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How emotion enhances the feeling of remembering

Tali Sharot, Mauricio R Delgado & Elizabeth A Phelps

Studies examining memories of arousing 'real-life' events show that emotion heightens the feeling of remembering, without necessarily enhancing the objective accuracy of the memories. We measured brain activity associated with the feeling of remembering emotional and neutral photos. Subjects indicated whether recognition was accompanied by a recollection of details about the study episode ('remember') or not ('know'). 'Remember' judgments were boosted for emotional photos, but accuracy did not differ. For neutral photos, 'remember' judgments were related to enhanced activity in the parahippocampal cortex, previously related to recognition of visual details, which one might expect to supply the retrieval clues for a 'remember' judgment. In contrast, 'remember' judgments for emotional photos were associated with enhanced activity in the amygdala, suggesting that subjects rely on arousal and perceptual fluency to evaluate these memories. For the first time, we identify the neural mechanisms underlying the enhanced feeling of remembering for emotional events.

Highly emotional events are often reported to be remembered clearly, vividly and with great detail. For this reason it has been suggested that, similar to a camera's flashbulb, emotion triggers a mechanism that conserves what occurred at that instant, so that the memory stays true to the original incident[1]. However, an emerging body of evidence[2,3] indicates that the feeling of remembering is heightened with emotion, so that the memory feels as if it has left "a scar upon the cerebral tissues" (as William James described it in 1890)[4] even if it is far from an exact picture of the actual event. In fact, a recent study[2] examining students' recollections of the events of September 11, 2001 found that they differed from memories of everyday events only in their ratings of vividness, recollection and belief in accuracy (which compose the "subjective sense of remembering"). Although a number of studies have examined the neural substrates underlying the effects of emotion on memory accuracy[5], here, for the first time, we study the mechanisms underlying emotion's independent effect on the subjective sense of remembering.

Most studies examining the subjective feeling of recollecting emotional events look at real-life arousing events, such as the Challenger explosion[6] and the terrorist attacks on the World Trade Center[2]. In the present study we use brain imaging and a controlled laboratory paradigm, known as the 'remember'/'know' procedure[7], to study the processes underlying the sense of remembering emotional and neutral stimuli. Subjects were asked to classify previously experienced stimuli as either (i) vividly 'remembered' stimuli that evoke a specific memory for the episodic context in which each stimulus was experienced, such as a thought, feeling or sensory detail, or as (ii) stimuli that are 'known' to have been experienced earlier but do not bring to mind a recollection of a specific episode. The dual process theory of recognition proposes that underlying the 'remember' and 'know' responses are two distinct memory processes: 'recollection' (recognition accompanied by associative information) and 'familiarity' (memory for an item in the absence of contextual information), respectively[8]. Results from neuroimaging studies[9–11] support the notion that 'remembering' engages neural substrates that are similar to those underlying associative retrieval[12,13], such as the hippocampus and parahippocampal cortex, and are different from those underlying 'knowing'.

Findings of a recent behavioral study[14] suggest that emotion affects 'remember' and 'know' judgments differently. Negatively arousing stimuli are 'remembered' more often than neutral stimuli, but independent 'know' judgments do not differ with arousal. However, it is unknown whether distinct neural substrates are involved in 'remembering' and 'knowing' emotional stimuli, and whether these neural correlates are similar to those underlying 'remembering' and 'knowing' neutral stimuli.

At least two options can be contemplated. According to one hypothesis, given that 'remember' judgments are increased for emotional stimuli[14], activity in regions related to associative retrieval (such as the hippocampus and parahippocampus cortex)[12,13] will be enhanced for 'remember' judgments of emotional stimuli relative to neutral stimuli. Alternatively, considering that the subjective sense of remembering is enhanced with emotion irrespective of actual accuracy[2,14], there is reason to hypothesize that different neural networks will be involved in 'remembering' emotional and neutral stimuli. For example, the amygdala, previously associated with memory[15,16] and processing of emotional material[17], may play a key role in the subjective sense of remembering arousing stimuli.

