# Role of Amygdala Connectivity in the Persistence of Emotional Memories Over Time: An Event-Related fMRI Investigation

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According to the consolidation hypothesis, enhanced memory for emotional information reflects the modulatory effect of the amygdala on the medial temporal lobe (MTL) memory system during consolidation. Although there is evidence that amygdala–MTL connectivity enhances memory for emotional stimuli, it remains unclear whether this enhancement increases over time, as consolidation processes unfold. To investigate this, we used functional magnetic resonance imaging to measure encoding activity predicting memory for emotionally negative and neutral pictures after short (20-min) versus long (1-week) delays. Memory measures distinguished between vivid remembering (recollection) and feelings of knowing (familiarity). Consistent with the consolidation hypothesis, the persistence of recollection over time (long divided by short) was greater for emotional than neutral pictures. Activity in the amygdala predicted subsequent memory to a greater extent for emotional than neutral pictures. Although this advantage did not vary with delay, the contribution of amygdala–MTL connectivity to subsequent memory for emotional items increased over time. Moreover, both this increase in connectivity and amygdala activity itself were correlated with individual differences in recollection persistence for emotional but not neutral pictures. These results suggest that the amygdala and its connectivity with the MTL are critical to sustaining emotional memories over time, consistent with the consolidation hypothesis.

Keywords: affect, arousal, connectivity, consolidation, emotional memory

The formation of emotional episodic memories, compared with nonemotional (neutral) memories, is characterized by at least 2 distinct advantages: increased resources during encoding (Dolcos et al. 2004a; Kensinger 2004) and arousal-driven enhancements leading to improved consolidation. According to the consolidation hypothesis, the latter effects reflect the modulatory influence of the amygdala on the medial temporal lobe (MTL) memory system, which boosts consolidation processes and the persistence of memories over time (McGaugh 2004; LaBar and Cabeza 2006).

These neurohormonal changes within the amygdala–MTL network, which constitute the "direct" route to emotional memory, are accompanied by a host of other changes during item encoding, including increased attentional and perceptual processing resources allocated to emotional stimuli (Dolan and Vuilleumier 2003). These cognitive and perceptual encoding enhancements exert an indirect influence over emotional memory strength and thus may be considered the "indirect" network supporting emotional memory. These "direct" and "indirect" networks are dissociable: whereas the direct network must be recruited by increased arousal, it has been suggested that components of the indirect network can be recruited by valence (whether an item is positive or negative) alone (Kensinger and Corkin 2004). Furthermore, although both networks are activated during encoding, the impact of the direct network should become more apparent as consolidation processes unfold over time. By manipulating the time between encoding and retrieval, the present study highlights the role of the direct network in creating and sustaining emotional memories.

Arousal enhances emotionally negative memories relative to neutral as time goes on, from 20 min to 1 week (Kleinsmith and Kaplan 1963), from immediate to 1 h (LaBar and Phelps 1998), from 1 day to 2 weeks (Anderson et al. 2006), and from immediate to 24 h (Sharot and Phelps 2004; Sharot and Yonelinas 2008) after encoding. Indeed, emotional memory is particularly resilient to time, with laboratory enhancements being reported up to 1 year after encoding (Dolcos et al. 2005). Emotional memories also tend to be accompanied by highly confident responding or a sense of reexperiencing (Ochsner 2000; Kensinger and Corkin 2003; Sharot et al. 2004; Dolcos et al. 2005), and these recollection benefits are also augmented relative to neutral over time (Anderson et al. 2006; Sharot and Yonelinas 2008).

These behavioral results are consistent with the claim that consolidation serves to mediate emotional memory enhancements over the course of hours to days (LaBar and Phelps 1998). Accordingly, postencoding consolidation manipulations influence memory after long (e.g., 24 h) but not after short (e.g., 1.5 h) delays (Bianchin et al. 1999). The passage of time, then, should yield functional dissociations in the relative importance of encoding and consolidation effects to predicting subsequent retrieval of emotional memories (Hamann 2001). One may predict that activity associated with arousal-mediated consolidation should increasingly distinguish between subsequently remembered and forgotten emotional items over time, whereas activity related to perceptual, attentional, or semantic encoding should make no improvement or even decay in its ability to make this distinction.

Although consolidation occurs after encoding, emotional arousal during encoding initiates firing rate increases within the amygdala that can persist for up to 2 h after encoding (Pelletier et al. 2005), spanning the period during which consolidation manipulations are particularly effective (McGaugh 2004). Furthermore, it has been demonstrated that amygdala activity facilitates the induction and expression of hippocampal long-term potentiation, which may be the underlying mechanism of memory consolidation (Nakao et al. 2004; Hu et al. 2007). These effects are time sensitive: long-term potentiation benefits most when the amygdala and hippocampus are coactivated during acquisition or encoding. Thus, initial coactivation of these structures determines how much the memory trace will be strengthened and persist over time. These results

give credence to the supposition that amygdala and MTL activity during encoding have implications for memory consolidation, consistent with previous interpretations of human data (Cahill et al. 1996; Hamann et al. 1999; Dolcos et al. 2004b).

One powerful way to study how encoding activity leads to successful memory is the subsequent memory paradigm (Paller and Wagner 2002). This paradigm involves measuring a participant's brain activity while they encode a list of items. The results from a subsequent memory test are then applied to each participant's encoding data, classifying each encoding trial as a subsequently remembered or forgotten trial. Greater activity for remembered than forgotten trials is taken as *encoding success activity* (ESA) or encoding activity that leads to successful subsequent memory. Critically, this method enables the researcher to draw conclusions about within-subject, event-related activity that specifically predicts memory for that item. In comparison, correlations between an individual's encoding activity and overall memory score enable conclusions about across-subject, individual differences supporting later memory.

Few studies have investigated the neural correlates supporting emotional memory or recollection changes over time. In 1 such study, positron emission tomography (PET) scans revealed that amygdala regional cerebral blood flow during encoding correlated with emotional recognition after a 4-week delay but not with emotional free recall after a 10-min delay (Hamann et al. 1999). The authors attributed this effect to the role of consolidation, but due to limitations of the PET method, they were unable to look at event-related activity predicting subsequent memory. A later event-related functional magnetic resonance imaging (fMRI) investigation found that ventral amygdala activity during emotional picture viewing correlated with emotional memory after a 2-week delay whereas dorsal amygdala activity correlated with emotional memory immediately after encoding (Mackiewicz et al. 2006). Because this experiment did not employ a subsequent memory design, these results are again derived from across-subject correlations. It remains to be seen how the amygdala participates at the trial level to identify which items will be remembered after short versus long delays. Furthermore, neither of these studies reported a corresponding behavioral effect, with improved emotional memory relative to neutral over time. Taken together, these results suggest that individual variations during emotional memory encoding are related to how well these traces persist over time, but the role of intertrial functional differences remains unclear.

