perceptual processing during encoding may draw attention to the salient features of the emotional materials, resulting in a richer, more detailed memory trace with more arousal

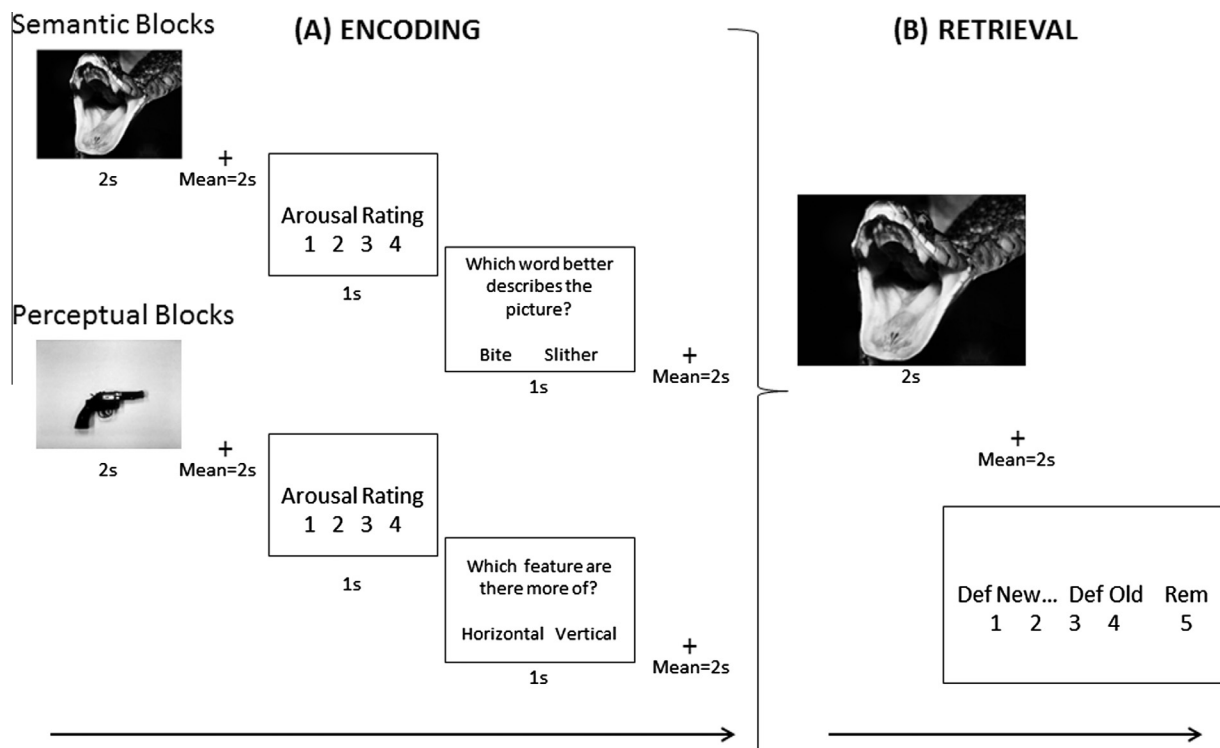


Fig. 1. Paradigm. Emotional and neutral pictures were assigned to semantic and perceptual encoding conditions, blocked across runs. Recognition memory was tested two days later.

attached to it. As such, when participants see that picture again, the retrieved memory may be more likely to have retained that vividness and arousal and re-engage the amygdala, MTL and visual cortices.

To investigate these three questions, we used the paradigm illustrated by Fig. 1. Emotional and neutral scenes were incidentally encoded under instructions to attend to either semantic or perceptual features during scene viewing. Following each scene, participants were asked to make an arousal rating and to answer a question specific to perceptual or the semantic condition. Two days later, memory for the scenes was tested with a task in which participants rated memory strength and indicated the occurrence of recollection (retrieval of contextual details).

The fMRI analyses focused on the three questions mentioned above. First, to investigate whether prior perceptual processing modulates the neural mechanisms of emotional memory strength, we used participants' rating of memory strength as a parametric regressor and identified regions where activity increased as a function of emotional memory success. On the basis of the aforementioned evidence linking the amygdala to emotion-induced memory retrieval enhancement (Buchanan, 2007) and effects of perceptual processing on emotional encoding (Ritchey et al., 2011; Todd et al., 2012) we predicted the amygdalar activity associated with emotional memory strength would be enhanced by prior perceptual processing. Second, to investigate whether prior perceptual processing enhances the neural mechanisms of emotional recollection, we compared activity for trials eliciting recollection to trials eliciting strong memories without recollection. On the basis of evidence linking emotional recollection to the amygdala and the hippocampus (Dolcos et al., 2005), we predicted that amygdalar and hippocampal activity associated with emotional recollection would be enhanced by prior perceptual processing. Finally, to investigate whether prior perceptual processing enhances amygdalar interactions with medial temporal and other cortical regions, we used the amygdala as a seed in a functional connectivity analyses. We predicted that prior perceptual processing would enhance amygdalar connectivity with regions strongly associated with retrieval success, such as hippocampal/parahippocampal regions, visual cortex, and ventral parietal cortex.

