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Amygdala Activity at Encoding Corresponds with Memory Vividness and with Memory for Select Episodic Details

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Abstract

It is well known that amygdala activity during encoding corresponds with subsequent memory for emotional information. It is less clear how amygdala activity relates to the subjective and objective qualities of a memory. In the present study, participants viewed emotional and neutral objects while undergoing a functional magnetic resonance imaging scan. Participants then took a memory test, identifying which verbal labels named a studied object and indicating the vividness of their memory for that object. They then retrieved episodic details associated with each object's presentation, selecting which object exemplar had been studied and indicating in which screen quadrant, study list, and with which encoding question the exemplar had been studied. Parametric analysis of the encoding data allowed examination of the processes that tracked with increasing memory vividness or with an increase in the diversity of episodic details remembered. Dissociable networks tracked these two increases, and amygdala activity corresponded with the former but not the latter. Subsequent-memory analyses revealed that amygdala activity corresponded with memory for exemplar type but not for other episodic features. These results emphasize that amygdala activity does not ensure accurate encoding of all types of episodic detail, yet it does support encoding of some item-specific details and leads to the retention of a memory that will feel subjectively vivid. The types of episodic details tied to amygdala engagement may be those that are most important for creating a subjectively vivid memory.

Keywords

Emotion; Encoding; fMRI; Parametric; Subsequent memory

Memories that we retrieve can differ both in their subjective vividness and in their objective details. But these dimensions do not have to be aligned, and the types of episodic details that we remember can vary greatly from event to event. We can remember a plane flight vividly, and our memory can include information about the spatial, temporal, and contextual details of an event. Or we can remember a plane flight vividly, despite being unable to remember where we were traveling to or how long ago the trip occurred. Or we can feel that our memory of a flight is not particularly vivid, yet we may be able to remember many accurate

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episodic details about the flight. As these examples highlight, there can be a complex relation between the subjective vividness and the diversity of episodic details remembered.

This relation may be particularly complex when memories are of an emotional nature (e.g., Dougal & Rotello, 2007; Talarico & Rubin, 2003). There are many examples of eyewitnesses who erroneously but confidently identify a perpetrator (e.g., Charles et al., 2003; Wells et al., 1998; Woocher, 1976) or of individuals who vividly recollect inaccurate details of past emotional experiences (e.g., Neisser & Harsch, 1992). These findings emphasize that the subjective vividness of a memory is not always tethered to the amount of accurate episodic information remembered about an event, a finding that suggests these two types of mnemonic features may be supported by distinct processes. Phelps and Sharot (2008) have described emotion as enhancing the "feeling of remembering," and have connected this enhancement to amygdala engagement. Indeed, some research focusing on the role of retrieval-related processes has suggested that the amygdala plays a particularly important role in guiding the subjective experience of recollection, whereas it may not be tied to the retrieval of all types of episodic details (Sharot et al., 2004; Sharot et al., 2007). Further evidence to suggest that emotion may enhance the subjective feeling of remembering rather than the recovery of accurate episodic detail has come from behavioral studies revealing that emotion can boost false recollection and can bias participants to believe they have encountered emotional information previously (Dougal & Rotello, 2007; Brainerd et al., 2008; Gallo et al., 2009). Contrary to this view, however, is evidence that amygdala engagement during retrieval can enhance the recovery of some episodic details (Kensinger & Schacter, 2007), including the emotional context in which an event was experienced (Smith et al., 2005). Thus, it is possible that the connection between the amygdala and the recollection of past emotional experiences reflects not only a change in the subjective qualities but also in the amount of episodic detail retrieved (see Dolcos et al., 2005 for further discussion).

Research examining the interplay between the subjective vividness and the diversity of episodic detail included within a memory has often focused on the role of the amygdala during retrieval (e.g., Sharot et al., 2004). Yet the amygdala is believed to exert much of its influence upon earlier phases of memory, including memory encoding. Higher amygdala activity corresponds with improved encoding of emotional events (see Hamann, 2001; LaBar & Cabeza, 2006 for reviews), and lesions to the amygdala result in an impairment in the recollection of emotional information (e.g., Richardson et al., 2004). The primary goal of the present study, therefore, was to examine how amygdala engagement at *encoding* would correspond with the subjective vividness of a memory or with the diversity of episodic details remembered.

This study was designed to contribute to ongoing debates about whether amygdala activity corresponds with successful encoding of episodic detail. Some studies have found a link between amygdala activity and memory for episodic features (e.g., Kensinger et al., 2007), but other studies have found that amygdala activity corresponds with item memory, but not with source memory (e.g., Dougal, Phelps, & Davachi, 2007; Kensinger & Schacter, 2006). We have hypothesized previously that amygdala activity may correspond with memory for only a subset of episodic features, and that the amygdala's correspondence to subsequent memory may therefore vary depending on the particular type of episodic detail assessed (Kensinger, 2009; see also Mather, 2007; Phelps & Sharot, 2008). In particular, amygdala activity during encoding may correspond with the ability for participants to remember details that are specifically tied to the emotional item itself (e.g., its sensory features) but amygdala engagement may not enable the encoding of other contextual details that are more peripherally related to the item (Kensinger, 2009). The present study allowed a direct examination of the validity of this hypothesis by assessing memory for multiple different

types of episodic details. We tested participants' abilities to encode those types of details most readily distinguished in assessments of episodic memory: memory for spatial context (operationalized as memory for screen quadrant), memory for temporal context (measured as memory for the study list in which an item was presented), memory for conceptual detail (operationalized as memory for the decision made about an item), and memory for item-specific detail (operationalized as memory for the visual features of the presented object exemplar).