Another key consideration in this line of research is the dynamic nature of arousal-mediated consolidation, which depends on interactions between the amygdala and the MTL memory system. Emotional memory enhancements are contingent on coactivation of the amygdala with hippocampal (Roozendaal et al. 1999) and parahippocampal (Roesler et al. 2002) regions, and manipulations of either component can impact memory function (McIntyre et al. 2003; Richardson et al. 2004). This interactive relationship has also been observed at the level of functional neuroimaging: correlations between memory-related activity in the amygdala and that in the hippocampus (Dolcos et al. 2004b; Kensinger and Corkin 2004) and parahippocampal gyrus (PHG) (Kilpatrick and Cahill 2003; Dolcos et al. 2004b) are greater during emotional item encoding than neutral. The dynamic process of consolidation, then, may be best captured via connectivity analyses, rather than simple contrasts.

The present study improves upon the previous literature by combining complementary methods to investigate the impact of study-test delay on encoding and consolidation-related activity supporting emotional memory. It employs a subsequent memory design to look at within-subject event-related activity and connectivity that distinguish between remembered and forgotten emotional items after short (20-min) versus long (1-week) delays, as well as across-subject differences that correlate with emotional memory persistence. We interrogate 3 main hypotheses: 1) activity in the amygdala and MTL memory system will be more predictive of long-delay emotional memory than short-delay emotional memory; 2) individuals who display greater amygdala responses to emotional stimuli during encoding will show greater preservation of recollection for emotional stimuli over time; and 3) functional connectivity between the amygdala and MTL memory system will be greatest for those items remembered at the long delay, representing the increasing importance of dynamic consolidation processes.

## Methods

### *Participants*

Nineteen young adults (9 female; mean age = 22.7 years, standard deviation [SD] = 3.2) participated in the study. Participants were healthy, right-handed, native English speakers, and with no disclosed history of neurological or psychiatric episodes. Participants gave written informed consent for a protocol approved by the Duke University Institutional Review Board. Due to image quality problems in their MRI scans, 2 of these participants were excluded from all analyses. Of the remaining 17 participants, 4 did not have enough trials (i.e., at least 10 per trial type) in each of the trial types of interest and thus could not be included in the fMRI analyses. All behavioral and neuroimaging analyses were conducted on the remaining 13 participants (7 female; mean age = 22.6 years, SD = 3.4).

### *Materials*

Stimuli consisted of 480 pictures. These were selected from the International Affective Picture System (Lang et al. 2001) as well as from an in-house, standardized database (Yamasaki et al. 2002) that allowed us to equate the pictures for visual complexity and content (e.g., human presence). Pictures were assigned on the basis of normative valence scores to emotionally negative (valence: 1.4–4) and neutral (valence: 4–6) conditions. In accordance with the picture selection procedure, valence scores (1 = negative, 5 = neutral, 9 = positive) were lower for negative ($M = 2.75$, SD = 0.69) than neutral pictures ($M = 5.04$, SD = 0.52; $t_{478} = 41.22$, $P < 0.001$). Additionally, arousal scores (1 = calm, 9 = excited) were greater for emotional ($M = 5.69$, SD = 0.89) than neutral pictures ($M = 3.82$, SD = 0.80; $t_{478} = 24.29$, $P < 0.001$).

### *Procedure*

Participants encoded pictures in the scanner, and their recognition memory for these pictures was tested after 2 different delays. During encoding, participants viewed 160 emotionally negative and 160 neutral pictures while functional MR images were recorded. The pictures were presented in color for 1 s, followed by a noise mask for 200 ms. Trials were separated by an intertrial fixation period that was quasi-exponentially distributed between 3 and 9 s, with a mean of 4750 ms, allowing for event-related fMRI analyses. Participants were instructed to indicate as soon as possible whether each picture was of an indoor or outdoor scene, and responses were collected until the onset of the next stimulus. The encoding session consisted of 5 functional runs, across which emotional and neutral pictures were evenly divided. To avoid the induction of long-lasting mood states, the pictures within each block were pseudorandomized so that no more than 3 pictures of the same valence were consecutively presented. Block presentation order was counterbalanced across subjects.

Twenty minutes after encoding, participants completed a recognition task for half of these pictures (80 emotional negative, 80 neutral) outside of the scanner. An additional 40 emotionally negative and 40 neutral pictures were presented as distracters. These pictures were presented for 1 s, followed by a 1500-ms fixation, during which participants were instructed to respond whether the item was old or new. Then a confidence screen appeared for 1500 ms, instructing the participants to rate their confidence on a 3-point scale, from 1 meaning "not sure" to 3 meaning "very sure." Trials were separated by a 1500-ms fixation period, and confidence responses were recorded until the onset of the next stimulus. This 2-step response procedure yielded 6 possible recognition response options (i.e., from "very sure new" to "very sure old"). All pictures were presented in gray scale in order to attenuate memory performance. One week later, participants were tested for their recognition of the remaining study items (80 emotionally negative, 80 neutral), also outside of the scanner. Study items were randomly assigned to 2 retrieval lists, and these lists were counterbalanced across subjects for whether they were presented at the 20-min or 1-week delay. Recognition sessions at each delay were identical in design.

### Behavioral Analyses

To measure overall differences in memory between conditions, $d'$ scores were evaluated for each trial type. Recollection and familiarity estimates were derived for each subject according to a dual-process receiver operating characteristic (ROC) curve-fitting procedure (Yonelinas et al. 1998). This model assumes that recollection and familiarity independently contribute to memory performance but are not mutually exclusive. In order to generate the ROCs, recognition data were rescaled from 1, indicating a highly confident "new" response, to 6, indicating a highly confident "old" response. Hit and false alarm rates were plotted according to this confidence scale, forming an ROC for each subject and condition. By fitting these data points to a function relating them to dual-process memory performance, we obtained parameter estimates of recollection and familiarity for each ROC. Estimates from each delay were then combined into a single measure by dividing the long-delay estimate by the corresponding short-delay estimate, yielding a measure of memories' resistance to forgetting or "persistence." For example, if a participant had a $d'$ of 2.4 after a short delay and a $d'$ of 1.2 after a long delay, the resulting "persistence score" was 0.5. A persistence score of 1 corresponds to the case when memory performance after a long delay is as high as memory performance after a short delay. Persistence scores were calculated for memory performance overall and separately for recollection (*recollection persistence score*) and for familiarity (*familiarity persistence score*). These 3 persistence scores were separately calculated for emotional and neutral pictures.

### fMRI Methods

#### Scanning

Images were collected using a 4-T GE scanner. Stimuli were presented using liquid crystal display goggles (Resonance Technology, Northridge, CA), and behavioral responses were recorded using a 4-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 commissure (AC) and posterior commissure (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 500-ms repetition time (TR), a 14-ms echo time (TE), 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 × 3.75 × 3.8 mm voxels.

