

Dissociable Medial Temporal Lobe Contributions to Social Memory

Leah H. Somerville, Gagan S. Wig, Paul J. Whalen,
and William M. Kelley

Abstract

■ Medial temporal lobe structures such as the hippocampus have been shown to play a critical role in mnemonic processes, with additional recruitment of the amygdala when memories contain emotional content. Thus far, studies that have examined the relationship between amygdala activity and memory have typically relied on emotional content of the kind that is rarely encountered in day-to-day interactions. The present event-related functional magnetic resonance imaging study investigates whether amygdala activity supports emotional memory during the more subtle social interactions that punctuate everyday life. Across four training sessions, subjects learned common first names for unfamiliar faces in the presence or absence of additional contextual information that was positive, negative, and neutral in valence (e.g., “Emily helps the

homeless,” “Bob is a deadbeat dad,” “Eric likes carrots”). During scanning, subjects performed a yes/no recognition memory test on studied and novel faces. Results revealed a functional dissociation within the medial temporal lobe. Whereas a region within the right hippocampus responded strongly to all faces that had been paired with a description, regardless of its valence, activity in the right amygdala was uniquely sensitive to faces that had been previously associated with emotional descriptions (negative and positive > neutral). This pattern of activity in the amygdala was preserved even when the emotional contexts associated with faces could not be explicitly retrieved, suggesting a role for the amygdala in providing a nonspecific arousal indicator in response to viewing individuals with emotionally colored pasts. ■

INTRODUCTION

The ability of humans to encode and represent knowledge about others is a critical component of social interaction. Often, our impressions of individuals are shaped by subtle emotional acts (e.g., witnessing a person opening a door for an elderly man). How emotional content is integrated and represented in memory has been a topic of considerable neuroscientific interest.

Several lines of research have investigated the neural underpinnings of emotional memories. A common and straightforward approach to investigating the relationship between emotion and memory has been to examine behavioral and neural responses to overtly emotional material. For example, overtly emotional material (e.g., a picture of a murder scene) is remembered better than neutral material (Ochsner, 2000; Cahill & McGaugh, 1998; Cahill, Prins, Weber, & McGaugh, 1994), and patient studies have highlighted the importance of the amygdala in this memory facilitation (Richardson, Strange, & Dolan, 2004; Adolphs, Tranel, Hamann, et al., 1999; Adolphs, Cahill, Schul, & Babinsky, 1997). Neuroimaging work has provided further support (Dolcos, LaBar, & Cabeza, 2004, 2005; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Cahill,

Haier, et al., 1996). For example, work by Canli et al. (2000) has demonstrated that moment-to-moment fluctuations in amygdala activity at encoding can predict both the arousal value of the material and the likelihood of later recognizing the material.

Another common approach to the study of emotional memory has paired highly emotional material (e.g., a picture of maggots) with neutral items (e.g., a picture of a chair) at encoding, and then later assessed neural activity during a recognition memory test on the neutral items (Smith, Henson, Dolan, & Rugg, 2004; Maratos, Dolan, Morris, Henson, & Rugg, 2001). This approach elegantly deconfounds the neural processes engaged when subjects experience emotional content from the neural operations that are brought to bear during memory retrieval. Erk et al. (2003) employed a similar paradigm but examined brain activity during the initial encoding experience. Studies that have adopted this approach have demonstrated that neutral items that were associated with negative contexts produced greater amygdala activation at encoding (Smith et al., 2004; Erk et al., 2003) and retrieval (Smith et al., 2004; Maratos et al., 2001) than did neutral items that were associated with neutral contexts. Similar analyses using positive contexts have noted analogous amygdala activity (Smith et al., 2004) or greater activation in other regions such

as the orbitofrontal cortex (Maratos et al., 2001) or parahippocampal and extrastriate visual regions (Erk et al., 2003).

One challenge in the interpretation of these disparate results for materials encoded under positive- and negative-valenced contexts is that the positive and negative contexts are not typically matched in terms of valence and arousal (i.e., negative contexts are typically more strongly negative and arousing than positive ones). Thus, differences in brain activity during retrieval of items encoded under positive and negative contexts could be attributed to differences in arousal properties or to the valence of the material itself.

To date, much of the work investigating the neural substrates of emotional memory has principally relied on overtly arousing materials to manipulate emotion. This approach, although highly reliable and robust, arguably reflects only the most extreme cases of emotion processing that humans regularly encounter. Additionally, in some studies, the semantic link between the emotional context and the to-be-learned neutral information is arbitrary (Smith et al., 2004; Erk et al., 2003). An open question is whether brain regions that support such emotional memories are similarly engaged during the more prosaic affective situations that individuals experience in daily life.

In the social domain, integrating information about individuals into long-term memory is critical to forming accurate evaluations of others. Often, our impressions of others are shaped by memorable past experiences (e.g., remembering an argument with a colleague). However, work in social psychology has demonstrated that evaluation of conspecifics can also be impacted by implicit factors (Uleman, Blader, & Todorov, 2005; Lewicki, 1984). In support of this notion, amnesic patients can exhibit affective preferences to individuals even in the absence of a conscious recollection of the encoding experience (Tranel & Damasio, 1993; Johnson, Kim, & Risse, 1985).

The current study manipulated emotional context by pairing socially relevant stimuli (faces and names) with positive, negative, or neutral biographical descriptors of each individual. Over four training sessions, subjects were trained to learn individuals' names either in the

presence or in the absence of a social context (Figure 1). Three weeks after training, subjects underwent functional magnetic resonance imaging (fMRI) scanning during a recognition memory test where only the faces were presented. Of interest was the neural activity that accompanied recognition of previously learned faces. Specifically, we were interested in whether neural activity in medial temporal regions previously implicated in memory retrieval for robust emotional experiences would vary depending on whether the previously learned context was emotional or neutral and whether the context could be consciously recollected.

METHODS

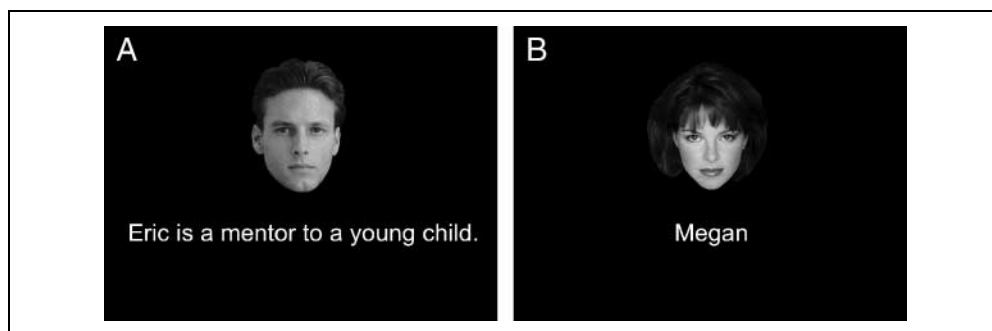
Subjects

Eighteen healthy adult participants were recruited from the local Dartmouth community. Two subjects were excluded from analysis, one due to a stimulus counterbalancing error and one due to unrecorded button presses during the fMRI scan. Of the remaining 16 subjects (aged 18–20 years, mean 19 years), 9 were women. Each participant provided informed consent for their participation in accordance with the guidelines set by the Committee for the Protection of Human Subjects of Dartmouth College and received course credit and/or cash compensation. All participants were right-handed, as measured by the Edinburgh Handedness Inventory (Raczkowski, Kalat, & Nebes, 1974), underwent a brief screening verifying the absence of any significant neurological history and lack of current usage of psychotropic medications, and had normal or corrected-to-normal visual acuity.