The present study examined whether amygdala engagement during encoding would correspond with the subjective vividness of a memory and with memory for these different types of episodic details. We addressed this question in two ways. First, we used parametric analyses to assess whether increases in amygdala activity would correspond with increases in subjective ratings of vividness or whether its activity would relate to increases in the number of different types of episodic details that could be remembered. Second, we used subsequent-memory analyses to examine whether amygdala engagement at encoding was tied to memory for specific types of episodic details. Based on proposals that the amygdala is tied to the ability to encode only select types of episodic details (e.g., Kensinger, 2009; Mather, 2007; Phelps & Sharot, 2008), we hypothesized that amygdala engagement would be tied to enhancements in the subjective richness of an episodic memory but that its engagement would not lead to a greater diversity of episodic details remembered. Rather, we hypothesized that the amygdala would only be tied to the ability to remember a subset of the episodic details that we assessed. Based on prior research, we hypothesized that the amygdala would correspond with the ability to retrieve item-specific details (consistent with Kensinger, 2009; Mather, 2007); it also seemed likely that amygdala engagement could benefit memory for the spatial location of the object, because some behavioral research has suggested that emotional objects may be bound to their spatial location during processing (e.g., MacKay et al., 2004; Mather, 2007).

A secondary goal of the present study was to examine whether the link between amygdala engagement and subsequent memory would differ depending upon the affective characteristics of the item being remembered. Emotional experiences are commonly divided into the dimensions of valence, referring to the pleasantness or unpleasantness of an event, and arousal, describing whether an event is exciting or agitating, or calming or subduing (e.g., Russell, 1980). Amygdala engagement during encoding has been proposed to be connected to the arousal elicited by an experience (Kensinger & Corkin, 2004; Anderson et al., 2006), but this does not negate the possibility that it could still show some tie to the subjective vividness of a memory even for items low in arousal, particularly when memory is assessed after a short delay. Similarly, amygdala activity has been tied to the ability to encode both positive and negative items (e.g., Kensinger & Schacter, 2008; Hamann & Mao, 2002), but this does not mean that its activity would correspond equally to the subjective vividness or episodic detail encoded for each of these valences of information.

To examine whether the link between amygdala engagement at encoding and subsequent memory vividness or memory detail was modulated by the valence or arousal of stimuli, we presented participants with four different categories of emotional stimuli: negative high arousal, negative low arousal, positive high arousal, and positive low arousal. We examined the correspondence between encoding-related activity and subsequent memory for all emotional items, collapsing across the characteristics of valence and arousal, and we also examined how that encoding-related activity might differ depending upon the valence and arousal of the to-be-remembered information.

Methods

Participants

Participants included 15 females and 11 males between the ages of 18 and 28. All participants were screened to exclude those with histories of neurological, psychiatric, or mood disorders. All participants received low scores on the Beck Depression Inventory (mean = 1.8, *SD* = 2.2; on this scale, scores greater than 10.0 are considered to indicate the presence of depressive symptoms; Beck et al., 1961). All participants indicated that they were taking no medications that would affect the central nervous system.

Due to malfunction with the stimulus presentation projector (1 participant), problems obtaining signal using the MRI head coil (1 participant), excessive head motion (2 participants), or chance memory performance (3 participants), 7 participants were excluded from analysis. The remaining 19 participants were 11 females and 8 males with a mean age of 22.7 years (*SD* = 2.5) and 15.3 years of education (*SD* = 1.6).

Materials

Stimuli comprised photo objects used in prior investigations of emotional memory (objects taken from those used in Waring & Kensinger, 2009 and Schmidt et al., in press). These images were taken from the Hemera photoset (www.hemera.com) and were supplemented with images from online databases (e.g., www.clipart.com, images.google.com). Normative data for these stimuli had been gathered previously, for use in prior studies (all stimuli were a subset of those used by Waring & Kensinger, 2009; Schmidt et al., in press), but because the stimuli were drawn from multiple datasets, we asked a separate group of 10 participants (5 female and 5 male, mean age = 20.1, mean years of education = 14.5) to rate all possible stimuli for valence and arousal. These ratings were made using a 7-point Likert scale, with low values indicating negative valence or low arousal, respectively. Based upon these ratings, 300 stimuli were selected because they could be clearly divided into five groupings: those that were negative and high arousal (average valence lower than 3.5, average arousal greater than 5), positive and high arousal (average valence greater than 6.5, average arousal greater than 5), negative and low arousal (average valence lower than 3.5, average arousal lower than 5), positive and low arousal (average valence greater than 6.5, average arousal lower than 5), and neutral (valence ranging from 3.5 to 6.5, arousal lower than 5). An ANOVA conducted on the four “emotional” categories (i.e., excluding neutral items) confirmed that there was a main effect of arousal ($p < .001$) and a main effect of valence ($p < .001$), but no interaction between arousal and valence ($F < 1.2$, $p > .25$; see Table 1 for valence and arousal ratings of stimuli in each category).