#### fMRI Analyses

Preprocessing and data analyses were performed using SPM2 software implemented in Matlab (www.fil.ion.ucl.ac.uk/spm/). After discarding

the 1st 6 volumes, the functional images were slice timing corrected and motion corrected and then spatially normalized to the Montreal Neurological Institute template and spatially smoothed using an 8-mm isotropic Gaussian kernel, and resliced to a resolution of 3.75 × 3.75 × 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 (GLM), as implemented in SPM2. Confounding factors (head motion, magnetic field drift) were also included in the model.

#### Effects of Arousal on Encoding Activity Predicting Memory at Short and Long Delays

The subsequent memory paradigm (Paller and Wagner 2002) was employed to identify ESA, which was defined as greater activity for pictures that were remembered rather than forgotten in subsequent memory tests. Eight main trial types were modeled, representing all possible combinations of arousal (emotional vs. neutral pictures), delay (short vs. long delays), and subsequent retrieval (hit vs. miss trials). Long-delay misses were disregarded in all fMRI analyses because this trial type is ambiguously related to short-delay hits and misses. That is, this trial type represents items that, had they been tested at the short delay, may have been classified as either short-delay hits or misses. However, because we did not retest any items, it is unclear which items would have fallen which way. Thus, both short- and long-delay hits were compared with a common baseline, short-delay misses.

To find ESA regardless of delay, short- and long-delay hits were collapsed and compared with short-delay misses for each emotion type, yielding ESA for emotional and neutral pictures for each participant. A random-effects paired t-test then revealed which regions showed a greater ESA for emotional than neutral pictures. This t-test ($P = 0.05$, extent threshold = 5 functional voxels) was inclusively masked with ESA for emotional pictures at $P = 0.05$, pulling out only those regions that contribute differentially to the encoding of emotional stimuli. Although probabilities are not completely independent, this procedure results in a threshold that approaches the joint probability estimate of $P = 0.0025$ (Fisher 1950; Lazar et al. 2002).

To assess the interaction between arousal and delay, contrasts between short- and long-delay hits for each emotion type were generated for each subject. Because short- and long-delay hits share a common baseline, this is functionally equivalent to comparing the subsequent memory effect at the short delay with that at the long delay for each emotion type. Paired t-tests compared this delay effect for emotional and neutral. These t-tests ($P = 0.05$, extent threshold = 5 voxels) were inclusively masked at $P = 0.05$ with the corresponding delay effect (e.g., long-delay emotional hits > short-delay emotional hits) and subsequent memory effect (e.g., long-delay emotional hits > short-delay emotional misses) as to isolate those memory-related areas that distinguish between emotional short- and long-delay hits but not between neutral short- and long-delay hits. Because of the triple threshold, the joint probability of these activations can be estimated as approaching $P = 0.000125$.

#### Individual Differences Associated with Sustained Recollection

In order to track regions whose activity correlated with individual differences in sustained recollection, we implemented the simple regression model in SPM2. Parametric maps contrasting all emotional or neutral items versus baseline were taken as the dependent variables for each subject, and their corresponding measures of sustained recollection served as covariates. Resulting regression maps for each emotion type were thresholded at $P = 0.05$ with extent threshold = 5 voxels within the MTL and at $P = 0.001$ with extent threshold = 5 voxels outside of the MTL. The probability threshold was lower in the MTL because we can reasonably expect to see recollection-related activity within these regions. The conjunction of these maps (via inclusive masking, both at $P = 0.05$, extent threshold = 10 voxels) was also taken to reveal general sustained recollection effects. The joint probability of this conjunction can be estimated as approaching $P = 0.0025$.

#### Functional Connectivity Analyses

Amygdala regions identified in the previous regression analysis were further interrogated via individual trial analysis to examine the

functional network of brain regions correlated with activity in this region. We created a GLM in which each individual trial was modeled by a separate covariate, yielding different parameter estimates for each individual trial and for each individual subject. The validity of the use of this design has been confirmed in previous studies (Rissman et al. 2004; Daselaar, Fleck, and Cabeza 2006; Daselaar, Fleck, Dobbins, et al. 2006). Parameter estimates from our peak amygdala voxel were correlated with trial-specific parameter estimates from all other voxels, generating correlation maps for each of our trial types of interest: emotional short-delay hits, emotional long-delay hits, neutral short-delay hits, and neutral long-delay hits. The correlation data was normalized via the Fisher transform (Fisher 1921), resulting in connectivity $z$ maps.

In order to assess differences in functional connectivity between our trial types, connectivity $z$ maps for short- and long-delay hits were statistically compared with each other for each subject. Data from the $z$ maps were 1st subtracted from each other, then divided by the standard error of the difference, $\sqrt{\left(1/\left(N_{short}-3\right)+1/\left(N_{long}-3\right)\right)}$. This yielded $z$ maps representing the difference in connectivity associated with subsequent hits at each delay. These connectivity difference maps for emotional versus neutral were compared with a paired $t$-test ($P = 0.05$, extent threshold = 4 voxels within the MTL, 10 voxels elsewhere), inclusively masked with corresponding group effect (e.g., long-delay emotional hit > short-delay emotional hit connectivity) at $P = 0.05$ (approaching the joint probability of $P = 0.0025$). This is consistent with the way in which we assessed the interaction of emotion and delay in our ESA analyses. In this way, we were able to isolate, for example, regions exhibiting greater amygdala connectivity for subsequent long-delay hits than for short-delay hits but only for emotional items. Individual differences in connectivity were assessed outside of SPM by exporting the difference map values for a specified functional ROI and correlating them with sustained recollection measures for each subject.
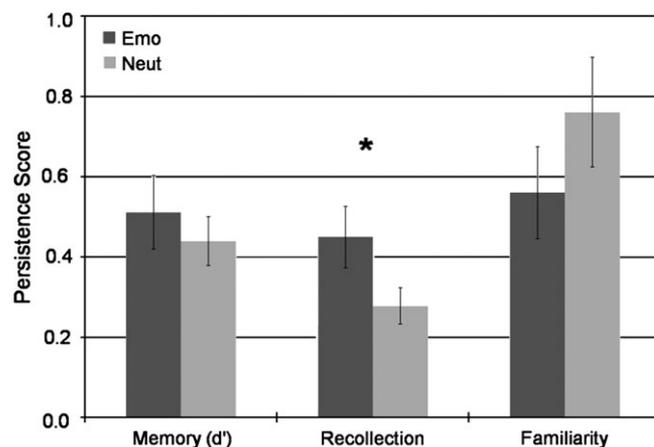
## Results

### Behavioral Results

Persistence scores were calculated by dividing long-delay $d'$ scores by short-delay $d'$ scores for each individual (see Methods). Although persistence scores did not show emotion effects overall, $P > 0.1$ (Fig. 1), differences were found when persistence scores were separately calculated for recollection and familiarity. As illustrated by Figure 1, whereas recollection persistence scores were greater for emotional than neutral pictures, $t_{12} = 2.75$, $P = 0.017$, familiarity persistence scores did not differ as a function of emotion, $P > 0.1$ (Fig. 1). These results are consistent with evidence that the memory-enhancing effect of emotion is driven mainly by recollection rather than familiarity (Ochsner 2000; Kensinger and Corkin 2003; Dolcos et al. 2005) and expand this evidence by showing that recollection benefits increase over time.