Stimuli

Participants learned the names of 120 unique faces presented during a series of training sessions. To manipulate the emotional context of these identities, additional information of positive, negative, or neutral valence was added to the face–name pairings during training procedures (see Figure 1A). For other identities, no context was provided (see Figure 1B).

Figure 1. Sample face stimuli studied during encoding sessions with an associated context (A) and without a context (B).



Faces

Face stimuli consisted of a standardized set of unfamiliar faces used in previous studies (Wig, Miller, Kingstone, & Kelley, 2004; Kelley et al., 1998). These nonfamous faces were compiled from the media, and were cropped below the chin line and around the outer hairline, creating a face centered on a black background. Faces were normalized for size and depict either a neutral expression or a slight smile.

Names

One hundred twenty common first names (60 male, 60 female) were assigned to faces for memorization during training sessions. Names were chosen from the United States Social Security Administration most popular names for births in the United States from 1970 to 1979 (www.ssa.gov/OACT/babynames/1999/top1000of70s.html). When pairs of very similar names were on the list (e.g., Eric and Erica), one of the names was omitted. Sixty names of each gender were then randomly selected from the remaining 97 female and 96 male names on the list.

Sentences

A list of potential sentences providing positive, negative, and neutral descriptions to individuals was created. Examples of such descriptive sentences included, "This person teaches piano lessons," "This person forgets appointments," and "This person is an organ donor." Given the different opinions, backgrounds, and experiences of each subject, we expected variability in valence and arousal judgments for these descriptions. To avoid making assumptions about an individual's personal reactions to these descriptions, sentence selection for the positive, negative, and neutral conditions was performed on a subject-by-subject basis based on valence and arousal ratings attained from each subject during their first session. More importantly, this technique allowed for matching of positive and negative sentences on the magnitude of valence ("distance from neutral") and arousal value.

Study Procedure

Session 1: Stimulus Prerating Session and Matching Procedure

Subjects rated the valence and arousal (intensity) of 185 descriptive sentences. Sentences were phrased in the format, "This person . . ." (e.g., "This person teaches piano lessons"), and subjects were instructed to rate the valence and arousal of a person possessing this characteristic. Valence was rated on a -4 to 4 integer scale: -4 (*very negative*), -2 (*negative*), 0 (*neither positive nor negative*), 2 (*positive*), 4 (*very positive*). Arousal was rated

on a 9-point integer scale used in a previous study (Kim, Somerville, Johnstone, Alexander, & Whalen, 2003): 1 (*least amount of emotional arousal I have ever felt*), 3 (*low emotional arousal*), 5 (*medium emotional arousal*), 7 (*high emotional arousal*), 9 (*the greatest amount of emotional arousal I have ever felt*). The concept of emotional arousal was explained to subjects as the degree to which reading a given sentence changed their emotional state or produced any visceral reaction. Valence and arousal ratings were collected on separate questionnaires and the order of administration of these two scales was counterbalanced between subjects.

After completion of these scales, a stimulus set of 90 sentences (30 negative, 30 positive, 30 neutral) was chosen for each individual subject based on their ratings of the 185 original sentences (Table 1). The mean valence rating for neutral sentences did not differ from the scale midpoint of zero, $t(15) = 1.00, p = .33$, and the arousal value was significantly less than the arousal value of both negative, $t(15) = 18.2, p < .0001$, and positive, $t(15) = 16.7, p < .0001$, sentences. Negative and positive sentences were chosen by matching for arousal and then selecting the 30 sentences with the most extreme negative and positive valence scores. Critically, the distance from zero for negative and positive ratings did not differ significantly within any individual subject (all $ps > .1$) or as a group [absolute value (negative) vs. positive: $t(15) = -1.19, p = .25$]. Arousal ratings of negative and positive sentences also did not differ significantly within any individual subject (all $ps > .15$) or as a group [negative vs. positive: $t(15) = 1.63, p = .12$].

Once sentence lists were created, 60 male and 60 female faces were randomly chosen from the 220 faces (106 female) in the stimulus face set and randomly assigned a gender-congruent name. The face-name pairings were then separated into four groups of 30 (15 males and 15 females each) and were randomly assigned the individualized contexts. At the conclusion of this procedure, each individual stimulus set contained 30 named individuals with negative contexts, 30 with positive contexts, 30 with neutral contexts, and 30 face-name pairings with no context.

Table 1. Mean Valence and Arousal Ratings for Selected Negative, Positive, and Neutral Sentence Contexts

	Negative	Positive	Neutral
Valence rating (-4 to 4 scale)	-2.81 (.625)	2.83 (.690)	$.0082$ (.033)
Arousal rating (1 to 9 scale)	5.75 (1.02)	5.70 (1.11)	1.499 (.740)

Absolute value of valence ratings and arousal values did not differ between negative and positive contexts. Neutral valence ratings did not differ from zero, and neutral arousal values were as low as individual ratings allowed. Numbers in parentheses are group standard deviations from the mean.

Sessions 2–5: Encoding Sessions

After individualized stimulus lists were programmed for presentation via Psyscope software (Cohen, MacWhinney, Flatt, & Provost, 1993), subjects returned to the laboratory (latency range, 2–7 days) for encoding sessions. As depicted in Figure 1, the 120 stimuli were presented to subjects on an Apple computer monitor (Apple Computer, Cupertino, CA). Each stimulus was present on the computer screen for 5 sec, after which the screen went blank. Subjects pressed the space bar to advance to the next trial. Stimuli were presented within a single 120-trial run and this run was repeated three times per session; presentation order was randomized during each run. Subjects were instructed to view the information on the screen and to try to learn the name of each face. They were told that for some faces, they would also receive additional information about the person to help them learn each name.

Following each study session, a self-paced name-recall test was administered. Each face was presented alone on the screen with a blinking cursor below it. Subjects were instructed to type the name of the individual and press the [Enter] key. Following their choice, the correct name replaced their answer on the screen for 2.5 sec as feedback.

Study sessions were administered in this fashion every 2–4 days (mean number of days between sessions, 2.95 ± 1.04) until the subject demonstrated memorization of the name–face pairings at criterion performance ($\geq 95\%$ correct name recall). Although many subjects reached criterion performance after three training sessions, for consistency, 15 of 16 subjects completed four training sessions. One subject completed only three sessions due to illness but had reached criterion performance following the third training session. After training sessions were completed, subjects returned 15–19 days later (mean number of days, 16.63 ± 1.36) for an fMRI scanning session.

Session 6: fMRI Scan and Recall Test

Imaging was performed on a 1.5-T whole-body scanner (General Electric Medical Systems Signa, Milwaukee, WI) with a quadrature head coil. Visual stimuli were generated with an Apple G3 Laptop computer running PsyScope software (Cohen et al., 1993). Stimuli were back projected from an Epson LCD projector (model ELP-7000) (Epson, Long Beach, CA) and viewable by an angled mirror mounted on top of the head coil. Two fiber-optic, light-sensitive keypresses, one held in each hand, were used to collect responses, which were recorded through the PsyScope Button Box (New Micros, Dallas, TX). Cushions were used to minimize head movement.