Behavioral Procedure

While undergoing an fMRI scan, participants viewed four encoding lists; across the lists, 30 photo objects were from each emotion category (7 or 8 presented in each list). Photo objects appeared for 2 sec in one of four quadrants on the screen and were followed by one of four question prompts: common, living, store, or fit. The prompt indicated which question the participant should answer about the object: Is it something common that you would see in an average month? Is it something living? Is it something that you could buy in a department store? Is it something that would fit in a file cabinet drawer? Participants pressed a button with their thumb to indicate “yes” and a button with their index finger to indicate “no”; button presses were made via a magnet-compatible button-box. Participants had 2 sec to make their response.

The presentation of these trials was pseudorandomly intermixed according to an optimal sequencing program written by Doug Greve (surfer.nmr.mgh.harvard.edu/opseq) to optimize

the detection of the hemodynamic response associated with each trial (Dale, 1999). The interstimulus interval (ISI) was also determined by this program and ranged from 2 to 14 sec (average of 4 sec); the ISI included a fixation cross which participants were asked to passively view.

Outside of the scanner, and after an approximately 30-minute delay, participants performed a recognition memory test. For 300 images (the 150 that had been presented in the scanner and 150 novel objects, 30 from each emotion category), participants were shown a series of verbal labels (e.g., “canoe”) and were asked to indicate whether the word named an object that had been seen during the fMRI scan. If participants indicated that the word did not name a studied item, they were presented with the next verbal label. If they indicated that the word did name a studied item, they were then asked a series of additional questions. They were asked to rate the vividness of their memory for the studied object, on a scale of 1 to 7. They were asked to select, from four alternatives, which particular exemplar of the object had been viewed during the fMRI scan (e.g., which canoe they had seen). They selected in which quadrant of the screen the image had appeared, in which study list the object had been presented, and which question they had been asked to answer about the image (see Figure 1 for depiction of task design). To avoid participant confusion, these retrieval questions were asked in a fixed order to each participant, although the order of the retrieval questions was rotated across participants.

fMRI Procedure

Participants were scanned on a 1.5 Tesla Siemens Avanto whole body MRI scanner (Erlangen, Germany), using a 32-channel high-resolution head coil. Stimuli were projected from a Macintosh iBook G4 using a Sharp200 color LCD projector with a collimating lens (Buhl Optical). The image was shown on a screen that was mounted at the end of the magnet bore. The screen was viewed via mirrors placed on the head coil. Anatomic images were acquired with a multi-planar rapidly acquired gradient echo (MP-RAGE) sequence and a T1-weighted inversion recovery echo planar image was acquired for auto alignment.

Functional images were acquired via a T2*-weighted echo planar imaging sequence sensitive to blood oxygenation dependant contrast (BOLD). The TR was 2000 ms, the effective TE was 40 ms, and the flip angle was 90°. The slices were acquired in an interleaved fashion, at an axial-oblique angle parallel to the AC-PC line. Twenty-six slices were acquired in a 3.125 mm × 3.125 mm × 3.84 mm matrix. The slices were 3.2 mm thick and had a 0.64 mm skip between slices.

Preprocessing and data analysis were completed using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). Preprocessing included: slice time correction, motion correction (which used a six parameter, rigid body transformation algorithm from SPM5), normalization (to the Montreal Neurological Institute template, with resampling at a 3mm isotropic resolution), and spatial smoothing (at a 5 mm isotropic Gaussian kernel).

fMRI Data Analysis

Analysis of the fMRI data focused on the emotional categories of items. The neutral items were included in the task to ensure that participants’ responses to the emotional items would be consistent with prior normative data. Prior pilot data from our laboratory has revealed that emotional reactions to stimuli are influenced by context (e.g., a high-arousal word is less arousing if presented in the context of high-arousal pictures), and so if no neutral items were presented, it seems plausible that this would alter the experience associated with each type of emotional item. Two types of analyses were performed on the data: parametric analyses and a structural ROI analysis of the amygdala.

Parametric Analyses—Two separate fixed-effects models were created. One model examined the neural activity corresponding with an increase in subjective memory vividness, while the second model examined the activity corresponding with an increase in the objective number of details remembered.

For each model, regressors were created for each of four event types (remembered negative arousing items, remembered positive arousing items, remembered negative nonarousing items, remembered positive arousing items[1]), and for each event type, a corresponding parametric regressor (modeled linearly) was included. All participants had at least 8 of each of these event types (range = 8-25). These parametric regressors tracked either the subjective memory vividness (for the first model) or the objective number of details remembered (for the second model). For the model examining associations with subjective memory vividness, ratings of 1-2, 3-4, 5-6, and 7 were analyzed as four separate levels. For the model examining associations with number of details, 0, 1, 2, and 3 details remembered were analyzed as four separate levels. Regressors of no interest were included for the neutral items and for the forgotten emotional items, so that activity associated with these items did not enter the error term.