### Imaging Results

#### Encoding Activity Predicting Memory for Emotional and Neutral Pictures After Short Versus Long Delays

Analyses comparing ESA (remembered > forgotten) for emotional versus neutral pictures were 1st performed collapsed over delay and then as function of delay (i.e., emotional–neutral × short–long interaction). Greater ESA for emotional than neutral stimuli collapsed over delays was found in bilateral amygdalae and the left inferior frontal gyrus (see Fig. 2), among other brain regions (see Table 1). Unexpectedly, no regions survived our interaction analysis, suggesting that ESA for emotional items does not vary by delay. Thus, the results did not support our 1st prediction that activity in the amygdala



**Figure 1.** Behavioral results. Memory at each delay was assessed using the corrected recognition score $d'$, and recollection and familiarity estimates were obtained via a dual-process ROC curve-fitting procedure (Yonelinas et al. 1998). Persistence scores for memory, recollection, and familiarity were then calculated by dividing long-delay estimates by their associated short-delay estimates (e.g., emotional memory persistence is equivalent to emotional long-delay $d'$ divided by emotional short-delay $d'$). Recollection persistence scores were significantly greater for emotional than neutral items, suggesting an emotional recollection effect. Error bars indicate standard error of the mean. *Significant at $P = 0.05$.

and MTL memory system would be more predictive of memory after a long delay than after a short delay in the case of emotional pictures. Instead, ESA for emotional pictures was comparable for short- and long-delay memory (see Fig. 2).

#### Individual Differences Associated with Recollection Persistence for Emotional Stimuli

To identify activity more directly associated with consolidation processes leading to recollection after a long delay, individual recollection persistence scores (long divided by short) were entered as a regressor in a whole-brain analysis. Consistent with our 2nd prediction, 1 of the brain regions showing significant correlations between encoding activity and recollection persistence scores was the amygdala (see Table 2). Moreover, left amygdala activity predicted recollection persistence scores in the case of emotional pictures but not in the case of neutral pictures (see Fig. 3). This suggests that people with greater amygdala response to emotional items during encoding are more likely to maintain strong, recollective memory traces for these items over time. Recollection persistence scores for emotional stimuli were also correlated with activity in the left fusiform gyrus (Table 2). Recollection persistence scores for neutral stimuli were not correlated with any regions, even using a more lenient threshold ($P = 0.005$ outside MTL). The conjunction of emotional and neutral regression maps revealed 2 regions predictive of recollection persistence scores for both emotional and neutral stimuli: left fusiform gyrus and posterior left inferior frontal gyrus. Thus, the left amygdala was involved in predicting recollection persistence scores only for emotional items.

#### Functional Connectivity Distinguishing between Remembered Items at Short Versus Long Delays

The peak amygdala voxel identified by the preceding regression analysis (Fig. 3) was taken as the seed voxel for an analysis that identified connections between the left amygdala and the rest of the brain that predicted subsequent memory as a function of emotion and delay. Consistent with our 3rd prediction, 1 of the
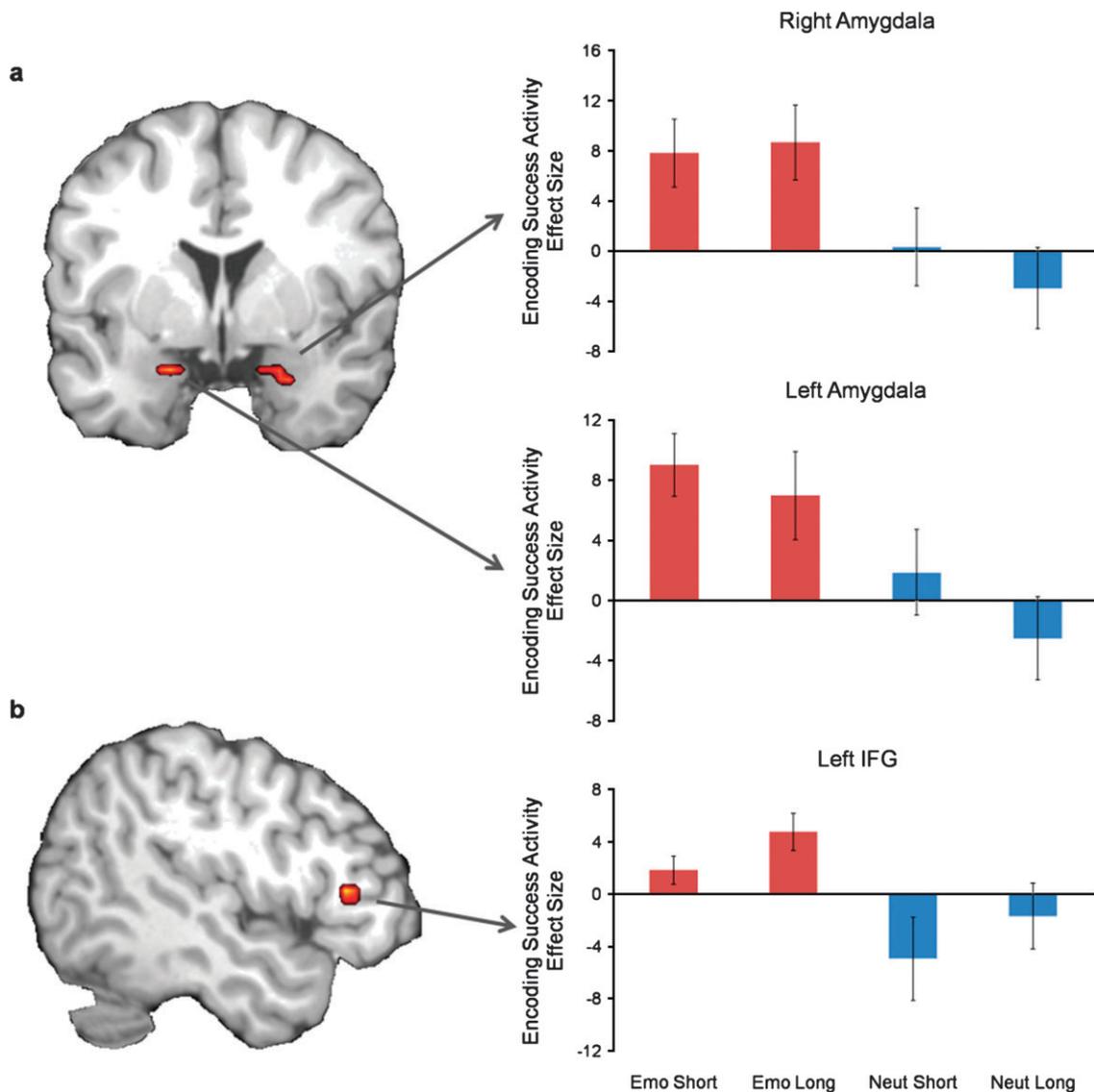
**Figure 2.** ESA for emotional items. Areas that show greater ESA for emotional (Emo) than neutral (Neut) items include (*a*) bilateral amygdalae and (*b*) left inferior frontal gyrus (IFG). Bar graphs represent functional ESA estimates, that is, group-averaged contrasts between hits at each delay (short and long) and short-delay misses. Error bars indicate standard error of the mean. See Table 1 for coordinates.