This study employed an event-related design to investigate trial-by-trial differences in brain activity during a recognition memory test. During each of three func-

tional runs, 40 old (studied) faces (10 each of four context types), 25 new (unstudied) faces, and 40 fixation trials were presented pseudorandomly, such that face stimuli in each category were presented no more than twice consecutively. Faces were presented centrally on an otherwise black screen for 2000 msec followed by 500 msec of central fixation. Fixation trials consisted of a central fixation point presented on the screen for 2500 msec. Fixation trials were included to introduce “jitter” into the time series so that unique estimates of the hemodynamic responses for the trial types of interest could be computed (Ollinger, Shulman, & Corbetta, 2001), and were interspersed between face trials creating a variable intertrial interval of 0, 2500, 5000, or 7500 msec. Subjects were instructed to determine as quickly and as accurately as possible whether the face was an old (studied) face or a new face, and to respond with a two-alternative forced-choice button press.

For each subject, a whole-brain, high-resolution, T1-weighted anatomical scan (3-D spoiled gradient; 124 sagittal slices, TE = 3.2 msec, TR = 8msec, flip angle = 15, voxel size = 1 mm^3) was collected for transformation of functional data to standardized anatomical space (Talairach & Tournoux, 1988). Functional images were collected in runs using a gradient spin-echo, echo-planar T2*-weighted sequence (TR = 2500 msec, TE = 35 msec, flip angle = 90, $3.75 \times 3.75 \text{ mm}$ in-plane resolution). During each functional run, 105 sets of axial images (25 slices, 4.5 mm slice thickness, 1 mm skip) were acquired allowing whole-brain coverage.

Postscan Memory Assessment

Following fMRI scanning, subjects underwent a surprise recall task assessing their recollection of the names and contexts for faces presented during scanning. Stimuli were presented on a Macintosh G3 laptop screen and subjects wrote their answers to each of the items on a numbered form with blanks. Both old and new faces presented during fMRI scanning were re-presented individually in a pseudorandom order. Specifically, subjects viewed each face, and were instructed to recall the face’s identity (i.e., name) as well as any additional information about the person (i.e., the context sentence). For purposes of sorting trials for the context-dependent memory analysis (see Results), a liberal scoring criterion was used. If a subject was able to successfully recall any portion of the context sentence (e.g., recalling “glasses” when the context was “... wears reading glasses”), the context was considered to be remembered. This approach was therefore conservative with respect to forgotten contexts; only those faces for which no context information was recalled were considered to be truly forgotten. Faces remained on the screen until the subject pressed the space bar advancing to the next trial.

fMRI Analysis

fMRI data were analyzed using Statistical Parametric Mapping software (SPM99, Wellcome Department of Cognitive Neurology, London, UK) (Friston, Holmes, et al., 1995). For each functional run, data were pre-processed to remove sources of noise and artifact. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned within and across runs to correct for head movement, and coregistered with anatomical data. Functional data were then transformed into a standard anatomical space (3-mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute), which approximates Talairach and Tournoux (1988) atlas space. Normalized data were then spatially smoothed (6 mm full width half maximum [FWHM]) using a Gaussian kernel. Analyses took place at two levels: formation of statistical images and regional analysis of hemodynamic responses.

First, for each participant, a general linear model, incorporating task effects (modeled with a canonical hemodynamic response function; Friston, Fletcher, et al., 1998) and covariates of no interest (a session mean, a linear trend, and six movement parameters derived from realignment corrections) were used to compute parameter estimates (beta) and *t*-contrast images (containing weighted parameter estimates) for each comparison at each voxel. These individual contrast images were then submitted to a second-level, random-effects analysis to create mean *t* images. An automated peak-search algorithm identified the location of peak activations based on *t* value and cluster size. To obtain signal change values for the positive-, negative-, neutral-, and no-context trials in an unbiased manner, medial temporal lobe regions of interest (ROIs) were defined based on peaks identified in the mean *t* image comparing all face trials to baseline. In this way, each trial type contributed equally to the generation of ROIs.

Significantly activated voxels ($p < .001$, uncorrected; minimum cluster size = 5 contiguous voxels) within 4 mm of a peak location were included in each region. Consistent with prior work (Kensinger & Corkin, 2004), small ROIs were used due to the circumscribed nature of amygdalar and hippocampal anatomy. Mean signal intensity values for each trial type of interest were then extracted from each ROI and were submitted to off-line statistical tests.

RESULTS

Behavioral Results

Training Sessions

Name recall improved across training sessions (Figure 2). An analysis of variance (ANOVA) revealed a significant effect of training session on recall performance, $F(3, 36) = 86.50$, $p < .0001$. Performance improved linearly from one session to the next, $F(1,12) = 126.25$, $p < .0001$, and planned comparisons revealed that performance during each subsequent session was significantly better than performance during the preceding session (all $ps < .005$). The presence of sentence contexts during learning, however, did not impact the rate at which face-name pairs were learned (Context \times Time interaction: $F < 1$).

Test Session

During fMRI scanning, subjects performed a simple yes/no recognition memory task on previously learned and new faces. There was no significant effect of context type (negative, positive, neutral, and none) on recognition accuracy, $F(3,45) = 1.53$, $p = .22$; Table 2). Similarly, response latencies did not differ as a function of context ($F < 1$), and direct contrasts between response times of each of the four context types did not yield significant

Figure 2. Name recall for faces across encoding sessions. Bars represent mean name recall for faces according to the type of context present during encoding. Error bars represent standard error of the mean (*SEM*). Although name recall improved across sessions, context type did not affect learning rate.

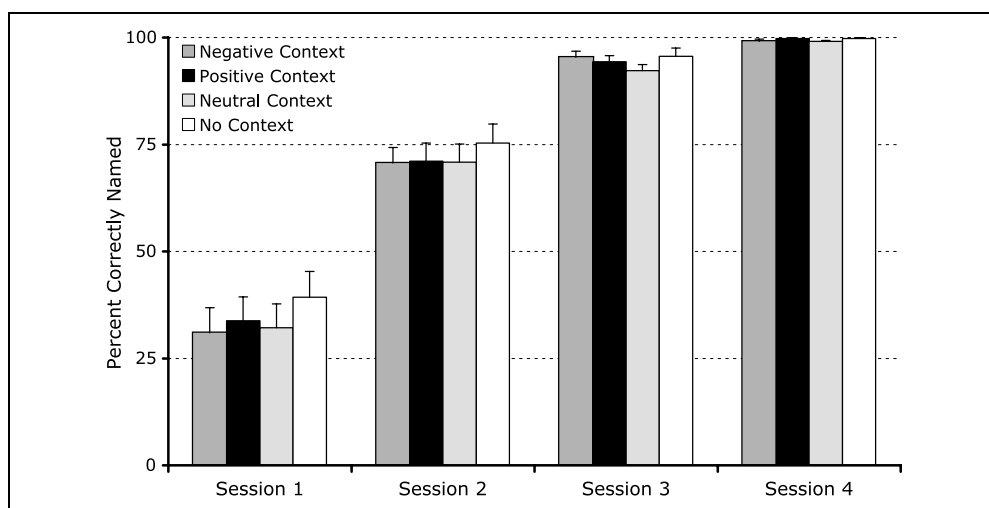


Table 2. Recognition Accuracy (Expressed as the Percentage of Faces Correctly Classified as Either Old or New) and Mean Reaction Times of Correct Responses by Context Type at Encoding

	<i>Negative</i>	<i>Positive</i>	<i>Neutral</i>	<i>No Context</i>	<i>New</i>
Recognition accuracy	95.83 (6.41)	93.96 (6.02)	93.65 (9.55)	95.52 (6.43)	94.92 (6.46)
Reaction time (msec)	941 (115)	934 (94.1)	953 (102)	937 (102)	974 (109)

Numbers in parentheses are group standard deviations from the mean.

results (all $ps > .15$). There was a trend for subjects to respond more slowly to new faces than to old faces, $t(15) = 2.02, p = .06$.