In this study, we used event-related functional magnetic resonance imaging (fMRI) to examine differential changes in blood oxygenation level–dependent (BOLD) signal associated with the subjective feeling of remembering emotional and neutral pictures. Subjects were first presented with emotional and neutral images outside the scanner. An hour later they viewed these photos in the fMRI scanner and made 'remember/know' recognition judgments. Our findings provide evidence that different subregions of the medial temporal lobe have independent contributions to recognition judgments based on the level of emotion-

Department of Psychology, New York University, Room 863, 6 Washington Place, New York, New York 10003, USA. Correspondence should be addressed to E.A.P. (liz.phelps@nyu.edu).

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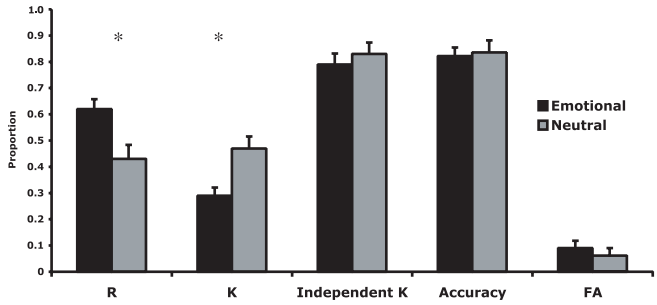

Figure 1 Behavioral results showing an enhanced sense of remembering with emotion, but no difference in accuracy for emotional and neutral photos. Accuracy indicates hits minus false alarms. R and K indicate, respectively, the proportion of 'remember' and 'know' responses from old items minus the proportion of 'remember' and 'know' responses from new items. Independent K indicates the probability of an item to receive a 'know' response given it was not recollected. False alarms (FA) for R responses were zero for both neutral and emotional stimuli. FA thus indicates proportion of false alarms for K responses from new photos. *$P < 0.002$.

ality of the stimuli. A heightened feeling of remembering is associated with enhanced activity in the amygdala for emotional material, but with enhanced activity in the parahippocampal cortex for neutral material.

RESULTS

Behavioral data

The behavioral results (**Fig. 1**) replicate previous findings[14]. Accuracy (as indexed by hit rates – false alarm rates) did not differ for neutral (mean = 0.84, s.d. = 0.16) and emotional (mean = 0.82, s.d. = 0.11) pictures. Emotional stimuli tended to be remembered (mean hit rate for R ('remember') = 0.62, s.d. = 0.14, and for K ('know') = 0.29, s.d. = 0.11 ; $P < 0.002$, paired *t*-test), whereas neutral stimuli did not differ on R and K judgments (mean hit rate for $R = 0.43$, s.d. = 0.19, and for K = 0.47, s.d.= 0.16). False alarms for R responses were zero for both neutral and emotional stimuli. False alarms for K responses did not differ for emotional (mean = 0.09, s.d. = 0.1) and neutral (mean = 0.06, s.d. = 0.12) photos. Scored under the independence of redundancy assumption[18], R responses (as indexed by hit R – false alarm R) were boosted for emotional stimuli (mean = 0.62, s.d. = 0.14 for emotional; mean = 0.43 s.d. = 0.19 for neutral; $P < 0.002$ paired *t*-test); independent K responses (the probability that an item received a 'know' response given that it did not receive a 'remember' response; as indexed by K/(1 – R)) did not differ for emotional (mean = 0.79, s.d. = 0.15) and neutral (mean = 0.83, s.d. = 0.16) stimuli. Reaction times did not differ for any of the included conditions.

A priori ROI analysis

A priori regions of interest (ROIs) included the posterior parahippocampus cortex and hippocampus, both previously related to associative memory decisions during recognition[9,12,13], and the amygdala, associated with memory[15,16] and processing[17] of emotional material.