For each model, a contrast was computed to reveal the positive parametric response for each condition. The resulting contrast images were then entered into an ANOVA conducted at the random-effects level that included arousal and valence as factors. The two ANOVAs (one for each model) examined the regions whose activity varied parametrically with subjective memory vividness, or with objective memory detail. These ANOVAs revealed the regions that showed this parametric relation across all emotional items, and they also revealed the regions in which this correspondence differed as a function of the arousal or valence of the to-be-remembered information. More specifically, to identify regions that showed a parametric correspondence that was not affected by an item's valence or arousal, analyses used exclusive masking to reveal the regions that showed a parametric correspondence to image vividness (or detail) but neither a main effect of valence, a main effect of arousal, nor an interaction between valence and arousal. Regions were considered to be significant if they were active in the parametric contrast at a threshold of $p<.001$ uncorrected and with an 8-voxel extent (using Monte Carlo estimates described by Slotnick et al., 2003 to allow for a $p<.05$ corrected significance value) and did not show a main-effect or interaction-effect in the ANOVA even when the threshold for those effects was lowered to a significance of $p<.05$. These regions, therefore, showed a parametric relation to all emotional items, and this relation was not significantly impacted by the item's valence or arousal.

To identify regions that showed a parametric correspondence to image vividness (or detail) that was modulated by valence, we looked for regions that were revealed by the ANOVA show a main effect of valence (at $p<.001$ uncorrected and an 8-voxel extent, as described above) but not an interaction between valence and arousal (using exclusive masking as described above). Similar exclusive masking methods were used to identify the regions that showed a main effect of arousal, making sure these regions showed only the main effect and not an interaction between valence and arousal. Finally, the results of the ANOVA were used to identify regions that showed an interaction between valence and arousal. When the ANOVA revealed a main effect, random-effects one-sample t-tests were then conducted to examine the direction of the effect (e.g., whether a main effect of arousal indicated a more positive parametric relation for high-arousal items or for low-arousal items). These t-tests

[1]Separate parametric models were set up to include regressors for the remembered neutral items, with regressors of no interest included for the forgotten neutral items and for the emotional items. These analyses revealed no activity within the amygdala, even at a liberal threshold ($p < .05$), and so these analyses will not be discussed further.

again used a $p<.001$ uncorrected and an 8-voxel extent to allow for a $p<.05$ corrected significance value using Monte Carlo estimates (Slotnick et al., 2003).

ROI analysis of the amygdala—Because the amygdala was a region in which we had an a priori interest, we defined two anatomical masks using the MARINA software (Walter et al., 2003). One mask included all voxels within the right amygdala while the other mask included all voxels within the left amygdala. Within these masks, we examined the pattern of subsequent memory performance that corresponded with amygdala engagement. We were particularly interested in examining the types of details for which there were links between amygdala engagement and subsequent memory.

ROI analyses were conducted using the REX – ROI extraction toolbox (hhtp://web.mit.edu/swg/software.htm), which extracts beta values for each condition of interest. For each participant, the beta values for each condition were rescaled by the constant beta value to obtain a measure of percent signal change. These rescaled values were then used to compute the group mean and *SE* percent signal change value for each condition.

Results

Behavioral Results: Recognition Accuracy

An ANOVA was conducted to examine how emotion (emotional, neutral) affected the corrected recognition rates (hits minus false alarms). This ANOVA indicated a significant main effect of emotion, $F(1,17) = 4.99$, $p < .05$, partial eta-squared = .23, with emotional items having higher corrected recognition rates than neutral items (see Table 2). Additional ANOVAs revealed that the benefit for emotional items emerged in the hit rates, $F(1,17) = 7.96$, $p < .04$, partial eta-squared = .32, whereas the false alarm rates did not differ, $p > .5$.

To assess how the valence and arousal of the emotional items affected recognition accuracy, ANOVAs were conducted for just the emotional items, including valence (negative, positive) and arousal (high, low) as factors. When this ANOVA was conducted on the corrected recognition rates (i.e., hits minus false alarms), there was only a main effect of valence, $F(1,17) = 6.55$, $p < .05$, partial eta-squared = .28, with negative items recognized more accurately than positive items (see Table 2). Additional ANOVAs revealed that the benefit for negative items stemmed from an effect of valence on the hit rate, $F(1,17) = 12.59$, $p<.05$, partial eta-squared = .32, whereas valence did not affect the false alarm rate, $p > .2$.

Behavioral Results: Memory Vividness

To examine how emotion affected the distribution of vividness responses, a repeated-measures ANOVA was conducted, examining how emotion (emotional, neutral) affected the proportion of vividness rating (not vivid (1-2), somewhat vivid (3-4), vivid (5-6), very vivid (7)). This ANOVA revealed a significant interaction between vividness rating and emotion, $F(3,20) = 3.22$, $p <.05$, partial eta-squared = .33. As can be seen in Table 3, for neutral items, responses that a memory was “very vivid” or “vivid” were less frequent than responses that a memory was “somewhat vivid” or “not vivid.” For emotional items this pattern was not upheld, revealing a pattern of more vivid memories for emotional items than for neutral items.

To examine whether this pattern of results was comparable for all emotional items, or whether it was specific to items with particular affective characteristics, another ANOVA was conducted just on the responses given to the emotional items with vividness rating (not vivid, somewhat vivid, vivid, very vivid), valence (positive, negative), and arousal (high,

low) as factors. This ANOVA revealed only a significant interaction between arousal and vividness rating, F (3,20) = 4.37, p <.05, partial eta-squared = .40, reflecting the fact that memory vividness was greater for items that were high in arousal (see Table 3).