Two further indices of declarative memory were acquired after the fMRI scan. Subjects viewed each of the faces again and were asked to recall the name of each face and any context that they remembered as having been paired with the face during the training sessions.

Name Recall

Contextual information, whether emotional or neutral, did not affect performance on the name recall task. There was no significant main effect of context type (negative, positive, neutral, none) on the proportion of correctly recalled names ($F < 1$). Additionally, a comparison of recall rates for names paired with emotional versus neutral contexts yielded nonsignificant results, $t(15) = .357, p = .73$, as did a contrast of “all contexts” versus no context, $t(15) = -0.312, p = .76$.

Context Recall

Although subjects were not explicitly instructed to memorize the sentence contexts that accompanied a subset of the faces during training, they were nonetheless tested to determine whether any incidental encoding of the context occurred. Similar to name recall, there was no effect of context type (negative, mean [M] = 31.86%; positive, $M = 28.75%$; neutral, $M = 30.83%$) on subsequent recall of the contexts ($F < 1$). Pairwise contrasts of the three individual context types did not yield significant differences (all $ps > .3$).

fMRI Results

The central aim of the present study was to test for region/context dissociations in the medial temporal lobe during memory retrieval. To accomplish this, an ROI analysis was employed. Specifically, medial temporal lobe ROIs were defined in an unbiased manner from a statistical activation map comparing all recognition trials to the baseline control condition (fixating a crosshair) (see Methods). This resulted in the identification of four regions within the medial temporal lobe (reported in Talairach and Tournoux [1988] atlas space): left hippo-

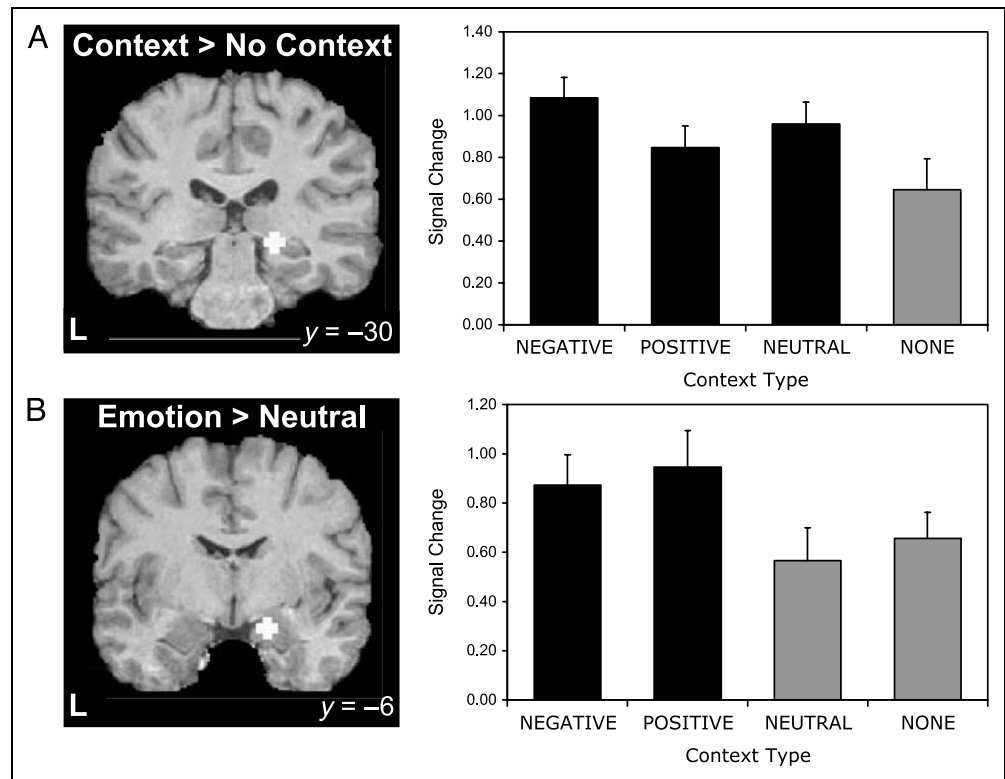
campus ($x = -21, y = -29, z = -4$), left amygdala ($x = -21, y = -4, z = -15$), right hippocampus ($x = 21, y = -29, z = -4$), and right amygdala ($x = 18, y = -7, z = -15$). For each subject, signal intensities for each ROI were calculated for each condition and examined statistically using repeated measures ANOVA. Left-hemisphere regions were considered separately from right-hemisphere regions because we had no *a priori* hypotheses concerning laterality effects, and a three-way ANOVA (examining the factors of Region, Context, and Hemisphere) revealed a near-significant three-way interaction, $F(3,45) = 2.60, p = .06$. This three-way interaction can be conceptualized as a differential region by context interaction as a function of hemisphere.

In the right hemisphere, we observed a functional dissociation between the hippocampus and amygdala. The ROI analysis revealed a significant main effect of context, $F(3,45) = 3.36, p < .05$, and a Region \times Context interaction, $F(3,45) = 3.18, p < .05$. The main effect of region was not significant, $F(1,15) = 1.32, p = .27$. Post hoc statistical tests revealed that the right hippocampus responded more strongly to faces that were previously studied with a context sentence than to faces that were only paired with a name at study, $F(3,45) = 8.60, p < .01$, but did not respond differentially as a function of whether the contexts were emotional or neutral (positive and negative contexts $>$ neutral contexts, $F < 1$) (Figure 3A). By contrast, the right amygdala was not generally responsive to faces encoded with sentence contexts, $F(3,45) = 1.85, p = .18$ (Figure 3B). Rather, activity in the right amygdala was uniquely sensitive to those faces that were encoded in emotional contexts: emotional vs. neutral context: $F(3,45) = 10.11, p < .005$; emotional vs. no context: $F(3,45) = 5.48, p < .05$. Within the emotional contexts, activity in the amygdala did not differ (negative vs. positive, $F < 1$).

This functional dissociation between right hippocampus and amygdala regions was not present in the left hemisphere. Overall, activity in the left hippocampus and amygdala was weaker than in their right-hemisphere homologues, $F(1,15) = 40.73, p < .0001$. Moreover, there was no main effect of context, $F(3,45) = 1.05, p = .38$, and no main effect of region ($F < 1$). The critical region by context interaction was also not significant ($F < 1$).

Although recognition accuracy was high across participants ($>93%$) following a 2-week delay, subjects' ability

Figure 3. Functional dissociation between activity in the right hippocampus (A) and right amygdala (B) while performing a recognition test on faces encoded with emotional contexts (negative, positive), neutral contexts, and no contexts. Images depict a single coronal slice through the center of each functionally defined ROI. Graphs depict mean signal change (arbitrary units) within each ROI (left). Error bars represent standard error of the mean (*SEM*).



to freely recall any contextual information previously associated with each face was relatively poor, with an average recall rate of 30.48%. When considered in relation to the differential right hippocampal and amygdala responses to faces previously paired with contexts, the memory results raise the possibility that activity in these regions occurred in the absence of conscious recollection of the contexts. To test this possibility formally, we examined right hippocampus and amygdala signal intensities separately as a function of whether a face's context could be remembered or forgotten. This was accomplished by collapsing positive and negative contexts into a single condition; activity in the right hippocampus and amygdala regions did not differ between positive and negative contexts, and collapsing across these two conditions further afforded the increased statistical power necessary to contrast the trials based on memory performance. Of interest in this analysis was whether neural activity differed depending on whether the face was recognized in the presence or absence of an ability to recall the contextual information. One subject was excluded from this analysis because of excessively poor recall performance (<5% context recall).