Structural ROI analysis. We identified the *a priori* ROIs using anatomical landmarks in each subject bilaterally. Beta weights were estimated by general linear model (GLM) analysis in each of the ROIs for each of the regressors: emotional stimuli indicated as 'remember' (ER), neutral stimuli indicated as 'remember' (NR), emotional stimuli indicated as 'know' (EK) and neutral stimuli indicated as 'know' (NK). Misses and false alarms were excluded from the imaging data analysis because of insufficient number of trials per condition.

In both right and left posterior parahippocampal cortex, all regressors were significantly greater than zero. Mean beta weights for neutral 'remember' trials were significantly greater than mean beta weights for emotional 'remember' trials in the right posterior parahippocampal cortex, as indicated by a paired *t*-test ($P < 0.002$).

In both right and left amygdala, only the regressor associated with emotional 'remember' trials was significantly greater than zero ($P < 0.01$). In individual subject analysis, 10 of the 13 subjects showed this pattern of results (estimates for ER > estimates for NR) in the right amygdala, $Z = 1.89$, $P < 0.05$ (one-tailed sign test with a correction of continuity[19]).

In the hippocampus bilaterally, all regressors were significantly greater than zero. Paired *t*-tests revealed no significant differences between mean beta values of the different trial types.

Functional ROI analysis. To further characterize the BOLD response, we contrasted all trials with fixation and identified the peak active voxel for this comparison in each of the structurally derived ROIs (**Figs. 2a**,**b**). We used this peak voxel to extract the time courses of activation in each ROI

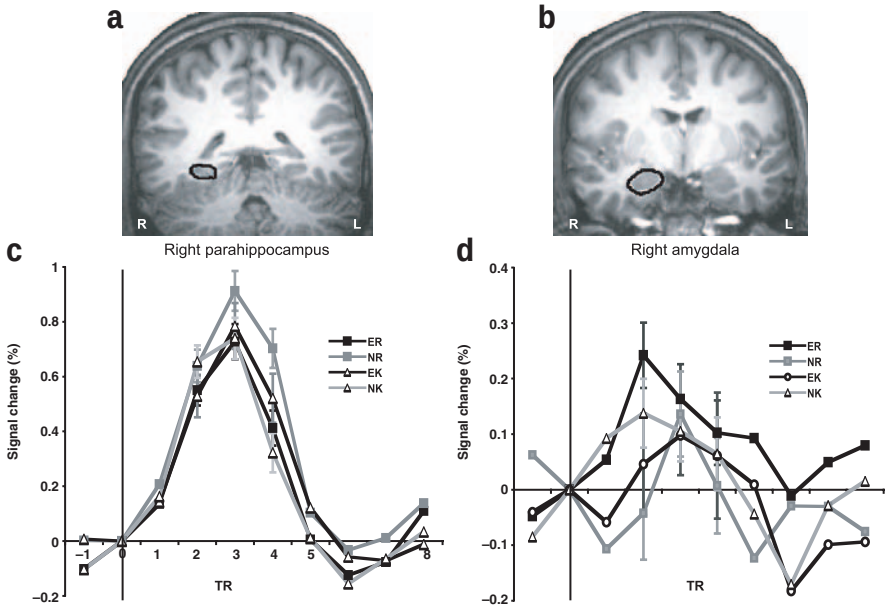

Figure 2 Regions of interest showing a differential pattern of activation across trial types. (**a**,**b**) A coronal slice of the structurally defined (**a**) right posterior parahippocampus and (**b**) right amygdala, that includes peak active voxels. Group average of time courses of activation for the different trial types from peak active voxel derived by contrasting all trials with fixation in the (**c**) right posterior parahippocampus, Talairach coordinates (*x*,*y*,*z*) for peak activation (28,–41,–15), and the (**d**) right amygdala, Talairach coordinates for peak activation (–28,5,–22). Horizontal axis indicates number of TR (*TR* = 2 s). Stimulus onset occurs at time 0; stimulus offset occurs at time 1, at which point subjects indicate their decision. Error bars, s.e.m.