Behavioral Results: Memory for Details

To examine how emotion affected memory for detail, a repeated-measures ANOVA was conducted with diversity of episodic details remembered (no details remembered, one, two, or three details remembered) and emotion (neutral, emotional) as factors. This ANOVA revealed a main effect of detail diversity, F(3,19) = 145.1, p<.001, partial eta-squared = .96, with more items remembered with one or two details than with zero or three (see Table 4). Importantly, there was no interaction between detail diversity and emotion (p > .15).

To examine whether this pattern of results was comparable for all emotional items, or whether it was specific to items with particular affective characteristics, another ANOVA was conducted on the responses given to only the emotional items. This ANOVA included detail diversity (no details remembered, one, two, or three details remembered), valence (positive, negative), and arousal (high, low) as factors. This ANOVA revealed only a significant main effect of detail diversity, F(3,20) = 152.5, p<.001, partial eta-squared = .96.

Parametric fMRI Results: Neural Activity Varying with Subjective Memory Vividness

An ANOVA was conducted on the parametric correspondence between fMRI signal change and subsequent vividness ratings in order to identify the regions that showed a few different patterns of results: regions that showed a parametric response to subsequent vividness ratings that was not influenced by valence or arousal; regions whose parametric relation to memory vividness was affected by valence; and regions whose parametric relation was affected by arousal (see Table 5 for listing of all regions that showed each of these patterns). Of most interest, activity in the right amygdala (see Figure 2), in regions throughout the medial and lateral PFC, and within the angular gyrus of the parietal lobe showed a parametric relation to vividness; these relations to subsequent memory vividness did not vary as a function of the valence or arousal of the emotional items[2]. Activity in a number of prefrontal regions showed a more strongly positive parametric relation to subsequent memory vividness for high-arousal items than for low-arousal items, whereas activity in the occipital and inferior temporal cortex showed a more strongly positive parametric relation to subsequent memory vividness for low-arousal items than for high-arousal ones. Importantly, no region within the amygdala showed a correspondence to subsequent memory vividness that was influenced by the item's valence or arousal.

Parametric fMRI Results: Neural Activity Varying with Increasing Diversity of Episodic Detail

A similar ANOVA was conducted on the parametric correspondence between fMRI signal change and memory for detail, to reveal the regions showing the different patterns of results described in the prior fMRI Results section (see Table 6 for listing of all regions that showed each of these patterns). At the standard threshold, only a single region, in the anterior cingulate gyrus, showed a parametric correspondence that did not differ as a function of

[2]When a parametric analysis was conducted for only the neutral items, the amygdala did not show a parametric relation to subsequent memory vividness, and an interaction contrast confirmed that the parametric relation in the right amygdala was significantly stronger for the emotional items than for the neutral items. As can be seen in Figure 3, the right amygdala was not activated in response to the neutral items. However, it is important to note that in the present study, because the number of neutral items was equated with the number of items from a single type of emotional category (e.g., to the number of positive low-arousal items), there were more emotional items than neutral items shown to participants. It is therefore possible that the different power in the two conditions made it easier to find strong parametric or subsequent-memory relations for the emotional items. Future studies may choose to re-examine this issue using a design that includes a comparable number of emotional and neutral items.

valence or arousal. When the threshold was reduced to $p<.005$, regions within the PFC and a region of the right posterior hippocampus[3] were demonstrated to show this parametric correspondence. Importantly, even at a reduced threshold of $p<.01$, amygdala activity was not revealed. Moreover, amygdala activity did not show a correspondence to memory for detail that varied as a function of item valence or arousal. (An ANOVA directly comparing the parametric relations for subjective memory vividness and objective memory for detail confirmed that the amygdala showed a main effect of memory type [vividness, detail], showing a stronger parametric relation to memory vividness than to memory detail).

There were a number of regions in which the parametric relation to episodic detail was modulated by valence or arousal (see Table 6 for listing of regions). Of most interest, regions of the occipital and inferior temporal lobes showed a stronger parametric relation for negative than for positive valence, and regions within the frontal and temporo-parietal cortices showed a stronger parametric relation for low-arousal than for high-arousal items.

Anatomical Region of Interest Analysis: Subsequent-Memory Activity within the Amygdala

Because a key interest of this study was to examine the link between amygdala engagement and subsequent memory, we defined the left amygdala and the right amygdala as anatomical ROIs, using the MARINA toolbox (Walter et al., 2003). Because activity in the left amygdala showed no correspondence to subsequent memory within the current paradigm, only activity from the right amygdala ROI will be reported.

Within the right amygdala ROI, one-tailed *t* tests examined whether activity to forgotten items was significantly less than activity to items remembered with different types of episodic details. The only significant difference emerged when comparing forgotten items to items for which the specific exemplar was remembered correctly ($t(17) = -1.75$, $p < .05$). All other *t* tests were nonsignificant (all $p > .15$). As can be seen in Figure 3, the right amygdala showed a strong relation to the ability to remember the image exemplar, but it showed no significant relation to the ability to remember the other episodic features[4].

Discussion

The results of the present study indicate that neural activity recruited during encoding is associated with the subsequent vividness and episodic detail with which an emotional item is retrieved. The results reveal that the processes that predict increasingly vivid memories are not the same as those that correspond with increasingly detailed memories. Critically, amygdala activity was found to correspond with an increase in the subjective vividness of a subsequent memory but not in the number of episodic details remembered about the emotional event. Here, we discuss the importance of these findings for understanding the way in which vivid or detailed emotional memories are formed.