2. Materials and method

2.1. Participants

Twenty-one young adults participated in the study. All participants were right-handed, native English speakers with no history of psychiatric or neurological illness. Participants provided written informed consent in accordance with the Institutional Review Board of Duke University Medical Center. One participant was excluded for excessive head motion and one was excluded for problems with image acquisition, leaving data from 19 participants included in analysis (9 female; ages 18–29, $m = 23.0$, $SD = 3.1$). In addition, one participant was removed only from analyses that directly compare “remember” versus “high-confidence old” judgments due to having no “remember” responses in the neutral-semantic condition.

2.2. Stimuli

Stimuli included 630 pictures from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008) as well as from an in-house, standardized database that allowed us to equate the pictures better for visual complexity and content (e.g., human presence). Pictures were assigned on the basis of a 9-point normative valence scale to emotionally negative (valence: 1–4), neutral

(valence: 4–6), and positive (valence: 6–9) conditions. In accordance with the picture selection procedure, standardized valence scores were lower for negative ($M = 2.85$, $SD = .62$) than neutral pictures ($M = 5.14$, $SD = .43$; $t(418) = 43.98$, $p < .001$), and higher for positive ($M = 7.02$, $SD = .54$) than neutral pictures ($t(418) = 39.85$, $p < .001$). Additionally, arousal scores (1 = calm, 9 = excited) were greater for negative ($M = 5.72$, $SD = .49$) than neutral pictures ($M = 3.51$, $SD = .49$; $t(418) = 45.95$, $p < .001$), greater for positive ($M = 5.68$, $SD = .59$) than neutral pictures ($t(418) = 40.91$, $p < .001$), and did not significantly differ between negative and positive pictures ($t(418) = .62$, $p = .54$).

2.3. Procedure

Participants performed both encoding and recognition memory tasks in the scanner, with a 2-day delay between tasks. During encoding, participants viewed 140 negative, 140 positive, and 140 neutral pictures. The encoding session consisted of 10 functional runs, across which negative, positive, and neutral pictures were evenly divided. Runs alternated between two distinct tasks, semantic and perceptual, described below. To avoid the induction of long-lasting mood states, the pictures within each block were pseudo-randomized so that no more than three pictures of the same valence were consecutively presented. The assignment of encoding stimulus lists to the semantic versus perceptual task was counterbalanced across participants.

Semantic and perceptual tasks are illustrated in Fig. 1A. In the semantic task, participants were instructed to analyze each picture carefully for its meaning and interpretation, so that after the picture was taken away, they could choose between two possible descriptions of the picture. In the perceptual task, participants were instructed to analyze each picture carefully for its perceptual features, particularly colors and lines, so that after the picture was taken away, they could decide, for example, whether there was more red versus green or more horizontal versus vertical lines in the picture. Critically, participants were cued before each run as to which task was next, so that they were able to tailor their processing of each picture to the current task.

Trial structure was similar between tasks (Fig. 1A). For each trial a picture was presented for 2 s. A jittered fixation interval followed each picture presentation, drawn from an exponential distribution with a mean of 2 s. After this interval the participant was instructed to rate the picture for its emotional arousal or intensity on a 4-point scale (1 = calm, 4 = excited). The rating screen remained on-screen for 1 s and was immediately followed by a question screen, which varied by task. In the semantic task, the question screen said, “Which word best describes the picture?” Two possible options were presented on-screen, both of which were written for each picture such that both could be related to the picture but only one described the true meaning of the picture. In the perceptual task, the question screen said, “Which feature are there more of?” Two possible options were presented on-screen: either two color names or the words horizontal and vertical. The question screen remained for 1 s, followed by another jittered fixation interval (mean = 2 s) before the next trial. Responses were collected until the next picture appeared.

Two days after encoding, participants completed a recognition task for the pictures (see Fig. 1B). An additional 70 emotionally negative, 70 positive, and 70 neutral pictures were presented as distracters. Pictures were each presented for 2 s, followed by a jittered fixation interval (mean = 2 s). Participants indicated whether the item was old or new using a 5-point scale, with 1 = definitely new, 2 = maybe new, 3 = maybe old, 4 = definitely old, and 5 = remember. Participants were instructed that a remember response indicated the recollection of a specific detail from when

they saw that picture during the encoding period, whereas a definitely old response did not include any specific details.

2.4. Behavioral analyses

Average arousal ratings and question accuracy were calculated separately for each trial type. To measure differences in memory responding between conditions, hit rates, false alarm rates, and d' scores were evaluated for each trial type. In signal detection models, sensitivity to the memory signal is measured as d' (the difference between z-transformed hits and false alarms) (Macmillan & Creelman, 2005). Because the effect of emotion on memory tends to be strongest when only highly confident responses or recollection estimates are considered (Dolcos et al., 2005; Ochsner, 2000) d' was evaluated with its criterion between 3 ('maybe old') and 4 ('definitely old'). That is, responses of 4 and R were taken as 'old' and the rest were taken as 'new' responses. Encoding response data and d' scores were entered into separate repeated-measures ANOVAs with emotion (negative, neutral, positive) and task (deep, shallow) as factors. Subsequent post hoc statistics consisted of repeated-measures ANOVAs with the corresponding factors and variables of interest.