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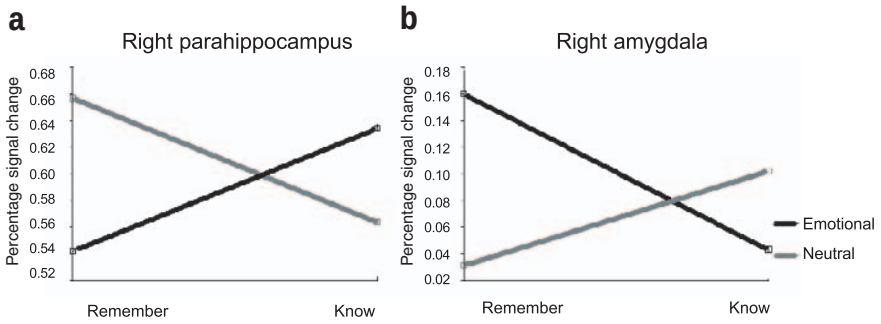

Figure 3 Mean activation values revealing a three-way interaction of response ('remember'/'know') × type of photo (emotional/neutral) × region (right amygdala/right parahippocampus). (**a**,**b**) Mean percentage signal change values, from 4 s to 8 s after stimuli onset, for each trial type from peak active voxel, derived by contrasting all trials with fixation (**a**) in the right posterior parahippocampus and (**b**) in the right amygdala.

for the different trial types[20]. Previous research has indicted that peak voxel activity is a better predictor of electrophysiological measures of activation than average cluster activations[21].

The time course of activation from the peak activated voxel in the right parahippocampus cortex suggests a difference between 'remember' and 'know' trials for neutral photos only, with higher activation for neutral photos indicated as 'remember' relative to 'know' (**Fig. 2c**). The time course of activation from the peak activated voxel in the right amygdala suggests a difference between 'remember' and 'know' trials for emotional photos only, with higher activation for emotional photos indicated as 'remember' relative to 'know' (**Fig. 2d**). Time course activations from the peak activated voxel in left parahippocampus, left amygdala and both right and left hippocampus indicate that activation does not differentiate between the different trial types.

Together, time courses of activation in the right amygdala and right parahippocampus suggest a three-way interaction (response: 'remember'/'know' × stimulus type: emotional/neutral × region: right amygdala /right parahippocampus). To confirm this, we determined the mean percentage signal change (averaged from 4 s to 8 s after stimuli onset) for each trial type and subject in the right amygdala and right parahippocampus, and conducted a three-way ANOVA that revealed a significant interaction $F_{1,12} = 17.518$, $P < 0.005$.

In addition, we conducted two two-way ANOVAs on mean percentage signal change values (response: 'remember'/'know' × stimulus type: emotional/neutral) in each region (right amygdala and right parahippocampus) separately. We found a significant interaction in the right amygdala ($F_{1,12} = 5.54$, $P < 0.05$) and an interaction that approached significance in the right posterior parahippocampus ($F_{1,12} = 3.46$, $P < 0.09$) (**Fig. 3**). Because the time course of activation in the right posterior parahippocampus (**Fig. 2c**) indicates that the greatest degree of differentiation between the different trial types occurs 8 s after stimuli onset (6s after stimuli offset), we conducted an ANOVA specifically on percentage signal change values at that time point, which revealed a significant interaction ($F_{1,12} = 7.62$, $P < 0.05$). Paired *t*-tests on these values show enhanced activation during neutral 'remember' trials relative to neutral 'know' trials ($t(12) = 2.55$, $P < 0.05$) and relative to emotional 'remember' trials ($t(12) = 3.23$, $P < 0.01$).

Correlations between the amygdala and MTL regions

Mean percentage signal change values from the peak voxel in the amygdala and posterior parahippocampus correlated only for 'know' trials ($r = 0.68$, $P < 0.01$ for EK trials; $r = 0.71$, $P < 0.01$ for NK trials). This is in accord with the above interaction, suggesting that these regions respond differently for 'remember' responses for emotional and neutral material, and thus should not be correlated for those trials. Activity in the amygdala and hippocampus correlated for emotional 'know' trials ($r = 0.62$, $P < 0.05$), but not for emotional 'remember' trials, presumably because activity in the amygdala is enhanced during these trials irrespective of activity in other medial temporal regions.