regions where amygdala connectivity modulated the persistence of emotional memory over time was found within MTL (see Table 3). As illustrated by Figure 4, greater connectivity between the amygdala and bilateral anterior parahippocampal regions predicted emotional memory after a long delay compared with a short delay, and this effect was specific to emotional items (Fig. 4). The peak of the left parahippocampal cluster appears to fall medially within entorhinal cortex, whereas the right parahippocampal cluster is closest to the intersection of entorhinal and perirhinal cortices. No MTL regions showed the opposite pattern of connectivity, with greater connectivity predicting memory for emotional stimuli after a short rather than long delay. Outside of the MTL, greater connectivity between the amygdala and right parietal and medial frontal regions also predicted memory for emotional stimuli after a long delay to a greater extent than memory after a short delay (Table 3). In the reverse analysis, compared with memory after a long delay, memory for emotional pictures after

a short delay was predicted by greater encoding connectivity between the amygdala and the left medial frontal gyrus.

To investigate this pattern of amygdala–MTL connectivity further, *z* scores representing the difference between connectivity associated with long- versus short-delay emotional hits were extracted from each identified parahippocampal region. Note that positive values indicate greater connectivity associated with long- than short-delay memory. These connectivity differences correlated across subjects with individual differences in recollection persistence scores for emotional stimuli but not recollection persistence scores for neutral stimuli (Fig. 5). This suggests that individuals whose memory for emotional stimuli after a long delay is predicted by greater amygdala–parahippocampal connectivity during encoding show better preservation of recollection for these stimuli after a long delay. These results give further support to the prediction that greater amygdala–MTL connectivity during encoding makes memories for emotional stimuli more resistant

**Table 1**

ESA (remembered > forgotten) collapsed over delay

| | BA | Hem | Coordinates (T and T) | | | | Voxels |
|---|---|---|---|---|---|---|---|
| | | | x | y | z | t | |
| ESA emotional > ESA neutral | | | | | | | |
| MTL | | | | | | | |
| Amygdala/PHG | 28 | R | 26 | 3 | −23 | 3.31 | 12 |
| Amygdala/PHG | 34 | L | −19 | 3 | −19 | 2.86 | 5 |
| Inferior frontal gyrus | 45 | L | −48 | 29 | 6 | 2.58 | 5 |
| Inferior temporal gyrus | 37 | L | −56 | −48 | −17 | 2.24 | 5 |
| Angular gyrus | 39 | R | 37 | −64 | 35 | 3.06 | 44 |
| ESA neutral > ESA emotional | | | | | | | |
| Hippocampus | | R | 30 | −33 | −2 | 4.72 | 19 |
| Cingulate gyrus | 24 | R | 4 | 22 | −4 | 4.79 | 16 |
| | 24 | L | −19 | −13 | 39 | 2.52 | 14 |
| Caudate | | L | −11 | 18 | 3 | 4.43 | 10 |
| | | R | 15 | 12 | 17 | 3.62 | 18 |
| Lentiform nucleus | | L | −26 | −18 | 4 | 2.53 | 7 |
| Temporal | | | | | | | |
| Middle temporal gyrus | 21 | R | 63 | −33 | 5 | 3.86 | 5 |
| | 21 | R | 45 | −54 | 3 | 2.18 | 6 |
| Inferior temporal gyrus/fusiform gyrus | 37 | L | −37 | −51 | −7 | 4.96 | 66 |
| Cerebellum | | R | 33 | −52 | −23 | 2.15 | 6 |
| Occipital | | | | | | | |
| Fusiform gyrus | 37 | L | −37 | −59 | −16 | 2.71 | 9 |
| Middle occipital gyrus | 19 | R | 30 | −76 | 11 | 3.6 | 6 |

Note: BA, Brodmann area; Hem, hemisphere; t, statistical t value; R, right; L, left; Talairach and Tournoux (T and T) coordinates reported.

**Table 2**

Activity predicting individual differences in recollection persistence

| | BA | Hem | Coordinates (T and T) | | | | Voxels |
|---|---|---|---|---|---|---|---|
| | | | x | y | z | t | |
| Correlations with recollection persistence for emotional stimuli | | | | | | | |
| Amygdala | | L | −22 | −4 | −13 | 2.85 | 11 |
| Fusiform gyrus | 19 | L | −37 | −77 | −9 | 5.31 | 9 |
| Correlations with recollection persistence for both emotional and neutral stimuli | | | | | | | |
| Inferior frontal gyrus | 6 | L | −45 | 2 | 35 | 3.93 | 10 |
| Fusiform gyrus | 19 | L | −37 | −77 | −9 | 5.31 | 15 |

Note: BA, Brodmann area; Hem, hemisphere; t, statistical t value; L, left; Talairach and Tournoux (T and T) coordinates reported.

to forgetting, consistent with the hypothesis that emotional arousal enhances consolidation processes.

## Discussion

The present study investigated how encoding activity predicting subsequent emotional memory is modulated by study-test delay. Participants were scanned while encoding emotional and neutral pictures, and recognition memory for nonoverlapping sets of these items was tested 20 min and 1 week after encoding. The experiment yielded 3 main findings. First, activity in the amygdala predicted emotional memory but not neutral memory, and this pattern was similar for emotional memory after both short and long delays. Second, corresponding to our behavioral finding of greater recollection persistence for emotional than neutral stimuli, activity in the left amygdala correlated with individual differences in the persistence of recollection over time for emotional but not neutral stimuli. Finally, greater connectivity between the left amygdala and bilateral anterior MTL memory regions during encoding predicted memory for emotional stimuli after a long delay to a greater extent than memory after a short delay. We discuss these 3 main results in turn.