Right hippocampal activity was greater for faces in which subjects were able to recall contextual information than for faces in which subjects could not recall contextual information, $t(14) = 1.75, p = .05$ (Figure 4). By contrast, activity in the right amygdala did not differ as a function of whether emotional contexts could be

explicitly recalled, $t(14) = 0.87, p = .40$. Moreover, amygdala activity was greater for faces paired with emotional contexts than neutral contexts even when the emotional contexts could not be explicitly recalled, $t(14) = 1.76, p < .05$. An overlapping region of the right amygdala ($x = 15, y = -9, z = -12$; identified by

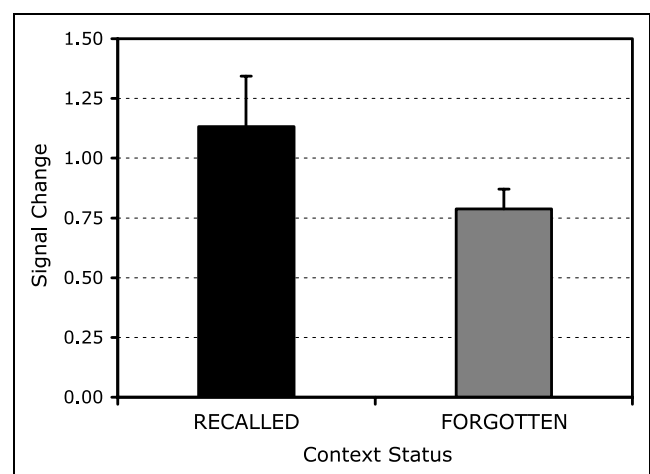


Figure 4. Neural activity in the right hippocampus (region depicted in Figure 3A) during recognition of faces learned with an emotional context differed as a function of whether the associated context could be remembered (RECALLED) or not (FORGOTTEN). Error bars represent standard error of the mean (*SEM*). Hippocampal activity was greater when contextual information could be recalled than when it was forgotten.

contrasting emotional to neutral trials) showed a similar pattern of effects: emotional and recalled > emotional and forgotten, $t(14) = 0.23$, $p = .82$; emotional and forgotten > neutral, $t(14) = 3.29$, $p < .01$ (Figure 5).

Tables 3–5 summarize significant activation in other brain regions demonstrating differential responses to old versus new faces (Table 3), to faces encoded with contextual information versus no contextual information (Table 4), and to faces encoded in emotional versus neutral contexts (Table 5).

DISCUSSION

The present results extend the study of emotional memory to social learning situations. A functional dissociation was observed between the right hippocampus and right amygdala, with greater hippocampal activity during recognition of faces previously presented with contextual information and more focused activity in the amygdala during recognition of faces that had been learned in the presence of an emotional context. Activity in the hippocampus was dependent on subjects' ability to consciously recollect the associated contextual information, whereas activity in the amygdala was not.

Hippocampal activity was comparable for all faces that were learned in the presence of a context, regardless of the context's valence or arousal. Moreover, the level of activity in this region depended upon subjects' ability to specifically recall the contextual information that had been paired with each face during training. This finding is consistent with recent work suggesting an associative role for the hippocampus in memory retrieval (Giovanello, Schnyer, & Verfaellie, 2004; Kirwan & Stark, 2004; Davachi, Mitchell, & Wagner, 2003). For example, Kirwan and Stark (2004) instructed subjects to memorize a series of face–name pairings and then tested them on their ability to discern intact face–name pairs from

recombined or novel face–name pairs. The authors report greater right hippocampal activity when individuals correctly remembered intact relationships between a face and a name than when that relationship was forgotten. Similarly, Giovanello et al. (2004) observed bilateral hippocampal activity during the recognition of intact versus recombined word pairs.

By contrast, amygdala activity was uniquely sensitive to faces that were previously learned with emotional contexts, a finding that supports a role for the amygdala in social evaluation. Consistent with this notion, increased amygdala activity has been observed in healthy individuals making trustworthiness judgments of faces (Wig et al., 2004; Winston, Strange, O'Doherty, & Dolan, 2002) and while viewing geometric shapes that appear to interact in socially meaningful ways (Martin & Weisberg, 2003). Additionally, patients with amygdala damage show impairments when judging individuals on trustworthiness and approachability (Adolphs, Tranel, & Damasio, 1998) and when extracting social meaning from interacting shapes (Heberlein & Adolphs, 2004).

When considering amygdala activity, it can be useful to examine its locus in the context of a relatively broad dorsal/ventral distinction (Kim, Somerville, Johnstone, Alexander, et al., 2003). The locus of the amygdala activation observed in the current study lies in the ventral region of the right amygdala, which, in humans, comprises the anatomical subregion of the basolateral complex (BLC; Mai, Assheuer, & Paxinos, 1997). In rats, the BLC has been shown to be a critical structure in the acquisition of conditioned fear responses (LeDoux, Cicchetti, Xagoraris, & Romanski, 1990). One possibility is that the learning phase of the present paradigm functioned as a form of "social conditioning" where an otherwise neutral stimulus (the face of a stranger) is imbued with a learning history that is either emotional or nonemotional. Rather than storing an explicit memory of the emotional content of an experience, the

Figure 5. Amygdala activity (A) is significantly greater when recognizing faces previously paired with emotional contexts compared to neutral contexts (15, –9, –12; thresholded, $p < .005$, uncorrected, activation displayed on a group-averaged anatomical image). (B) Mean signal change in the right amygdala as a function of whether the contextual information associated with each face could be remembered (RECALLED) or not (FORGOTTEN). The response to faces learned with a neutral context (NEUTRAL) is depicted for reference. Error bars indicate standard error of the mean (SEM). Whereas amygdala activity was greater during recognition of faces learned with emotional contexts than during recognition of faces learned with neutral contexts, activity was not dependent on subjects' ability to consciously recollect the context.