2.5. fMRI methods

Scanning Images were collected using a 4T GE scanner. Stimuli were presented using liquid crystal display goggles (Resonance Technology, Northridge, CA), and behavioral responses were recorded using a four button fiber optic response box (Resonance Technology). Scanner noise was reduced with earplugs and head motion was minimized using foam pads and a headband. Anatomical scanning started with a T2-weighted sagittal localizer series. The anterior (AC) and posterior commissures (PC) were identified in the midsagittal slice, and 34 contiguous oblique slices were prescribed parallel to the AC-PC plane. High-resolution T1-weighted structural images were collected with a 24-cm field of view (FOV), a 256^2 matrix, 68 slices, and a slice thickness of 1.9 mm. Functional images were acquired using an inverse spiral sequence with a 2-s TR, a 31-ms TE, a 24-cm FOV, a 64^2 matrix, and a 60° flip angle. Thirty-four contiguous slices were acquired with the same slice prescription as the anatomical images. Slice thickness was 3.8 mm, resulting in $3.75 \times 3.75 \times 3.8$ mm voxels.

Statistical analyses Preprocessing and data analyses were performed using SPM5 software implemented in Matlab (www.fil.ion.ucl.ac.uk/spm/). After discarding the first 6 volumes, the functional images were slice-timing corrected and motion-corrected, spatially normalized to the Montreal Neurological Institute (MNI) template, spatially smoothed using an 8 mm isotropic Gaussian kernel, and resliced to a resolution of $3.75 \times 3.75 \times 3.8$ mm voxels. For each subject, evoked hemodynamic responses to event types were modeled with a delta (stick) function corresponding to stimulus presentation convolved with a canonical hemodynamic response function within the context of the general linear model, as implemented in SPM5. Main event types were modeled at the fixed effects level, representing all possible combinations of emotion (negative, neutral, positive), encoding task (semantic, deep), and memory accuracy (hits, misses, false alarms, correct rejections). Given our focus on the amygdala and available fMRI evidence that this region contributes similarly to emotional memory for positive and negative pictures (e.g., Anders, Lotze, Erb, Grodd, & Birbaumer, 2004; Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Grafton, & Kilts, 1999; Hamann & Mao, 2002), positive and negative trials were collapsed into a single emotion category in all statistical analyses. Confounding factors (head motion, magnetic field drift) were included in the model. Because the theoretical focus of current analysis is on effects of arousal, rather

than valence, positive and negative scenes were combined at the random effects level to form the emotional event type.

Our first goal was to investigate how perceptual versus semantic processing modulates the effects of emotion on retrieval-related activity. Given that the focus of this first goal was on quantitative memory differences, we used a parametric approach to identify activity that varied with memory strength and then investigated how this activity was affected by emotion and the encoding task. For each participant, a linear parametric regressor was used to model the recognition response to old items, with 1 = *definitely new*, 2 = *maybe new*, 3 = *maybe old*, and 4 + 5 collapsed together for *definitely old*. High-confidence responses were collapsed together in this model in order to investigate effects of memory strength, rather than recollection. Estimates for the parametric regressor were generated for each participant, and then entered into group-level t -tests to evaluate the effects of emotion (emotional versus neutral pictures) as a function of previous encoding task (perceptual versus semantic processing). To specify further the interaction between emotional arousal and prior processing type on memory success, a second model was run in which arousal ratings made for each scene during encoding were entered as a parametric regressor, and activations during high-confidence trials were contrasted as a function of encoding task (perceptual versus semantic).

Our second goal was to test whether prior perceptual versus semantic encoding of emotional stimuli differentially influences recollection- versus familiarity-based neural activations. Thus, whereas our first goal focused on quantitative differences in memory (memory strength), our second goal focused on qualitative differences (recollection versus familiarity). For this goal, we used an ANOVA approach with emotion (emotion, neutral), encoding task (perceptual, semantic), and memory type (recollection versus familiarity). As in previous fMRI studies (e.g., Yonelinas, Otten, Shaw, & Rugg, 2005), we measured recollection using Remember (5) responses (mean number of trials in each bin: 11 for neutral perceptual, 36 for emotional perceptual, 17 for neutral semantic, and 44 for emotional semantic) and Familiarity using high-confidence (4) recognition responses (mean number of trials in each bin: 18 for neutral perceptual, 37 for negative perceptual, 21 for neutral semantic, and 40 for negative semantic). High-confidence (4) responses were described to the participants as being equally familiar as the Remember responses and differed only in recollection of specific details from the encoding period. Thus, this comparison is the cleanest way to discriminate between recollection and familiarity and can be interpreted in concert with the parametric strength analysis, which collapsed across these response types. Main effects and interactions were assessed by weighting condition types in the ANOVA framework. For visualization purposes only, regions-of-interest analyses were performed by extracting the mean beta value from all significantly active voxels within the functional cluster of interest and plotting these as a function of experimental condition.

Our third goal was to investigate the effects of perceptual versus semantic processing on amygdala connectivity during successful emotional memory retrieval. A seed region for the functional connectivity analysis was selected from a general emotion (emotional, neutral) by retrieval success (hits, misses) interaction in the direction of emotional > neutral and hit > miss. This analysis identified a right amygdala cluster, which showed greater hit-miss differences for emotional than neutral stimuli ($xyz = 23, 11, -19$) and was unbiased with respect to the effects of encoding task. Subsequently, each trial was modeled as a separate event, yielding different beta values for each trial and each subject in the seed cluster of interest (Rissman, Gazzaley, & D'Esposito, 2004), and correlations were examined between the time series activity of the seed with all other voxels in the brain. A box was built using all the

voxels directly adjacent to the peak coordinate within the functional amygdala cluster from the general test of successful emotional memory (emotional > neutral, hits > misses). A correlation map was created for each condition that displayed the correlation magnitude between every voxel and the amygdala seed region over time. Correlation maps were subsequently entered into SPM to identify brain regions showing differential connectivity as a function of experimental condition. To determine amygdala connectivity effects for successful emotional retrieval, connectivity analysis were examined within the successful retrieval network, defined as hits > misses.