Notably, there was a trend for a significant correlation between the amygdala and hippocampus for emotional 'new' trials ($r = 0.42$, $P = 0.07$, one tailed), consistent with previous research suggesting a correlation between these regions during the encoding of emotional stimuli[22] (see **Supplementary Note** and **Supplementary Table 1** online for additional analyses of 'new' trials).

Table 1 Regions elsewhere in the brain showing differential BOLD signal by trial type

Region	NR > ER	ER > NR	NK > EK	EK > NK	NR > NK	NK > NR	ER > EK	EK > ER
Cerebellum			(12,–71,–19)				(12,–65,–15)	
L cingulate gyrus	(–14,–62,15)				(–8,–56,21)			
R cingulate gyrus	(10,–10,40)							
L inferior parietal							(47,–29,25)	
L insula							(–38,–10,15)	
R middle frontal gyrus					(0,56,2)			(45,–26,–15)
L middle occipital gyrus		(–45,–65,–7)						
R middle occipital gyrus		(50,–65,–5)						
R postcentral gyrus							(58.–19,30)	
L superior frontal gyrus							(–9,43,45)	
R superior frontal gyrus				(4,37,50)				(22,7,57)
R supramarginal gyrus	(46,–52,30)							(46,–56,31)
R superior temporal gyrus				(55,–46,22)				

Listed are regions with 19 or more significant voxels at $P < 0.002$. Tailarach coordinates (*x*,*y*,*z*) for peak activation are given. ER, emotional photos indicated as 'remember'; NR, neutral photos indicated as 'remember'; EK, neutral photos indicated as 'know'; NK, neutral photos indicated as 'know.'

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Involvement of other cortical areas

We identified regions throughout the rest of the brain that showed greater BOLD response for one trial type than the other using paired contrasts (**Table 1**). An additional analysis was conducted comparing all 'remember' to all 'know' trials (**Supplementary Table 2** online). Greater activation associated with 'remember' responses relative to 'know' responses was evident in the left and right cingulate gyrus, left caudate nucleus, post- and precentral gyri, and other parietal and frontal regions. Greater activity related to 'know' responses as compared with 'remember' responses was found in parietal and frontal regions (**Supplementary Table 2** online).

DISCUSSION

Studies examining memories of highly arousing real-life events[2,6] have shown that the subjective sense of remembering emotional events can be heightened relative to that for neutral events, even when the objective accuracy of these memories is the same. We have shown this behavioral pattern of results under controlled laboratory conditions (also see ref. 14). Here, for the first time, we report a differentiation in the neural systems accompanying the subjective feeling of recollecting emotional and neutral stimuli that may underlie the enhancement in the feeling of remembering with emotion.

This result suggests that discrete subregions within the medial temporal lobe can independently differentiate recognition judgments associated with the subjective sense of remembering for emotional and neutral material. Specifically, our findings indicate that the amygdala responds selectively to emotional 'remembered' photos. The amygdala has been linked in the past with emotional arousal[17] and enhanced perceptual sensitivity to emotional stimuli[23,24]. Although earlier studies indicate that the amygdala may play a role in emotional memory, specifically the modulation of encoding and consolidation of hippocampal-dependent memories[5], there is no evidence that it is involved in the retrieval of perceptual details. Thus the enhancement of activity in the amygdala suggests that subjects may rely upon arousal signals and heightened perceptual fluency to evaluate their memories of emotional stimuli.

An alternative explanation for our findings is that amygdala activation correlates with enhanced accuracy for emotional stimuli rather than with a heightened feeling of remembering. We find this possibility less likely, as our behavioral results show a boost in the subjective sense of remembering with emotion, but no effect on accuracy. Furthermore, previous behavioral studies have reported an enhancement in the subjective sense of remembering for emotional events, which was independent from effects on accuracy[1–3].