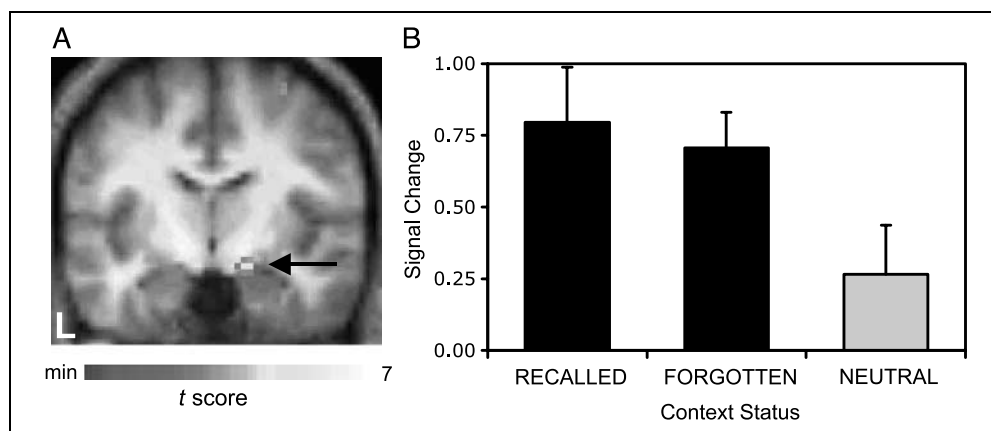


Table 3. Identification of BOLD Signal Contrast for Old versus New Faces

<i>Brain Region</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>z Score</i>
<i>Old > New</i>				
Parietal cortex				
Right BA 5	9	-21	51	4.59
Left BA 7	-36	-59	44	4.00
Right BA 7	18	-43	71	3.62
Right BA 23	15	-54	19	3.77
Frontal cortex				
Left BA 44/45	-53	21	13	5.67
Medial BA 8	-3	26	41	4.49
Left BA 8	-24	49	45	3.40
Left BA 10	-30	62	11	3.80
Motor cortex				
Right BA 4	36	-18	48	5.83
Anterior cingulate				
BA 32	15	-1	39	3.41
Subcortical				
Pons	-3	-52	0	4.19
Cerebellum				
Left cerebellum	-18	-50	-18	5.71
Right cerebellum	12	-83	-26	4.04
<i>New > Old</i>				
Frontal cortex				
Left BA 44	48	10	22	3.55
Medial BA 11	3	34	-17	3.53
Motor cortex				
Left BA 6	-45	-5	9	4.74
Left BA 4	-42	-23	56	4.20
Parietal cortex				
Right BA 40	65	-40	24	3.81
Occipital cortex				
Left BA 18	-36	-87	2	3.73
Left BA 18	-27	-82	-14	3.53
Temporal cortex				
Left BA 20	-59	-18	-19	5.20
Right BA 39	62	-55	11	4.70
Right BA 39	53	-43	28	3.60

Table 3. (continued)

<i>Brain Region</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>z Score</i>
Subcortical				
Left thalamus	-12	20	1	6.24
Cerebellum				
Right cerebellum	6	-69	-37	3.64
Right cerebellum	21	-53	-20	3.57

Activations determined to be significant ($p < .001$), minimum five voxels are listed along with the best estimate of their location. BA = approximate Brodmann's area location. Coordinates are from the Talairach and Tournoux (1988) atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach and Tournoux atlas.

amygdala may code social evaluations as crude emotional representations (i.e., emotional "coloring"). Somewhat analogous to increases in BLC activity in response to a conditioned stimulus, the BLC in humans appears, in the current study, to respond differentially to faces based on their learned emotional salience. In the social

Table 4. Identification of BOLD Signal Contrast for Old Faces Encoded with Contextual Information versus No Contextual Information

<i>Brain Region</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>z Score</i>
<i>Context > No Context</i>				
Parietal cortex				
Right BA 23/30	-3	-43	19	4.01
Frontal cortex				
Left BA 47	-24	31	-14	3.89
Left BA 44	-45	13	30	3.80
Right BA 11	33	25	-19	3.61
Motor cortex				
Right BA 6	-3	-6	56	3.54
Anterior cingulate				
BA 32	-9	16	32	4.52
<i>No Context > Context</i>				
Cerebellum				
Left cerebellum	-21	-77	-29	3.73

Activations determined to be significant ($p < .001$), minimum five voxels are listed along with the best estimate of their location. BA = approximate Brodmann's area location. Coordinates are from the Talairach and Tournoux (1988) atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach and Tournoux atlas.

Table 5. Identification of BOLD Signal Contrast for Old Faces Encoded with Emotional Contexts versus Neutral Contexts

<i>Brain Region</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>z Score</i>
<i>Emotional Context > Neutral Context</i>				
Parietal cortex				
Right BA 7	33	-27	46	3.97
Right BA 40	50	-34	27	3.70
Frontal cortex				
Right BA 45	45	27	15	4.48
Left BA 10	-15	66	14	3.59
Motor cortex				
Right BA 4	27	-23	65	4.07
<i>Neutral Context > Emotional Context</i>				
Parietal cortex				
Left BA 39	-36	-66	23	3.53
Motor cortex				
Left BA 6	-45	17	52	4.04
Subcortical				
Right thalamus	15	-17	12	3.57
Cerebellum				
Left cerebellum	-21	-77	-29	3.73

Activations determined to be significant ($p < .001$), minimum five voxels are listed along with the best estimate of their location. BA = approximate Brodmann's area location. Coordinates are from the Talairach and Tournoux (1988) atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach and Tournoux atlas.

domain, amygdala activity may play a predictive role in guiding future social interactions by tagging certain individuals as emotionally significant. This possibility is consistent with prior behavioral work in amnesic patients showing that, even in the absence of explicit memory for the source of underlying social evaluative judgments, the evaluative coloring can be retained (Tranel & Damasio, 1993; Johnson et al., 1985).

Interestingly, positive and negative "learning histories" yielded comparable levels of amygdala activity in the present study. Thus, to the degree that the amygdala functioned to signal the emotional significance of social stimuli, it did not appear to differentiate affective valence per se. Indeed, Tranel and Damasio (1993) reported a patient with bilateral medial temporal lobe damage including the amygdala who was nonetheless capable of forming nonconscious representations of affective valence. In the present study, there were no

clusters in the medial temporal lobe that were differentially active when faces learned with positive contexts and faces learned with negative contexts were directly contrasted. This was true even when examined with a more lenient statistical threshold ($p < .005$, uncorrected). However, whole-brain exploratory analyses revealed greater activation in bilateral regions of the insular cortex during recognition of faces learned with negative contexts than during recognition of faces learned with positive contexts. The insular cortex has been linked to a variety of unpleasant visceral responses including the perception of pain (Ostrowsky et al., 2002), disgust (Phillips et al., 1997), and vomiting (Fiol, Leppik, Mireles, & Maxwell, 1988). The reverse pattern (greater activation during recognition of faces learned with positive contexts) was not observed in any brain region.

More importantly, the presence of affective valence differences in the insula and the absence of such effects in the amygdala were observed here for material that was well controlled for overall arousal and absolute valence ratings. Emotional stimuli can, and often do, covary in terms of their valence and arousal, thus complicating the understanding of which dimension is indeed most relevant when amygdala activity is observed. Although reports of amygdala activity are most often observed as signal increases for negative stimuli (Maren & Quirk, 2004; Morris & Dolan, 2004; Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Whalen, Shin, et al., 2001; Canli et al., 2000; Whalen, Rauch, et al., 1998; Breiter et al., 1996; Morris et al., 1996), a growing number of reports have also demonstrated signal increases for positive stimuli (Moran, Wig, Adams, Janata, & Kelley, 2004; Whalen, Kagan, et al., 2004; Hommer et al., 2003; Hamann, Ely, Hoffman, & Kilts, 2002; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Yang et al., 2002; Hamann, Ely, Grafton, & Kilts, 1999).

Collectively, these findings suggest that the amygdala may be more sensitive to arousal than valence during emotional memory retrieval. In situations where stimuli are overtly emotional (e.g., the International Affective Photo Series; Lang, Bradley, & Cuthberg, 1997), negative stimuli, on average, are likely to be more arousing than their positive counterparts. When the affective distinction between negative and positive stimuli is subtle, as was the case in the present study, it affords an opportunity to more closely match items for their arousal level. When matched for arousal in this way, amygdala activity was comparable for both positively and negatively contextualized faces. This finding appears to generalize to other sensory domains as well. Anderson, Christoff, Stappen, et al. (2003) used odors that varied in their valence and arousal properties to avoid the confounds associated with overtly emotional pictures, and showed that the amygdala was uniquely sensitive to the intensity of odors regardless of their valence.

It should be noted that other work (Kim, Somerville, Johnstone, Polis, et al., 2004) has controlled for overall

valence and arousal levels and observed valence differences (negative > positive) in a more ventral region of the left amygdala during initial exposure to ambiguously valenced facial expressions (e.g., surprise) when such expressions were contextualized with clarifying contexts (e.g., “She just lost \$500”). The disparate findings linking amygdala activity to both arousal and valence computations highlight the need for future work to consider more fine grained functional anatomic distinctions within the amygdala—an approach that will likely require the enhanced spatial resolution afforded to higher field strength imaging.