To control for family-wise error resulting from multiple comparisons, we performed a Monte Carlo simulation (Slotnick et al., 2003). This procedure determines the height and cluster extent threshold sufficient to yield a corrected threshold of $p < .05$. Based on the results of the simulation, clusters were considered if they exceeded an uncorrected threshold of $p < .001$ with 10 or more contiguous voxels (3.75 mm isotropic) for whole-brain analyses. In the case of the targeted analysis that assesses differences between “remember” versus “definitely old” responses on MTL activity, activations were considered if they exceeded an uncorrected threshold of $P < .005$ with 3 or more contiguous voxels in the focal, hypothesized region of interest (ROI) (bilateral MTL). Conjunction analyses were assessed by entering individual contrasts at $p < .001$ uncorrected, such that they formed a joint threshold probability of $p < .000001$. All activations are presented according to neurological convention. In the figures, statistically significant activity is projected onto a single-subject T1 structural image template. Brodmann Area (BA) and gyral localizations of activations

were determined using the WFU PickAtlas and the Talarach Client (<http://www.talairach.org/client.html>).

3. Results

3.1. Behavioral results

All behavioral results were reported in a previous paper (Ritchey et al., 2011); for convenience only, we reiterate them here. Average arousal ratings at encoding were entered into a repeated-measures ANOVA with factors of emotion (negative, neutral, positive) and task (semantic, perceptual). There was a significant main effect of emotion, $F(2,38) = 206.31$, $p < .001$, $\eta_p^2 = .92$. Follow-up tests revealed that negative pictures were rated as more arousing than neutral, $F(1,19) = 335.38$, $p < .001$, or positive, $F(1,19) = 37.63$, $p < .001$, pictures. Positive pictures were also rated as more arousing than neutral pictures, $F(1,19) = 185.47$, $p < .001$. Critically, there was no main effect of task, $F(1,19) < 1$, $p > .1$, $\eta_p^2 = .02$, or interaction of emotion and task, $F(2,38) < 1$, $p > .1$, $\eta_p^2 = .04$, indicating that the task manipulation did not alter the participants' perceived emotional responses to the stimuli.

Recognition memory accuracy (d') was entered into a repeated-measure ANOVA with factors of emotion (emotional, neutral) and processing (semantic, perceptual). There was a marginally significant effect of emotion ($F(1,18) = 3.3$, $p = .085$), and a significant emotion \times processing interaction ($F(1,18) = 7.47$, $p = .014$). Follow-up t -tests showed that the memory-enhancing effect of emotion was significant in the perceptual ($t(18) = 2.58$, $p = .019$)

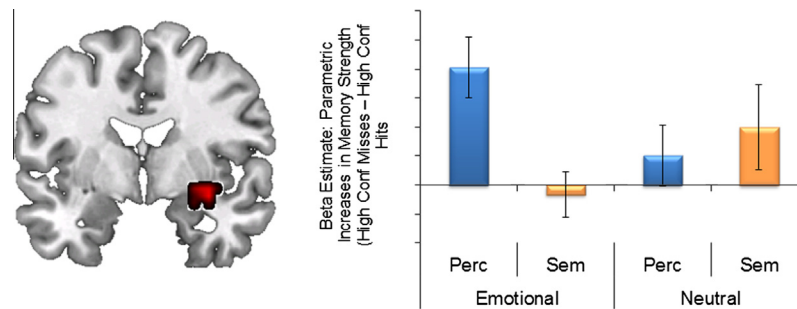


Fig. 2. Prior perceptual processing enhances memory success-related amygdalar activity. Mean beta estimates of activations in right (R) amygdala during successful retrieval of emotional and neutral pictures are overlaid on a T1 template and plotted as a function of previous encoding strategy. Error bars reflect standard error.

Table 1
Regions increasing parametrically with memory strength (high conf. new to high conf. old).

	H	BA	Voxels	MNI			t-value
				X	Y	Z	
Emo: Perceptual > Semantic							
Inferior Frontal Gyrus	R	47	17	30	23	-11	4.29
Inferior Frontal Gyrus*	L	47	22	-38	19	-4	4.02
Clastrum*	R		23	34	0	-11	3.89
Amygdala*	R			26	0	-15	3.37
Postcentral Gyrus	R	5	5	4	-45	68	3.8
Caudate*	L		5	-4	0	23	3.61
Clastrum	R		7	38	-11	11	3.57
Putamen*	R		14	30	-15	-8	3.44
Emo: Semantic > Perceptual							
<i>No regions</i>							
Neutral: Perceptual > Semantic \cap Emotional: Perceptual > Semantic							
<i>No regions</i>							

Note: H = Hemisphere; BA = Brodmann Area.