### ESA is Not Modulated by the Interaction of Emotion and Delay

When collapsed over delay, ESA for emotional pictures revealed a network of regions including bilateral amygdalae and left inferior frontal gyrus. This finding is consistent with extensive evidence that the amygdala is critical to the formation of emotional memories (Cahill et al. 1996; LaBar and Phelps 1998; Hamann et al. 1999; Canli et al. 2000; Dolcos et al. 2004b) and that the left prefrontal cortex contributes to superior encoding for emotional stimuli (Dolcos et al. 2004a; Kensinger and Corkin 2004). Contrary to our predictions, however, we did not find any differences in ESA for short- versus long-delay memory that were unique to emotional stimuli. This suggests that our emotional memory network contributes equally well during encoding to recognition memory shortly after encoding as well as 1 week later. In other words, basic activity estimates do not reveal any functional differences corresponding to our behavioral finding that recollection for emotional items is relatively preserved over time.

We had originally expected that long-delay hits would be the more targeted product of consolidation than short-delay hits and that there would be greater ESA associated with ensuing consolidation for long- than short-delay hits. It is possible that we did not find any such regions because of consolidation's dynamic nature: arousal-mediated consolidation is the product of interactions between the amygdala and MTL memory system (McGaugh 2004) and might not be captured sufficiently by basic activity estimates. This idea will be addressed further in our discussion of functional connectivity results.

### Amygdala Activity Predicts Individual Differences in Recollection Persistence for Emotional Stimuli

Activity in the left amygdala in response to viewing emotional pictures was significantly correlated with individual differences in recollection persistence for emotional stimuli, our most behaviorally salient measure of temporal changes in emotional memory. This relationship was unique to emotional items; in fact, no MTL regions were significantly correlated with the persistence of recollection for neutral stimuli. Because our recollection persistence scores divide long-delay recollection by short-delay recollection, baseline memory variability across subjects is ameliorated, such that this measure corresponds most truly to differences that develop across the 1-week delay. Thus, our results imply that individuals who exhibit relatively strong amygdala activation in response to emotional items are less likely to forget these items after a 1-week delay. This finding is consistent with the finding that patients lacking functional amygdalae do not show enhancements in the emotional memory effect over time (LaBar and Phelps 1998).

These results successfully replicate and improve upon previous investigations into the interaction of emotion and delay in determining ESA. Across-subject correlations between amygdala activity and long- but not short-delay emotional memory are consistent with the results of previous studies (Hamann et al. 1999; Mackiewicz et al. 2006), but until now, these correlations have not been linked to behavioral changes in emotional memory over time. The present study is the 1st to pinpoint encoding activity in the left amygdala as specifically predictive of emotional recollection, in particular, the degree to which recollection for emotional stimuli persists over time. Thus, our results more strongly argue for amygdala activity as the catalyst
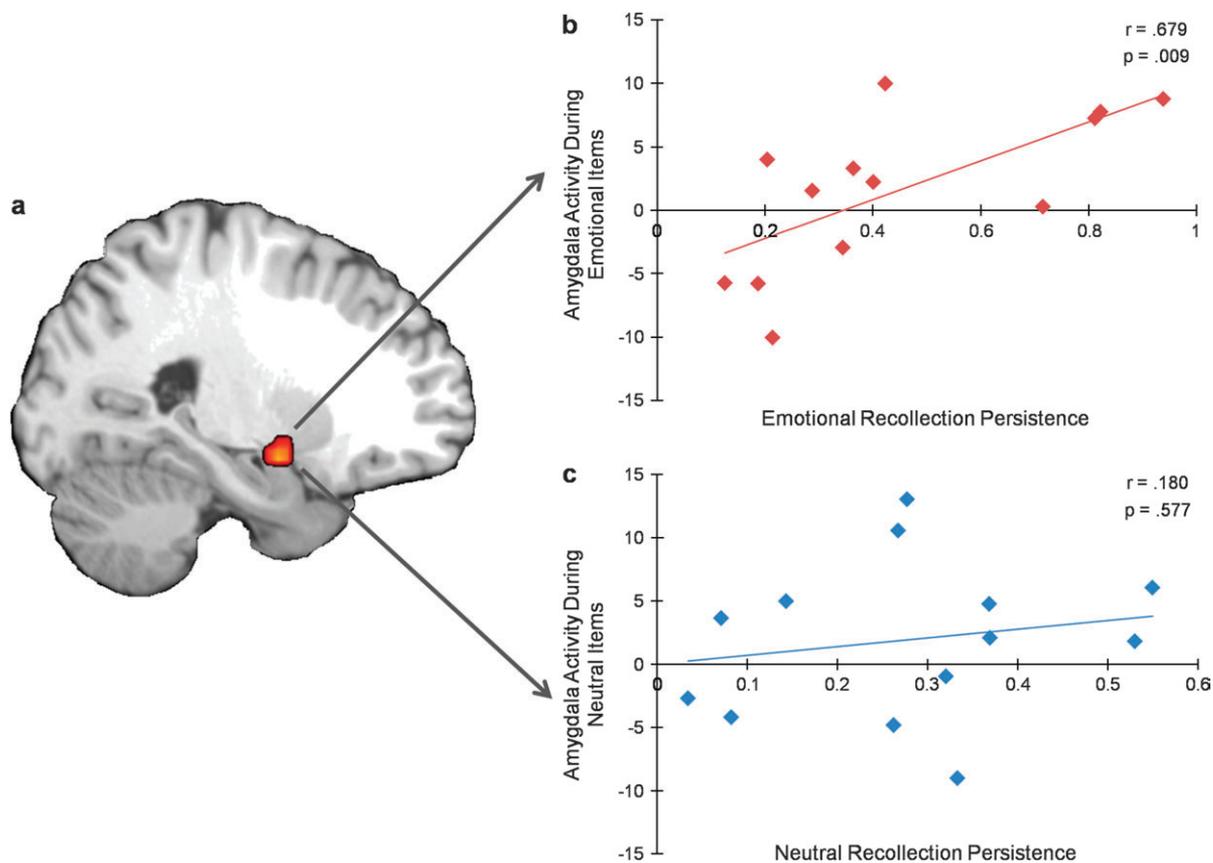
**Figure 3.** Activity-associated individual differences in recollection persistence for emotional stimuli. (*a*) Left amygdala region whose activity correlates across subjects with individual differences in recollection persistence for emotional items. See Table 2 for coordinates. (*b*) Scatterplot depicting the relationship between individual recollection persistence scores for emotional stimuli and mean activity in the left amygdala region in response to emotional pictures. (*c*) Scatterplot depicting the relationship between individual recollection persistence scores for neutral stimuli and mean activity in the left amygdala region in response to neutral pictures.