In contrast, for neutral photos, activity in the posterior parahippocampus was enhanced for 'remember' judgments relative to 'know' judgments. Activity in this region has been associated with processing[25] and recognition[26] of scene details, suggesting that subjects rely on recognition of visual details to evaluate these memories. This is the type of information that might be expected to supply the retrieval cues necessary for a 'remember' judgment. Activity in the parahippocampus has also been shown to be distinct during recognition of items previously encountered and those only falsely believed to have been encountered[27].

Activity in the hippocampus did not differ during recognition of emotional and neutral photos for either 'know' or 'remember' judgments. Although enhanced activity associated with making associative judgments has been reported in both the hippocampus and parahippocampus during retrieval[12], studies examining false memory propose that the hippocampus plays a role in the recovery of semantic information, whereas the parahippocampal gyrus plays a role in the recovery of perceptual information[27]. When making a 'remember' judgment for either a neutral or emotional picture, a subject may rely on semantic information to a similar extent.

One should note, that some studies have shown distinct activation for 'remember' and 'know' judgments for neutral stimuli in the hippocampus proper[9,11]. However, the one neuroimaging study[10] that used the same method of the 'remember/know' procedure used here—three alternative choices (remember/know/new) in one step—did not. It has been suggested that in this paradigm participants use the 'remember' and 'know' markers to indicate strong and weak memory rather than recollection and familiarity[9]. Although this is possible, the fact that activity in the parahippocampus distinguished 'remember' and 'know' judgments for neutral photos, as found previously by using a two-step method (in which the subject makes first a yes/no response and then a remember/know response)[9], puts this prospect into question. However, further research is needed to determine whether the distinct activity underlying the subjective sense of remembering neutral and emotional photos is related specifically to processes of familiarity and recollection and/or to the perceived strength of the memory.

In sum, our results suggest that the same judgment regarding the subjective sense of remembering is associated with distinct neural activity for emotional and neutral stimuli. 'Remember' judgments are associated with enhanced activity in the amygdala for emotional material and with enhanced activity in the parahippocampal cortex for neutral material. We suggest that this pattern of BOLD activation is related to the heightened subjective experience of remembering an emotional event[2,3,6]. When making a 'remember' judgment for a neutral photo, an individual may rely upon the recognition of perceptual details, which is linked to activity in the posterior parahippocampus[27,28] and is related to successful retrieval[27]. In contrast, when making a 'remember' judgment for an emotional photo, an individual may rely on the feeling of arousal and enhanced perceptual fluency, related to the amygdala[23,24], which may boost the subjective experience of retrieval without necessarily enhancing accuracy *per se*.

METHODS

Participants. Twenty-one healthy right-handed subjects (age range 20–35) were recruited through posted advertisements. Eight of these subjects were eliminated from the analysis because they did not undergo a sufficient number of trials per critical condition (at least 9) to allow reliable analysis of the imaging data. The remaining 13 subjects (5 male, 8 female) were included in the analysis. All subjects gave informed consent and were paid for their participation.

Stimuli. Stimuli consisted of 75 negatively arousing photos and 75 neutral photos selected from the International Affective Photo Series (IAPS), based on their standard scores for emotional arousal and emotional valence[29]. The IAPS pictures were supplemented with our own set of neutral pictures to equate the two sets for the presence of humans and for visual complexity. All photos were rated for valence and arousal by 11 of the participants after scanning. Valence was rated on a scale from 1 (positive) to 9 (negative). Neutral photos were rated as neutral (mean = 3.75, s.d. = 1.07) and emotional photos as negative (mean = 7.69, s.d. = 0.52); $t(10) = 14.23$, $P < 0.0001$. Arousal was rated on a scale from 1 (not at all arousing) to 9 (very much arousing). Neutral photos had lower arousal ratings (mean = 3.03, s.d. = 0.83) than did emotional photos (mean = 6.79, s.d. = 1.15); $t(11) = 10.67$, $P < 0.0001$.