Creation of Subjectively Vivid Memories

When it comes to remembering an emotional event vividly, amygdala engagement is a strong predictor: The more active the amygdala was during encoding, the more subjectively vivid a memory later was rated. Interestingly, this tie between amygdala activity and subsequent memory vividness held across all types of emotional items, regardless of their

[3]When the right hippocampus was defined as an anatomic region-of-interest, using the MARINA toolbox (Walter et al., 2003), analyses on extracted beta values indicated that the hippocampus corresponded with subsequent memory for each type of episodic detail assessed, and that it showed this correspondence to subsequent memory for both the emotional items and also for the neutral items.

[4]This pattern of activity was the same when the area of activity depicted in Figure 2 was analyzed as a 5mm spherical ROI; however, in this functional ROI the pattern did not reach statistical significance.

valence or arousal, suggesting that this link is not restricted to any one type of emotional experience. Although high-arousal experiences are often remembered more vividly than low-arousal ones (e.g., Kensinger & Corkin, 2003; Sharot et al., 2007), the amygdala appears to show a link to memory vividness for all types of emotional experiences.

Beyond the amygdala, it was particularly interesting that the angular gyrus showed a parametric relation to subsequent memory vividness. The coordinates within the angular gyrus found here (−45, −70, 37) were close to those associated with a subjective feeling of recollection in a prior study (Slotnick, 2010, coordinates: −48, −67, 28), despite the fact that Slotnick (2010) examined the link to memory vividness during retrieval. Thus, the present results are consistent with the proposal that activity within the angular gyrus supports subjective memory vividness, rather than the binding of episodic details (Slotnick, 2010; see also Wheeler and Buckner, 2004; Montaldi et al., 2006; Vilberg & Rugg, 2008).

Although a number of regions, including the amygdala and the angular gyrus, showed a parametric relation to memory vividness that did not vary as a function of valence or arousal, other regions showed a correspondence that was stronger for a specific type of emotional experience. Of most interest, activity within many prefrontal regions was more strongly associated with increasing memory vividness for high-arousal items than for low-arousal ones, whereas occipital and inferior temporal regions showed the opposite pattern. This pattern suggests that different processes support the encoding of vivid recollections of emotional events depending upon the arousal of the experience. To better understand the reason for this pattern of results, it is useful to consider the neural findings in conjunction with the behavioral results. The behavioral results revealed that high-arousal items are remembered with more subjective vividness than low-arousal items, yet they are not remembered with more episodic detail. In other words, participants appeared biased to believe they had encoded a rich episodic memory of high-arousal items even when the contextual details had not been successfully encoded. The fact that it was prefrontal rather than sensory cortices which showed the stronger tie to memory vividness for high-arousal items sheds light on this behavioral effect: It may not be the increased encoding of sensory details that leads a person to create a subjectively vivid memory for a high-arousal event but rather the encoding of other types of information (e.g., internal details, autobiographical elaborations) supported by prefrontal engagement. This pattern would be consistent with prior evidence that high-arousal affect can increase confidence and the subjective feeling of recollection without having an accompanying influence on memory for sensory detail (e.g., Sharot et al., 2004; Sharot et al., 2007; Talarico & Rubin, 2003).

Creation of Episodically Detailed Memories

When examining the regions that corresponded with an increasing diversity in the episodic details remembered, there was a notable absence of amygdala activity. In fact, at the standard threshold, only activity within the left anterior cingulate cortex showed a link to increasing diversity in episodic detail for all types of emotional experiences. At a reduced threshold, activity in the hippocampus and lateral prefrontal cortex was also revealed. The activity in these regions is consistent with prior studies demonstrating their role in binding together different types of contextual elements of an episode. The hippocampus is often associated with episodic binding (e.g., Davachi, 2006; Slotnick 2010; but see Spaniol et al., 2009), and the lateral prefrontal cortex has frequently been associated with the encoding of source information (reviewed by Mitchell & Johnson, 2009). Although the anterior cingulate cortex is less frequently associated with this role in binding, there is some evidence from animal models to suggest that this region may play a role in the binding of context as well (e.g., Frankland et al., 2004). Thus, some regions that have been previously implicated in episodic memory formation for neutral items also appear to play a role in the binding of

multiple different types of episodic details for all emotional events, regardless of their valence or arousal.

In a number of regions, however, the parametric relation to increasing diversity of episodic detail was modulated by valence or arousal. In terms of valence effects, occipital and inferior temporal activity showed a stronger parametric relation for negative than for positive valence. This pattern is consistent with prior proposals that negative information may be more likely than positive information to be encoded with an orientation toward sensory processing (e.g., Mickley & Kensinger, 2008; Mickley Steinmetz & Kensinger, 2009). In terms of arousal effects, there was a stronger parametric relation to diversity of episodic detail for low-arousal than for high-arousal items in regions throughout the frontal and temporo-parietal cortices. This finding is interesting for two reasons. First, the regions more strongly linked to episodic detail diversity for low-arousal items than for high-arousal items include many regions that have been implicated in elaborative and semantic processing. The fact that these regions would be disproportionately connected to detailed memory for low-arousal items is consistent with the proposal that low-arousal events are remembered in an episodically rich fashion when they are processed elaboratively (e.g., Kensinger, 2004; Buchanan et al., 2006). Second, the findings emphasize that the pattern noted above for memory vividness (with an increased correspondence between prefrontal activity and memory vividness for *high*-arousal items) is specific to vividness and does not extend to memory for a diverse set of episodic details. For detail, there is more activity throughout the frontal as well as the temporo-parietal cortices for *low*-arousal items. Thus, the effect of arousal on the processes linked to subjective vividness is distinct from its effect on the processes linked to the encoding of a diverse set of episodic details.