* Denotes that this region also showed a significant parametric effect within the emotional perceptual condition alone (i.e., positive relationship with memory).

but not semantic ($t(18) = .90, p = .38$) condition. This finding is consistent with evidence that perceptual processing can enhance emotional memory (e.g., Reber et al., 1994). Our fMRI analyses focus on the neural mechanisms of this enhancing effect of perceptual processing.

3.2. fMRI results

Memory strength. To test our first prediction that amygdalar activity associated with emotional memory strength would be enhanced by prior perceptual processing, we used participants' memory strength ratings as a linear parametric regressor and compared the effects of perceptual versus semantic processing. Consistent with our prediction, this contrast yielded a cluster in right amygdala (Fig. 2). Other regions identified by this contrast are listed in Table 1. To confirm that the amygdala region identified was specific to emotional memories, we tested for a similar effect for neutral pictures but no difference was found, even at a liberal $p < .05$ threshold. Thus, memory-enhancing activation in the amygdala is modulated by prior perceptual processing for emotional, but not neutral, stimuli.

To further confirm that the right amygdala finding was mediated by arousal, rather than by other features of the emotional stimuli, we ran a second analysis using the arousal rating for each picture (unique to each subject and trial) as a parametric regressor and tested for regions showing greater parametric increases in activity during correct retrieval of all perceptually- versus semantically-encoded pictures, as a function of the previous arousal rating. This contrast yielded a cluster in right amygdala (see Table 2), which, importantly, overlapped with the right amygdala region identified by the previous analysis.

Recollection. To test our second prediction that recollection-related activity in amygdala and hippocampus would be enhanced by prior perceptual processing, we ran an ANOVA with factors of emotion (emotional, neutral), memory response ("remember," "definitely old") and prior encoding task (perceptual, semantic). Consistent with our second prediction, the right amygdala and left hippocampus showed a three-way interaction effect in the direction of emotional > neutral, remember > definitely, and perceptual > semantic. Other regions showing three-way interactions

Table 2
Regions during hits increasing parametrically with prior arousal rating.

	H	BA	Voxels	MNI			t-value
				X	Y	Z	
Perceptual > Semantic							
Precentral Gyrus	R	6	6	56	-4	38	5.04
Amygdala	L		26	-34	-4	-23	4.72
Insula	R	13	18	41	-4	-4	4.61
Amygdala	R		15	26	0	-23	4.33
Claustrium	L		10	-38	-19	4	3.99
Precentral Gyrus	L	44	5	-45	4	8	3.73
Hypothalamus	R		5	4	0	-15	3.33
Semantic > Perceptual							
Precuneus	L	7	148	-11	-68	38	4.89
Superior Frontal Gyrus	R	8	13	23	23	57	4.43
Middle Temporal Gyrus	R	19	57	38	-64	19	4.31
Superior Frontal Gyrus	R	9	22	26	34	34	3.87
Insula	L	13	5	-30	19	-11	3.75
Superior Frontal Gyrus	L	10	10	-26	56	8	3.7
Medial Frontal Gyrus	R	10	10	15	56	19	3.59
Cuneus	R	7	5	23	-79	30	3.57
Caudate	L		5	-8	15	-4	3.52

Note: H = Hemisphere; BA = Brodmann Area.

Table 3
Interaction between emotion and prior processing on recollection versus familiarity responses.

	H	BA	Voxels	MNI			t-value
				X	Y	Z	
Emo > Neut, Perc > Sem, Remember > Def. Old							
Middle Occipital Gyrus	R	19	18	56	-64	-11	3.82
Insula	R	13	8	38	-23	27	3.42
Fusiform Gyrus	L	36	11	-49	-41	-30	3.33
Parahippocampal Gyrus	L	36	5	-34	-23	-23	3.06
Hippocampus	L			-38	-26	-15	2.73
Amygdala/Uncus	R	34	5	15	-4	-23	3.04
Fusiform Gyrus	R	37	11	49	-53	-23	3.02
Fusiform Gyrus	L	37	14	-49	-60	-19	2.97
Emo > Neut, Sem > Perc, Remember > Def. Old							
No Regions							

Note: H = Hemisphere; BA = Brodmann Area.

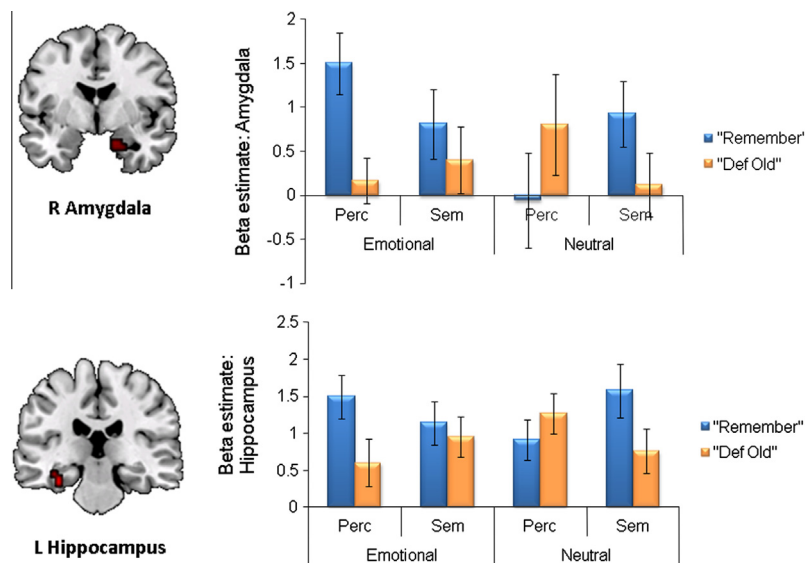


Fig. 3. Effects of prior processing strategy on recollection and familiarity-related activations in amygdala and hippocampus. Mean beta estimates of activations in right (R) amygdala and left (L) hippocampus are overlaid on a T1 template and plotted as a function of memory decision, emotion, and prior encoding strategy. Error bars reflect standard error.