Behavioral task. For each participant, 120 photos (60 negatively arousing) were used as studied items and 30 photos (15 negatively arousing) as new items. Old and new photo sets were counterbalanced across participants. An hour before the scanning session, participants went through an incidental encoding task consisting of 120 trials, which included presentation of a neutral or an emotional photo for 2 s, presentation of a rating task judging the visual complexity of the photo for 2 s, and fixation for 10 s.

Participants were trained at making the 'remember'/'know' judgments before entering the scanner[30]. The scanning session began with a structural scan,

followed by six functional scans of 5 min 50 s each. Each of the functional scans consisted of 25 14-s trials, which included the presentation of a photo for 2 s followed by 2 s to indicate a response ('new', 'remember' or 'know') when the photo disappeared from screen, by pressing the appropriate button on a button box (corresponding buttons were counterbalanced between subjects), and a fixation cross for 10 s. Stimuli were presented in a random order via a mirror mounted on the scanner head coil at a viewing distance of 50 cm.

MRI scanning and data analysis. The study was conducted at the New York University Center for Brain Imaging using a 3T Siemens Allegra scanner and a Siemens head coil. Anatomical images were acquired using MPRage scans, followed by 3-mm-thick axial slices (parallel to the AC-PC plane). Functional scans used a gradient-echo sequence, T*R* = 2 sec, TE = 30 ms, FA = 90, matrix = 64 × 64, FOV = 192 mm, slice thickness = 3 mm. A total of 35 axial slices parallel to the AC-PC plane were sampled. The in-plane resolution was 3 mm × 3 mm.

Imaging data was analyzed using Brain Voyager software (2000, version 4.9). Data were temporally and spatially smoothed (4 mm full-width half-maximum) and motion corrected. Individual data were transformed into Talairach space for group analysis. For each participant, a time series was created indicating the temporal position of the different trial types: neutral photos indicated as 'remember' (NR), emotional photos indicated as 'remember' (ER), neutral photos indicated as 'know' (NK), emotional photos indicated as 'know' (EK), and fixation (FIX). Data for individual trial types were convolved with the canonical hemodynamic response using a GLM. All of the above trial types correspond to correct hits.

A priori regions of interest (ROIs)—the amygdala, posterior parahippocampus cortex and hippocampus—were identified structurally. They were hand drawn on the anatomical images for each subject according to landmarks described previously[31]. For each subject in each ROI, beta values were derived using a fixed-effects GLM for each of the regressors. Group analysis was conducted on these beta values using paired *t*-tests ($P < 0.01$), along with one-sample *t*-tests to determine whether the beta values were significantly greater than zero ($P < 0.01$).

Active voxels within these ROIs were identified by contrasting all trials with fixation using a random effects GLM. Time courses of activation were extracted from the peak voxel in each ROI for the different trial types[20]. Previous research has indicted that peak voxel activity is more predictive of electrophysiological measures of activation than is average cluster activations[21].

Mean activation values (percentage signal change from 4 s to 8 s after stimulus onset) were determined for each trial type and subject. A three-way ANOVA was conducted on these values for regions for which the time course of activation suggested a differentiation of the different trial types (response: 'remember'/'know' × type of photo: emotional/neutral × region: right amygdala/right parahippocampus), and a two-way ANOVA (response × type of photo) was conducted in each of these regions separately. We also correlated peak voxel activity in the amygdala with peak voxel activity in the parahippocampus and hippocampus.

Additionally, to identify other voxels in the brain that showed stronger BOLD responses during one trial type than the other, we conducted a whole-brain exploratory analysis on group data using a random-effects GLM with direct paired contrasts (19 or more contiguous significant voxels at $P < 0.002$)[11]. Findings from the exploratory analyses should be regarded as tentative because of these relatively relaxed criteria.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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