The Role of the Amygdala in the Creation of Episodic Memories

A primary goal of the present paper was to clarify the role that the amygdala played in the encoding of vivid and episodically detailed memories. The results discussed so far indicate that amygdala engagement tracks linearly with the subjective vividness of a subsequent memory, but does not correspond with an increasing diversity of retained episodic details. The reason for this disconnect was elucidated by the anatomical ROI analyses. When ROI analyses were used to examine the correspondence between amygdala activity and subsequent-memory performance, these analyses revealed that – at least after a short delay – the amygdala showed a relation to memory for the exemplar type but not for any other episodic features. This pattern of results confirms what has been proposed previously (e.g., Kensinger, 2009; Mather, 2007): Amygdala activity seems to correspond with the ability to encode a select set of details (i.e., exemplar type), rather than with the ability to encode multiple different types of details. These results are consistent with the proposal that amygdala activity is tied to the successful encoding of some pieces of an experience, but that its engagement does not equally benefit all episodic details (see Kensinger, 2009 for a review).

The data also are consistent with the proposal by Phelps and Sharot (2008) that for emotional items, “quality and strength of memory for a few details may mediate judgments of recollection” (pg. 147). It is plausible that the details enhanced by amygdala activity are those that are weighted heavily when deciding about the vividness of a memory. For instance, the degree to which you remember what an exemplar looked like may influence the subjective vividness of a memory to a greater extent than the degree to which you remember the quadrant of the screen or the study list on which the image was located. The fact that it was the exemplar details that were encoded well when the amygdala was active may also relate to the fact that this information is likely to be the most stimulus-bound feature of all those features assessed. It may be these intrinsic item features that are most likely to be enhanced by amygdala engagement (discussed by Kensinger, 2009; Mather, 2007), perhaps

because those are the features that it will be most adaptive to remember quickly (discussed by Phelps & Sharot, 2008).

Limitations and Future Directions

It will be important for future research to examine whether the link between amygdala engagement and subsequent memory changes as the delay interval lengthens. Some of the effects of the amygdala on memory tested after a short duration may be mediated via its connections with regions such as the fusiform gyrus (Talmi et al., 2008), whereas after a long delay, the effects of the amygdala may be more likely to reflect direct modulatory effects on hippocampal function (e.g., McGaugh, 2004). Thus, it is possible that amygdala engagement during encoding would show a connection to memory for a broader set of episodic details after a long delay (when it is affecting hippocampal processing) than after a short delay (when it is more likely to be influenced by processing in regions like the fusiform gyrus, which may be specialized for item-specific visual features). Indeed, Ritchey et al. (2008) have shown that the relation between amygdala engagement and subsequent memory can be influenced by delay interval: They found that connectivity between the amygdala and the hippocampus was particularly important in sustaining vivid recollection of emotional stimuli across long (1-week) as compared to short (20-min) delays. However, because no prior study has distinguished the subjective feeling of recollection from the ability to recall different types of episodic details, it remains an open question whether both of these dimensions are affected by a lengthening delay interval.

It will also be important for future research to examine how the parametric effects revealed here relate to subsequent-memory effects typically reported with regard to the emotional enhancement in memory (e.g., Canli et al., 1996; Mickley & Kensinger, 2008). With the current methodology, it was not possible to obtain enough forgotten items for each emotion category (e.g., for positive low-arousal items) to directly compare the subsequent-memory patterns for each of these classes of stimuli. Therefore, the present study could not measure the both parametric relations to successfully-encoded items of each emotion category and also the subsequent-memory contrasts comparing remembered and forgotten items from each emotion category. Given the limited number of objects that fell into each of the emotion categories assessed here, in order to have enough remembered items to include in the parametric analyses, we had to sacrifice the ability to acquire signal from a sufficiently large number of forgotten items to allow subsequent-memory contrasts to be computed for each emotion category of item. It will be important for future research to develop a stimulus set and a task that would allow for both the parametric and the subsequent-memory measurements to be made simultaneously for items of each emotional category as well as for neutral items. Additionally, development of software that enables the extraction of bold signal from group level parametric analyses will further understanding of these parametric effects and how they relate to subsequent memory effects.

It would also be wise for future research to be conducted to examine whether the parametric relation between amygdala activity and subjective memory vividness is specific to emotional items or can also generalize to memory for neutral stimuli. In the present study, the number of neutral items was equated with the number of items from a single emotional category (e.g., to the number of negative high-arousal items) and so was smaller than the overall number of emotional items. This design element could have enabled us to detect parametric relationships for the emotional stimuli but not for the neutral stimuli simply because of these power differences.