**Table 3.**

Regions exhibiting emotion- and delay-specific connectivity with amygdala

| | BA | Hem | Coordinates (T and T) | | | | Voxels |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | | *x* | *y* | *z* | *t* | |
| Emotional long- versus short-delay hits > neutral long- versus short-delay hits | | | | | | | |
| MTL | | | | | | | |
| PHG | 28 | R | 30 | −1 | −26 | 3.49 | 5 |
| | 28, 34 | L | −19 | −8 | −22 | 2.07 | 4 |
| Medial frontal gyrus | 8 | R/L | 7 | 38 | 37 | 2.54 | 30 |
| Parietal | | | | | | | |
| Postcentral gyrus | 2 | R | 59 | −24 | 36 | 4.26 | 15 |
| Inferior parietal lobule | 40 | R | 56 | −38 | 37 | 2.85 | 12 |
| Emotional short- versus long-delay hits > neutral short- versus long-delay hits | | | | | | | |
| Medial frontal gyrus | 9 | L | −19 | 44 | 15 | 3.4 | 18 |

Note: BA, Brodmann area; Hem, hemisphere; *t*, statistical *t* value; R, right; L, left; Talairach and Tournoux (T and T) coordinates reported.

for the temporal persistence of emotional memory, an interpretation compatible with the consolidation hypothesis (McGaugh 2004).
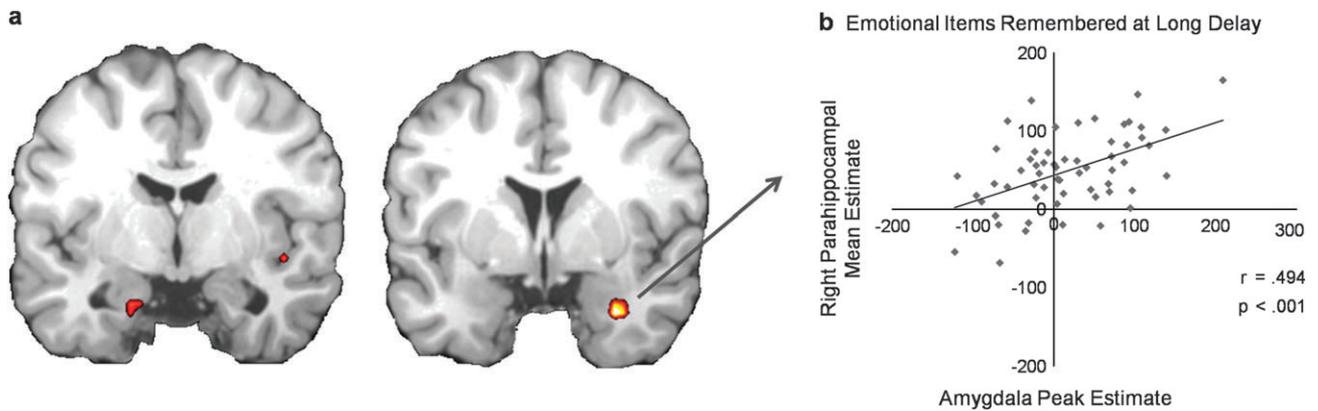
### *Functional Connectivity between Amygdala and MTL Memory System Supports Emotional Memory After Long Delay*

Functional connectivity analyses revealed that the degree to which connectivity between the left amygdala and bilateral anterior MTL memory regions predicted subsequent memory was determined by both emotion and delay. Specifically, connectivity between these regions during encoding predicted memory for emotional pictures after a long delay rather than after a short delay, and this effect was greater for emotional than for neutral items. Although previous neuroimaging studies have shown that amygdala–MTL connectivity during encoding is associated with successful emotional memory encoding (Hamann et al. 1999; Kilpatrick and Cahill 2003; Dolcos et al. 2004b; Kensinger and Corkin 2004), this is the 1st study to demonstrate that the beneficial influence of this connectivity heightens over time. Furthermore, the enhancing effect of amygdala–MTL connectivity on memory for emotional stimuli after a long delay was significantly correlated with individual differences in recollection persistence scores for emotional stimuli. This finding directly links connectivity findings at the group level to individual differences in emotional memory performance.

Taken together, these connectivity results can also be interpreted under the consolidation hypothesis, which posits that emotional memories benefit from arousal-mediated interactions between the amygdala and MTL memory system that act to improve memory consolidation (McGaugh 2004). Because consolidation unfolds across time, its role in predicting emotional memory should grow stronger over time, echoing the pattern of connectivity observed here.

The present results fit well with findings from animal studies of consolidation, although it should be noted that the latter

**Figure 4.** Functional connectivity with the amygdala. (*a*) Bilateral anterior parahippocampal regions whose connectivity with the amygdala interacts with emotion and delay, such that connectivity during long-delay hits is greater than during short-delay hits, but only for emotional items. See Table 3 for coordinates. (*b*) Scatterplot depicting the relationship between mean single-trial activation estimates (i.e., beta weights) from the indicated right PHG region and the seed amygdala voxel across emotional long-delay hits. These data points were extracted from an individual representative participant for display purposes.

typically investigate consolidation via posttraining behavioral or pharmacological manipulations. In the present study, we examined consolidation processes as they began during the encoding phase and distinguished these processes from other encoding processes by measuring the persistence of memory traces over time. However, it is possible that the present results could be attributed to differences in memory strength established during encoding itself. For example, emotional stimuli evoked greater ESA than neutral stimuli in left inferior frontal gyrus, a region often associated with semantic encoding (Gabrieli et al. 1998). This encoding benefit and others may have resulted in superior memory strength for emotional items, causing the emotional memories to decay more slowly than neutral memories over time. Thus, although we frame the present results in terms of consolidation, we acknowledge that memory strength differences could influence ESA and connectivity contributing to emotional memory changes over time.

Interestingly, the MTL memory regions showing emotion- and delay-specific connectivity with the amygdala are bilaterally located within the anterior PHG, not within the hippocampus proper. In particular, these regions appear to be centered either within entorhinal cortex or near the border between entorhinal and perirhinal cortices. Although its connectivity with the hippocampus has been emphasized within the literature, the amygdala interacts with the hippocampus via its projections to entorhinal cortex (Pare et al. 1995). These regions are likewise involved in arousal-mediated consolidation (McGaugh et al. 2002; Roesler et al. 2002; McIntyre et al. 2003). In particular, the anterior PHG is a site of information transfer from neocortex to the hippocampus, and amygdala activity facilitates correspondence between perirhinal and entorhinal cortex, an improvement associated with learning (Paz et al. 2006). Moreover, our finding is consistent with previous functional neuroimaging evidence that correlations between amygdala and entorhinal activity during encoding predict subsequent emotional memory compared with neutral memory (Dolcos et al. 2004b; see also Kilpatrick and Cahill 2003).

An interesting question for future research is whether the specific MTL subregions modulated by amygdala connectivity vary depending on the particular type of episodic memory investigated. For example, there is evidence that encoding activity in the hippocampus predicts better subsequent recollection, whereas encoding activity in anterior parahippocampal regions predicts greater subsequent familiarity (Ranganath et al. 2004). A similar dissociation exists within the emotional memory literature, with hippocampal ESA corresponding to incidental source memory and anterior parahippocampal and amygdala ESA for item-only memory (Kensinger and Schacter 2006). Although the present finding that amygdala connectivity with anterior parahippocampal regions is associated with individual differences in emotional recollection may seem inconsistent with these findings, it is important to note that the anterior parahippocampal region most strongly associated with item encoding is the perirhinal cortex rather than the entorhinal cortex (Davachi et al. 2003). In contrast, the entorhinal cortex is assumed to have memory functions intimately related to the hippocampus (Aggleton and Brown 1999), and it is assumed to support the encoding of contextual information (Eichenbaum et al. 2007).