Table 4
Amygdalar connectivity during successful emotional retrieval, as a function of prior processing strategy.

	H	BA	Voxels	MNI			t-value
				X	Y	Z	
Perceptual > Semantic							
Hippocampus/Amygdala	L		21	−26	−8	−15	6.28
Fusiform Gyrus	L	20	9	−41	−38	−19	5.14
Angular Gyrus	L	39	24	−45	−68	15	4.81
Ventral Occipital Cortex	L	19		−41	−79	19	4.55
Cerebellum	R		18	23	−49	−19	4.74
Cingulate Gyrus	L	25	9	−11	23	−15	4.42
Posterior Parahippocampal Gyrus	L	36	6	−23	−45	−8	3.75
Semantic > Perceptual							
Superior Frontal Gyrus	L	10/9	12	−19	49	30	6.61
Medial Frontal Gyrus	L	9	10	0	38	49	5.51
Cingulate Gyrus	L	31	7	0	−38	27	4.78

Note: H = Hemisphere; BA = Brodmann Area.

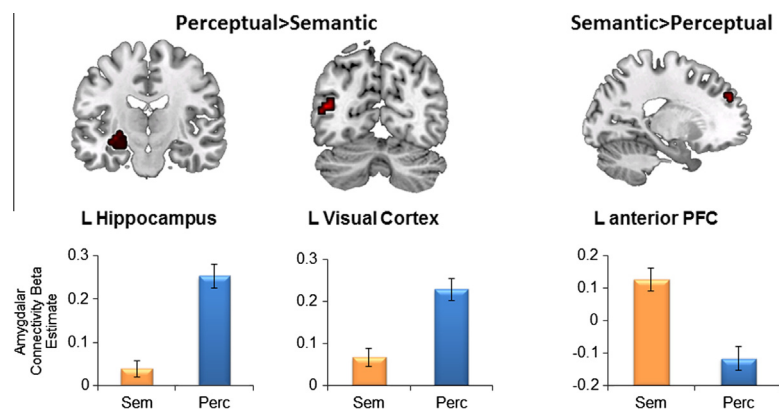


Fig. 4. Amygdalar connectivity during successful emotional retrieval (hits), as a function of prior processing strategy. Functional connectivity with amygdala was stronger in left (L) hippocampus and L visual cortex during successfully retrieved pictures previously encoded with perceptual relative to semantic processing, but stronger in L anterior prefrontal cortex (PFC) for prior semantic relative to perceptual processing. Error bars reflect standard error.

are listed in Table 3. As seen in Fig. 3, both the amygdala and hippocampus showed greater activity during remember relative to definitely old responses for emotional trials, with a larger difference for perceptually- relative to semantically-encoded trials. Interestingly, the reverse pattern was observed for neutral trials, where semantic encoding increased activation during later “remember” trials, but perceptual encoding increased activation during later “definitely old” trials. No regions showed the reverse-weighted 3-way interaction effect, with emotional > neutral, remember > high confidence old, and semantic > perceptual.

3.3. Functional connectivity

A functional connectivity analysis was conducted to test our third prediction, that the way in which emotional items are encoded will influence how brain regions later interact to promote successful retrieval. We used a right amygdala region defined by the general emotional memory analysis as a seed (see Methods) and measured its connectivity with regions showing hit-miss differences. Consistent with our third prediction, during high-confidence retrieval of emotional pictures, amygdalar connectivity with hippocampal/parahippocampal regions, visual cortex, and ventral parietal cortex was enhanced by prior perceptual processing (see Table 4 and Fig. 4a). Conversely, prior semantic processing yielded greater amygdalar connectivity with left anterior PFC (Fig. 4b).

4. Discussion

We investigated neural activations during retrieval of emotional and neutral pictures, which were incidentally encoded 2 days prior under instructions to focus on either perceptual or semantic properties. The study yielded three main findings. First, relative to prior semantic processing, prior perceptual processing enhanced neural activity related to memory strength in the right amygdala for emotional but not neutral pictures. This finding was replicated when pictures were not classified as emotional or neutral based on norms but rather when analyzed as a function of subject- and trial-specific arousal ratings. Second, in the right amygdala and left hippocampus, prior perceptual processing of emotional pictures produced a stronger effect on recollection- than familiarity-related activations. In contrast, prior semantic processing of neutral pictures impacted recollection-related activations. Finally, during successful emotional retrieval, prior perceptual encoding enhanced amygdala connectivity with regions strongly associated with retrieval success, including hippocampal/parahippocampal regions, visual cortex, and ventral parietal cortex, whereas prior semantic encoding increased amygdala connectivity with left anterior frontal cortex. These main findings will be discussed in turn.