Despite robust differences in amygdala activity between faces learned with an emotional context and faces learned with neutral contexts, an effect of emotional context on learning rate, recognition memory, and recall memory was not observed. Subjects performed uniformly well (above 90% accuracy) for each context type on the recognition test. One possibility is that the absence of memory differences based upon emotionality could be due to ceiling effects (see also Dolan, Lane, Chua, & Fletcher, 2000). A longer delay between study and test may have produced more accurate responses to faces encoded with emotional contexts, consistent with the assertion that effects of emotion on memory lie in enhanced retention of emotional memories over time (Sharot & Phelps, 2004).

Consistent with this notion, a subset of subjects ($n = 8$) returned for a second session following a 95 (± 10)-day latency, and was given the same memory tests as the initial session. At this time, subjects were also asked to judge the valence of the individual (good, bad, or neutral), regardless of whether or not they could consciously recollect contextual information about each face. Subjects correctly identified the valence of individuals learned in emotional contexts more often than those learned in neutral contexts, $F(1,7) = 5.99$, $p < .05$. At this time delay, the effect was independent of explicit memory, as recognition memory for the face ($F < 1$), recall of the name ($F < 1$), and recall of the context, $F(1,7) = 1.35$, $p = .28$, did not differ as a function of emotion. Although preliminary, these findings suggest that over longer intervals, memory for the coloring of an individual may persist even when the contextual information has long since been forgotten. Indeed, a recent study by Adolphs, Tranel, and Buchanan (2005) suggests that the amygdala plays a key role in the representation of gist-based emotional memory. Whereas amygdala damage impairs memory for the gist of information embedded in emotional contexts, it spares recollection of the nonemotional details.

More generally, considering the current design, the lack of an explicit memorial advantage for the emotionally contextualized faces may not be surprising. Emotional enhancement of memory has typically been observed in those studies assessing memory for *explicitly* emotional stimuli both behaviorally (Ochsner, 2000;

Cahill & McGaugh, 1998; Cahill, Prins, et al., 1994) and using neuroimaging (Dolcos et al., 2004; Kensinger & Corkin, 2004; Canli et al., 2000; Cahill, Haier, et al., 1996). However, other studies, including the current one, assessing memory for neutral information that has been contextualized with emotional information, have yielded mixed results. Consistent with the current data, previous studies have not found a memorial advantage for items learned in a negative context (Smith et al., 2004; Erk et al., 2003; Maratos et al., 2001), and evidence of a memorial advantage for items learned in a positive context has been reported in some studies (Smith et al., 2004; Erk et al., 2003) but not others (Maratos et al., 2001).

An alternative possibility is that amygdala activity during a memory retrieval task does not directly impact accuracy for emotional and neutral information, but might instead affect the confidence with which individuals make their judgments (i.e., belief in their accuracy). Although we did not collect confidence ratings in the present study, recent work by Sharot, Delgado, and Phelps (2004) showed that emotional photos were judged to be remembered with high confidence more often than neutral photos although overall recognition accuracy did not differ as a function of emotionality. Importantly, high-confidence “remember” judgments for emotional photos elicited enhanced activity in the amygdala—a finding the authors attribute to heightened arousal. Put differently, amygdala activity during memory retrieval increases arousal, which, in turn, leads individuals to be more confident in their memory decisions regardless of whether such decisions are accurate. Amygdala involvement, particularly in high-confidence remember responses to emotional stimuli, has also been reported in subjects following a 1-year delay (Dolcos et al., 2005), extending this finding to long retention intervals. Such an account may explain why recognition accuracy in the present study did not diverge as a function of emotionality although amygdala activity did differ. This would also explain the pattern of amygdala activity observed during face recognition (negative = positive > neutral) as positive and negative contexts were equally arousing, and both were more arousing than the neutral contexts.

In summary, the present results demonstrate an integral role for medial temporal lobe structures during the retrieval of socially relevant experiences. Whereas the hippocampus provides access to consciously recollectable information about others, the amygdala appears to provide a nonspecific arousal or relevance signal when remembering individuals with emotionally colored pasts. More importantly, the amygdala elicits this signal even in situations where conscious recollection of the details of the emotional experience is inaccessible. Thus, the amygdala may act independently of the hippocampus and in concert with other cortical regions (e.g., insular cortex) to ensure that when vivid, conscious

recollections of our past experience with others fail, we may still engage in appropriate social actions in subsequent encounters, avoiding the “short tempered” and perhaps inviting the “blood donor” to lunch.

Acknowledgments

We thank Neil Macrae, Megan McCulloch, Tammy Moran, Jed Dobson, Kate Demos, and Joe Moran for their assistance. This work was supported by NIH Grant MH64667 (W. M. K.) and the Dartmouth Brain Imaging Center. L. H. S. is a National Science Foundation graduate research fellow.

Reprint requests should be sent to Leah Somerville, Dartmouth College, 6207 Moore Hall, Hanover, NH 03755, or via e-mail: leah.somerville@dartmouth.edu.

The data reported in this experiment have been deposited with the fMRI Data Center (www.fmridc.org). The accession number is 2-2006-1213C.

REFERENCES

- Adolphs, R., Cahill, L., Schul, R., & Babinsky, R. (1997). Impaired declarative memory for emotional material following bilateral amygdala damage in humans. *Learning and Memory, 4*, 291–300.
- Adolphs, R., Tranel, D., & Buchanan, T. W. (2005). Amygdala damage impairs emotional memory for gist but not details of complex stimuli. *Nature Neuroscience, 8*, 512–518.
- Adolphs, R., Tranel, D., & Damasio, A. R. (1998). The human amygdala in social judgment. *Nature, 393*, 470–474.
- Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., Anderson, A., Lee, G. P., & Damasio, A. R. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia, 37*, 1111–1117.
- Anderson, A. K., Christoff, K., Panitz, D., De Rosa, E., & Gabrieli, J. D. (2003). Neural correlates of the automatic processing of threat facial signals. *Journal of Neuroscience, 23*, 5627–5633.
- Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., Gabrieli, J. D., & Sobel N. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience, 6*, 196–202.
- Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., & Rosen, B. R. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron, 17*, 875–887.
- Cahill, L., Haier, R. J., Fallon, J., Alkire, M. T., Tang, C., Keator, D., Wu, J., & McGaugh, J. L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings of the National Academy of Sciences, U.S.A., 93*, 8016–8021.
- Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences, 21*, 294–299.
- Cahill, L., Prins, B., Weber, M., & McGaugh, J. L. (1994). Beta-adrenergic activation and memory for emotional events. *Nature, 371*, 702–704.
- Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *Journal of Neuroscience, 20*, RC99.
- Cohen, J. D., MacWhinney, B., Flatt, M., & Provost, J. (1993). Psycscope: A new graphic interactive environment for designing psychology experiments. *Behavioral Research Methods, Instruments, and Computers, 25*, 257–271.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences, U.S.A., 100*, 2157–2162.
- Dolan, R. J., Lane, R., Chua, P., & Fletcher, P. (2000). Dissociable temporal lobe activations during emotional episodic memory retrieval. *Neuroimage, 11*, 203–209.
- Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron, 42*, 855–863.
- Dolcos, F., LaBar, K. S., & Cabeza, R. (2005). Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proceedings of the National Academy of Sciences, U.S.A., 102*, 2626–2631.
- Erk, S., Kiefer, M., Grothe, J., Wunderlich, A. P., Spitzer, M., & Walter, H. (2003). Emotional context modulates subsequent memory effect. *Neuroimage, 18*, 439–447.
- Fiol, M. E., Leppik, I. E., Mireles, R., & Maxwell, R. (1988). Ictus emeticus and the insular cortex. *Epilepsy Research, 2*, 127–131.
- Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *Neuroimage, 7*, 30–40.
- Friston, K. J., Holmes, A., Worsley, K., Poline, J., Frith, C., & Frackowiak, R. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping, 2*, 189–210.
- Giovanello, K. S., Schnyer, D. M., & Verfaellie, M. (2004). A critical role for the anterior hippocampus in relational memory: Evidence from an fMRI study comparing associative and item recognition. *Hippocampus, 14*, 5–8.
- Hamann, S. B., Ely, T. D., Grafton, S. T., & Kilts, C. D. (1999). Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience, 2*, 289–293.
- Hamann, S. B., Ely, T. D., Hoffman, J. M., & Kilts, C. D. (2002). Ecstasy and agony: Activation of the human amygdala in positive and negative emotion. *Psychological Science, 13*, 135–141.
- Heberlein, A. S., & Adolphs, R. (2004). Impaired spontaneous anthropomorphizing despite intact perception and social knowledge. *Proceedings of the National Academy of Sciences, U.S.A., 101*, 7487–7491.
- Hommer, D. W., Knutson, B., Fong, G. W., Bennett, S., Adams, C. M., & Varnera, J. L. (2003). Amygdalar recruitment during anticipation of monetary rewards: An event-related fMRI study. *Annals of the New York Academy of Sciences, 985*, 476–478.
- Johnson, M. K., Kim, J. K., & Risse, G. (1985). Do alcoholic Korsakoff's syndrome patients acquire affective reactions? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 11*, 22–36.
- Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., & Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*, 927–936.
- Kensinger, E. A., & Corkin, S. (2004). Two routes to emotional memory: Distinct neural processes for valence