### Caveats

The present results should be treated with 2 main caveats. First, because we chose to simplify the design by employing only negative and neutral stimuli, we cannot distinguish between the contributions of valence and arousal to the present results. However, previous research has shown that the amygdala responds primarily to arousal (Anderson et al. 2003; Dolcos et al. 2004b; Kensinger and Corkin 2004), a dimension shared by both positive and negative stimuli. Furthermore, the amygdala–MTL network predicts memory for both emotionally negative and positive stimuli (Hamann et al. 1999). Therefore, we predict that the inclusion of positive pictures would not qualitatively change the results in the amygdala and MTL or their interpretation and that these results are generalizable to both emotionally negative and positive memories.

Second, the present results do not address the issue of sex differences in emotional memory. Previous evidence indicates that emotional memory effects are lateralized by sex, with the left amygdala predicting emotional memory enhancements for females and the right amygdala for males (for a review see Cahill 2003). Preliminary analyses have failed to reveal any influence of sex on the present results (data not reported). However, because sex differences were not of primary interest
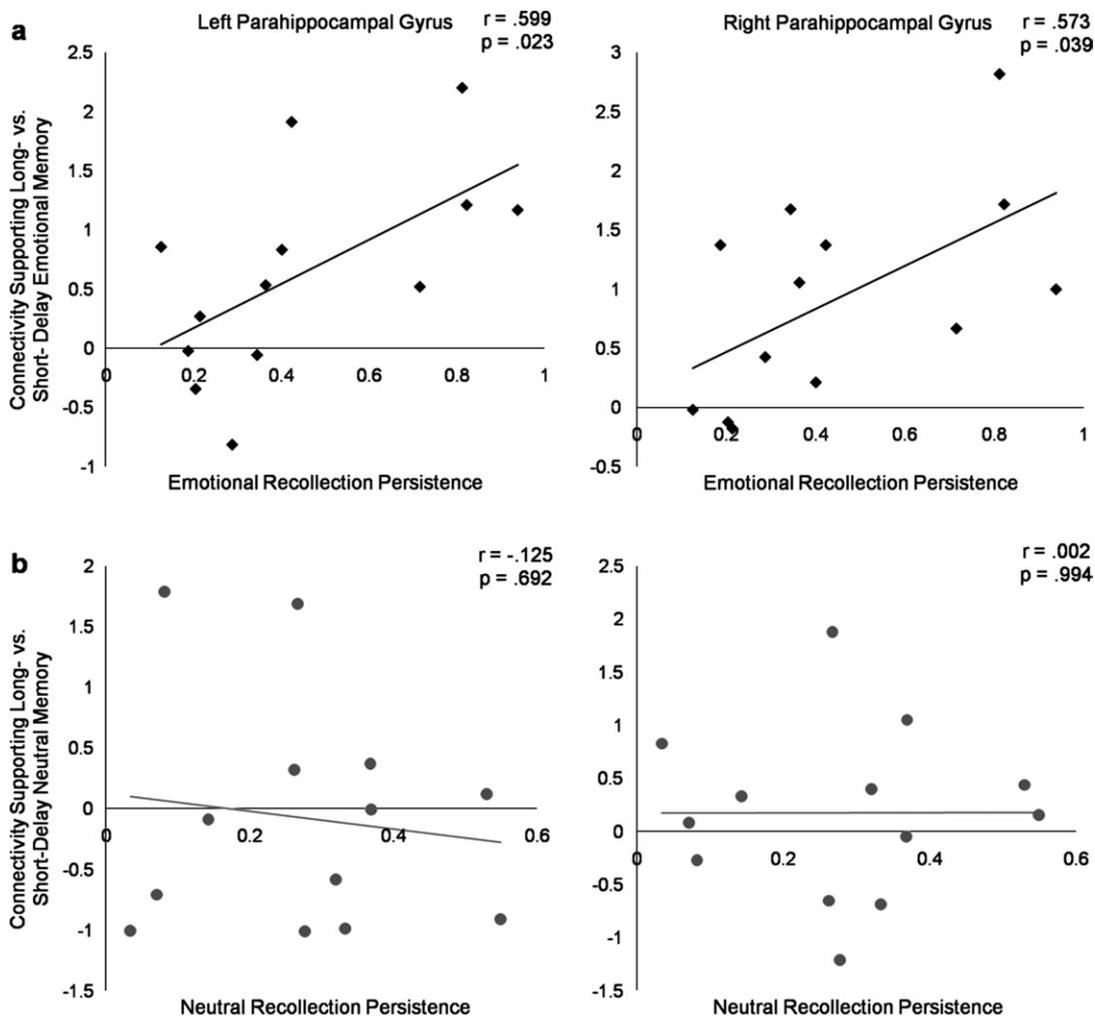
**Figure 5.** Functional connectivity differences associated with emotional recollection persistence. (*a*) In these across-subject scatterplots, the *y*-axis denotes the difference in connectivity between the amygdala and left or right PHG during emotional long- versus short-delay hits. The *x*-axis indicates individual recollection persistence scores for emotional stimuli. Note that increasing levels of emotional recollection persistence are associated with increasing disparity between connectivity supporting emotional memory after long versus short delays. (*b*) In these across-subject scatterplots, the *y*-axis denotes the difference in connectivity between the amygdala and left or right PHG during neutral long- versus short-delay hits. The *x*-axis indicates individual recollection persistence scores for neutral stimuli. Note that there is no relationship between connectivity differences and neutral recollection persistence.

in the present study, this null result should be treated with caution; it could be ascribed to low statistical power due to relatively small sample sizes for males and females. Future investigations should attempt to verify whether or not sex plays a role in determining patterns of amygdala–MTL connectivity in support of emotional memory.

### Conclusions

The present study investigated how encoding activity and functional connectivity differentially predicts emotional memory after short versus long delays. We report 3 main findings: 1) ESA for emotional items is similar for short- and long-delay memory; 2) activity in the left amygdala predicts individual differences in emotional recollection persistence; and 3) functional connectivity between the left amygdala and bilateral anterior PHG is greater for emotional items remembered after 1 week than those remembered after 20 min. These results suggest that amygdala activity, along with its connectivity with the MTL memory system, sustain emotional memory enhance-

ments over time. This interpretation is consistent with the consolidation hypothesis, which emphasizes the role of amygdala–MTL interactions in promoting emotional memory consolidation.

### Notes

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