Based on previous evidence linking the amygdala, perceptual processing, and emotional memory encoding (Kensinger et al., 2007; Ritchey et al., 2011; Todd et al., 2012), we predicted that

amygdala activations would be increased during retrieval of emotional scenes that were previously processed with a perceptual, relative to semantic, encoding strategy. Consistent with this prediction, activity in right amygdala was associated with successful retrieval of perceptually-encoded emotional pictures (Fig. 2). This region was identified by two different parametric analyses, one using participants' memory strength ratings and the other using their arousal ratings. The advantage of the first analysis is that it tests for differences that emerge as a function of subtle increases in memory success, whereas a binary hit-miss measure could introduce noise from individual differences in criterion or response bias. In addition, combining definitely old and remember responses allowed us to examine the effects of memory strength separately from recollection-related effects. The advantage of the second analysis is that it links the amygdala activation more directly to subjective arousal.

The finding that amygdala activations during emotional retrieval are enhanced by prior perceptual processing is consistent with evidence linking arousal to increased sensory processing (e.g., Bradley et al., 2003; Lang et al., 1998). In addition, a few recent studies have linked arousal-related perceptual processing directly to successful emotional memory formation in the amygdala (Kensinger et al., 2007; Ritchey et al., 2011; Todd et al., 2012). The current study goes beyond this previous work by showing enhanced amygdala activity during emotional retrieval of perceptually-encoded scenes. This finding is of particular interest because the processing manipulation occurred during encoding, and hence the difference in amygdala activity cannot be explained by processes elicited by the retrieval cue. Rather, it has to be mediated by the nature of the emotional memory representations stored during perceptual processing and recovered during retrieval. In addition, the effect cannot be explained by assuming that perceptual processing elicited greater arousal during encoding because participants' arousal ratings were similar in the perceptual and semantic encoding conditions. One interesting question for future research is whether perceptual encoding increases later arousal associated with the memory itself.

Although the amygdala findings reported here echo previous results from the encoding period (Ritchey et al., 2011), there are some apparent differences in how perceptual and semantic processing affect emotional memory-related activity during encoding versus retrieval. For instance, during encoding, it was previously observed that the right ventrolateral prefrontal cortex supported subsequent memory for emotional items that were semantically encoded rather than perceptually encoded (Ritchey et al., 2011). Here we did not observe any differences in ventrolateral prefrontal activity during the retrieval of these items, suggesting that the role of this region in supporting semantically-encoded emotional memories is limited to the encoding period. This discrepancy may be related to differences in the kinds of processes that support memory encoding and recognition, in that encoding may especially benefit from elaborative processes linked to the ventrolateral prefrontal cortex (Prince, Daselaar, & Cabeza, 2005) whereas these processes may be less important during recognition.

Why did perceptual processing during encoding enhance amygdala activity during retrieval? One possibility is that perceptual processing during encoding boosted the storage of emotion-related visual details (e.g., the red blood in a gory scene, the white fangs of a snake), enhancing memory of these details and arousal during retrieval, which increased amygdala activity. An alternative hypothesis is that perceptual processing promoted the storage of the emotional experience associated with the picture in the amygdala, leading to enhanced recapitulation of this emotional information during retrieval. In other words, according to the first hypothesis, the amygdala activation reflects the emotional experience elicited by remembered visual details, whereas according to

the second hypothesis, it reflects the reactivation of the original emotional experience. Another alternative hypothesis (see also Ritchey et al., 2011) is that semantic encoding promotes additional cues one can rely onto make a memory decision (e.g., associations with prior knowledge structures), but for perceptually-encoded pictures, the main determinant of subsequent memory is the degree of arousal and amygdala activity during memory formation. In turn, the degree of arousal elicited by a picture may be more likely to discriminate between remembered and forgotten items in the perceptual condition. Finally, because many of our findings reflect differences between memories formed via perceptual versus semantic processing, the present results might be partially explained by emotion-related decrements in semantic processing, in addition to enhancements in perceptual processing. Under this hypothesis, emotion may have interfered with semantic processing during encoding (c.f., Sakaki, Gorlick, & Mather, 2011), weakening the LOP effect for emotional items and disrupting memory-related activity during retrieval. Investigating these hypotheses warrants further research. It should also be noted that one caveat of the current analysis is that negative and positive valence were pooled together. There is some evidence (e.g., Kensinger et al., 2007) that negative emotions recruit perceptual regions more than positive emotions. Future research will be needed to divide the effects reported here by valence, to determine whether the effects are stronger for negatively compared with positively valenced emotions.

Turning to the second main finding, we tested whether prior perceptual versus semantic encoding of emotional stimuli differentially influences neural activations linked with distinct memory phenomena – specifically, recollection versus high confidence familiarity. Based on previous studies showing that emotion enhances hippocampal responses during retrieval (Buchanan, 2007), as well as evidence specifically linking recollection responses to emotion-related activations in hippocampus (Dolcos et al., 2005) and amygdala (Dolcos et al., 2005; Ochsner, 2000), we hypothesized that the influence of emotion on recollection, and its neural correlates, is related to increased perceptual processing during encoding. Consistent with this prediction, a three-way interaction was found in both amygdala and hippocampus, with increased activity during perceptually-encoded recollection of emotional scenes. As with the first finding, a notable aspect of this result is that the perceptual versus semantic processing variable occurred only during encoding; thus neural activations in these regions cannot be explained only by differences in emotional versus neutral retrieval cue or in online retrieval processes (recollection versus high confidence familiarity).