- and arousal. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 3310–3315.
- Kim, H., Somerville, L. H., Johnstone, T., Alexander, A. L., & Whalen, P. J. (2003). Inverse amygdala and medial prefrontal cortex responses to surprised faces. *NeuroReport*, *14*, 2317–2322.
- Kim, H., Somerville, L. H., Johnstone, T., Polis, S., Alexander, A. L., Shin, L. M., & Whalen, P. J. (2004). Contextual modulation of amygdala responsivity to surprised faces. *Journal of Cognitive Neuroscience*, *16*, 1730–1745.
- Kirwan, C. B., & Stark, C. E. (2004). Medial temporal lobe activation during encoding and retrieval of novel face–name pairs. *Hippocampus*, *14*, 919–930.
- Lang, P. L., Bradley, M. M., & Cuthbert, B. N. (1997). *International affective picture system* [Pictures]. Gainesville, FL: NIMH Center for the Study of Emotion and Attention.
- LeDoux, J. E., Cicchetti, P., Xagoraris, A., & Romanski, L. M. (1990). The lateral amygdaloid nucleus: Sensory interface of the amygdala in fear conditioning. *Journal of Neuroscience*, *10*, 1062–1069.
- Lewicki, P. (1984). Nonconscious biasing effects of single instances on subsequent judgments. *Journal of Personality and Social Psychology*, *48*, 563–574.
- Mai, J. K., Assheuer, J., & Paxinos, G. (1997). *Atlas of the human brain*. New York: Thieme.
- Maratos, E. J., Dolan, R. J., Morris, J. S., Henson, R. N., & Rugg, M. D. (2001). Neural activity associated with episodic memory for emotional context. *Neuropsychologia*, *39*, 910–920.
- Maren, S., & Quirk, G. J. (2004). Neuronal signalling of fear memory. *Nature Reviews Neuroscience*, *5*, 844–852.
- Martin, A., & Weisberg, J. (2003). Neural foundations for understanding social and mechanical concepts. *Cognitive Neuropsychology*, *20*, 575–587.
- Moran, J. M., Wig, G. S., Adams, R. B., Jr., Janata, P., & Kelley, W. M. (2004). Neural correlates of humor detection and appreciation. *Neuroimage*, *21*, 1055–1060.
- Morris, J. S., & Dolan, R. J. (2004). Dissociable amygdala and orbitofrontal responses during reversal fear conditioning. *Neuroimage*, *22*, 372–380.
- Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, *383*, 812–815.
- Ochsner, K. N. (2000). Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. *Journal of Experimental Psychology: General*, *129*, 242–261.
- Ollinger, J. M., Shulman, G. L., & Corbetta, M. (2001). Separating processes within a trial in event-related functional MRI. *Neuroimage*, *13*, 210–217.
- Ostrowsky, K., Magnin, M., Ryvlin, P., Isnard, J., Guenot, M., & Mauguiere, F. (2002). Representation of pain and somatic sensation in the human insula: A study of responses to direct electrical cortical stimulation. *Cerebral Cortex*, *12*, 376–385.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 11458–11463.
- Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., Calder, A. J., Bullmore, E. T., Perrett, D. I., Rowland, D., Williams, S. C., Gray, J. A., & David, A. S. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature*, *389*, 495–498.
- Raczkowski, D., Kalat, J. W., & Nebes, R. (1974). Reliability and validity of some handedness questionnaire items. *Neuropsychologia*, *12*, 43–47.
- Richardson, M. P., Strange, B. A., & Dolan, R. J. (2004). Encoding of emotional memories depends on amygdala and hippocampus and their interactions. *Nature Neuroscience*, *7*, 278–285.
- Sharot, T., Delgado, M. R., & Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nature Neuroscience*, *7*, 1376–1380.
- Sharot, T., & Phelps, E. A. (2004). How arousal modulates memory: Disentangling the effects of attention and retention. *Cognitive, Affective, and Behavioral Neuroscience*, *4*, 294–306.
- Smith, A. P., Henson, R. N., Dolan, R. J., & Rugg, M. D. (2004). fMRI correlates of the episodic retrieval of emotional contexts. *Neuroimage*, *22*, 868–878.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain* (M. Rayport, Trans.). New York: Thieme.
- Tranel, D., & Damasio, A. R. (1993). The covert learning of affective valence does not require structures in hippocampal system or amygdala. *Journal of Cognitive Neuroscience*, *5*, 79–88.
- Uleman, J. S., Blader, S., & Todorov, A. (2005). Implicit impressions. In R. Hassin, J. S. Uleman, & J. A. Bargh (Eds.), *The new unconscious* (pp. 362–392). New York: Oxford University Press.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., McLaren, D. G., Somerville, L. H., McLean, A. A., Maxwell, J. S., & Johnstone, T. (2004). Human amygdala responsivity to masked fearful eye whites. *Science*, *306*, 2061.
- Whalen, P. J., Rauch, S. L., Etkoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, *18*, 414–418.
- Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion*, *1*, 70–83.
- Wig, G. S., Miller, M. B., Kingstone, A., & Kelley, W. M. (2004). Separable routes to human memory formation: Dissociating task and material contributions in the prefrontal cortex. *Journal of Cognitive Neuroscience*, *16*, 139–148.
- Winston, J. S., Strange, B. A., O’Doherty, J., & Dolan, R. J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience*, *5*, 277–283.
- Yang, T. T., Menon, V., Eliez, S., Blasey, C., White, C. D., Reid, A. J., Gotlib, I. H., & Reiss, A. L. (2002). Amygdalar activation associated with positive and negative facial expressions. *NeuroReport*, *13*, 1737–1741.