Interestingly, there is some evidence that although emotion may enhance the subjective feeling of remembering and associated recollection responses on memory tests, it does not necessarily increase (and in some cases it impairs) accuracy for contextual details (e.g., Rimmele, Davachi, Petrov, Dougal, & Phelps, 2011). The current analysis modeled only correct “remember” and “definitely old” responses, and the data did not yield sufficient trial numbers to model incorrect responses in these categories (i.e., high confidence false alarms). It would be of interest in future studies to investigate the contribution of perceptual versus semantic processing to subjective versus objective recollection. Furthermore, several studies have shown that emotion does not have a uniform effect on all types of contextual details, and may systematically impair memory for some details while enhancing others (e.g., see Kensinger, 2009; Mather, 2007). The current study instructed participants to endorse a “remember” response if they retrieved the scene with high confidence along with details of the scene's initial occurrence. However, these details were not specified, and as such the current data do not speak to this debate. Further work is needed to determine the role of perceptual versus semantic

processing on the retrieval of distinct forms of contextual detail that accompany the experience of recollection.

In concert with the second main finding, it is noteworthy that the neutral trials showed the reverse pattern as the emotional trials. Specifically, for neutral trials, it was semantic encoding that enhanced recollection-related activity in the same MTL regions. In the memory literature, there is currently mixed evidence as to whether semantic processing benefits recollection more than familiarity. The standard view has been that semantic processing benefits later recollection (e.g., Gallo, Meadow, Johnson, & Foster, 2008; Gardiner, 1988; Rajaram, 1993), possibly by promoting elaborative processing and/or by linking the new episodic encounter with previous knowledge. However, there is also evidence that this difference depends on the paradigm used to measure recollection and familiarity. For instance, a recent study showed that simply by modifying slightly the instructions to make recollection-based (“remember”) versus familiarity-based (“know”) responses, both memory phenomena can be enhanced by semantic processing (Sheridan & Reingold, 2012). Although the current results do not definitively resolve this debate, they are consistent with the standard view that, for affectively neutral information, semantic processing benefits recollection, linked with activity in MTL memory regions, while perceptual processing benefits familiarity. Taken together, the data also suggest that the kinds of information that trigger recollection for emotional events may not be the same as for neutral events.

Turning to the final goal of the study, we investigated whether prior perceptual versus semantic processing would influence not only univariate estimates of amygdala activation levels but also functional integration between amygdala and other regions within the memory retrieval network. Consistent with our third prediction, prior perceptual processing enhanced amygdalar connectivity with several components of the successful retrieval network, including hippocampal/ parahippocampal regions, visual cortex, and ventral parietal cortex. The enhancement of amygdalar connectivity with the hippocampus extends the results of Dolcos et al. (2005), who found greater amygdala-hippocampus interactions during the retrieval of emotional than neutral pictures. The present results show that this effect is more pronounced when the pictures were processed perceptually rather than semantically during encoding. One interesting question is whether the amygdala-hippocampus interactions are related to the memory operations promoted by a visual recognition test. A classic and well-supported principle is that memory retrieval benefits from recapitulation of the cognitive processes engaged at encoding (Craik, 1983; Kolers, 1973; Morris, Bransford, & Franks, 1977); thus, emotional enhancement of visual cues may have a particularly strong effect on amygdala-hippocampus interactions during recognition. Future research should investigate how prior perceptual encoding of emotional events affects amygdala-MTL interactions during other forms of memory retrieval, such as recall.

The increase in amygdala connectivity with visual cortex is relevant to the two aforementioned accounts of the perceptual-processing effect on amygdala activity: (1) prior perceptual processing enhanced visual memory retrieval, which increased emotion during retrieval and emotion-related amygdalar activity; and (2) prior perceptual processing enhanced the storage of emotional information in the amygdala, which is reactivated during retrieval. The finding of that prior perceptual processing enhanced amygdalar connectivity with visual cortex is more consistent with the first account, which assumes an effect of visual cortex on the amygdala. Our functional connectivity analyses do not allow inferences about the directionality of the effects, but future studies could investigate this question using other types of analyses (e.g., dynamic causal modeling).

Finally, the finding that prior perceptual processing enhanced amygdalar connectivity with ventral parietal cortex (angular gyrus) is interesting given that this region is strongly associated with retrieval success and recollection (Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008). The contributions of ventral parietal cortex to episodic memory retrieval are a topic of debate. According to an episodic buffer account (Vilberg & Rugg, 2008), ventral parietal cortex mediates the maintenance of multimodal information within working memory, which is more demanding for recollected memories, whereas according to an attention-to-memory (AtoM) model (Cabeza, 2008; Cabeza, Ciaramelli, & Moscovitch, 2012; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008), this region mediates bottom-up attentional processes, which are captured by vivid memories. Both accounts could explain the current finding, by assuming enhanced visual memory would simultaneously increase episodic buffer load and bottom-up attention capture.

In conclusion, the current study is consistent with growing evidence that sensory processing may provide a pathway through which emotional arousal enhances memory retrieval. Given the role of sensory vividness in emotional-memory related conditions such as PTSD, we expect that characterizing the neural systems mediating this role in will help advance a mechanistic understanding of these complex disorders.

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