Conclusion

The present study revealed dissociable processes that correspond to the creation of subjectively vivid versus episodically detailed memories for emotional items. Most notably, activity in the amygdala corresponded with the former but not the latter, because amygdala activity was linked to the ability to encode only one of the episodic details assessed in this study (memory for the specific exemplar). Although the parametric relation in other regions was modulated by valence or arousal, the link between amygdala engagement and subsequent memory characteristics was stable for all emotion types. Thus, although memories for high-arousal events can be more likely to be remembered vividly than memories for low-arousal events, these differences may not be tied to arousal-based differences in amygdala engagement during encoding but rather to differences in engagement of other regions. These results emphasize that amygdala activity does not create a “picture-perfect” memory. Amygdala activity boosts the likelihood of encoding only a subset of episodic details. Yet, its activity tracks with the subjective vividness of the memory that is retained, perhaps because the subjective vividness of a memory is closely tied to the ability to remember the types of details that the amygdala helps to encode.

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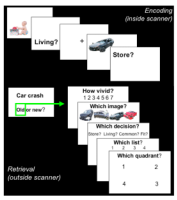

Figure 1.

During encoding (top panel), participants viewed images presented in one of four quadrants, in one of four lists, and were asked one of four questions about each image. At retrieval (bottom panel), participants were shown the verbal labels corresponding to items that could have been studied and were asked to indicate whether that label referred to a studied object ("old") or not ("new"). For labels judged to be old, participants then rated the vividness of their memory for the corresponding encoding episode, and selected the image exemplar, the question asked, the list in which the image was presented, and the quadrant in which the image was presented.

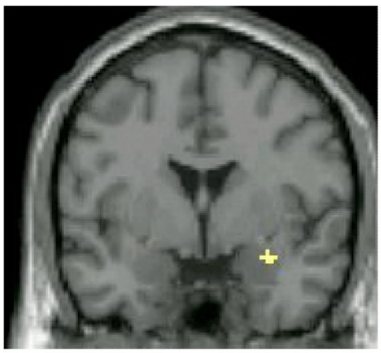

Figure 2.
Activity in the right amygdala (Talairach coordinates: 34, −3, −12) showed a positive parametric relation to subjective memory vividness for the emotional items.

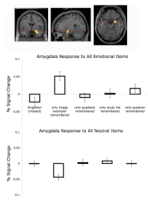

Figure 3.
For emotional items, activity in the right amygdala corresponded with subsequent-memory only for the image exemplar but not for the other episodic details. For neutral items, amygdala activity did not show any correspondence to subsequent memory.

Table 1

Mean Valence and Arousal Ratings for Stimuli Used in Experiment. Values in Parentheses Represent Standard Error of the Mean.

	Valence	Arousal
Neutral	5.3 (.03)	3.5 (.03)
Negative high arousal	2.7 (.04)	6.2 (.04)
Negative low arousal	3.0 (.04)	3.3 (.04)
Positive high arousal	7.2 (.04)	6.1 (.03)
Positive low arousal	7.1 (.03)	3.1 (.04)

Table 2

Mean proportion (*SE*) of items correctly endorsed ("hits") or correctly rejected. Corrected recognition rates reflect the hit rate minus the false alarm rate. (Note that the category of "emotional" collapses across negative high arousal, negative low arousal, positive high arousal, and positive low arousal).

	Hits	Correct Rejections	Corrected Recognition (Hits minus False Alarms)
Neutral	.55 (.03)	.87 (.03)	.43 (.04)
Emotional	.63 (.02)	.86 (.02)	.49 (.02)
Negative high arousal	.70 (.03)	.82 (.02)	.52 (.04)
Negative low arousal	.65 (.02)	.88 (.03)	.53 (.03)
Positive high arousal	.60 (.02)	.84 (.03)	.44 (.03)
Positive low arousal	.59 (.02)	.89 (.02)	.48 (.03)

Table 3

Mean proportion (*SE*) of vividness ratings given to correctly recognized emotional and neutral items (Note that the category of "emotional" collapses across negative high arousal, negative low arousal, positive high arousal, and positive low arousal).

	Not Vivid	Somewhat Vivid	Vivid	Very Vivid
Neutral	.27 (.06)	.36 (.04)	.18 (.03)	.18 (.04)
Emotional	.21 (.02)	.26 (.04)	.27 (.03)	.26 (.04)
Negative high arousal	.24 (.04)	.25 (.04)	.22 (.04)	.32 (.04)
Negative low arousal	.25 (.03)	.27 (.04)	.24 (.03)	.24 (.04)
Positive high arousal	.23 (.03)	.24 (.04)	.24 (.04)	.30 (.04)
Positive low arousal	.17 (.03)	.27 (.04)	.27 (.04)	.30 (.05)

Table 4

Mean proportion (*SE*) of correctly recognized items that were remembered with each number of details (Note that the category of "emotional" collapses across negative high arousal, negative low arousal, positive high arousal, and positive low arousal).

	No Details	One Detail	Two Details	Three Details
Neutral	.11 (.02)	.35 (.02)	.42 (.03)	.12 (.02)
Emotional	.11 (.02)	.31 (.02)	.49 (.03)	.11 (.02)
Negative high arousal	.12 (.02)	.34 (.04)	.43 (.03)	.11 (.01)
Negative low arousal	.10 (.03)	.28 (.03)	.50 (.04)	.12 (.02)
Positive high arousal	.08 (.02)	.30 (.03)	.55 (.04)	.06 (.01)
Positive low arousal	.12 (.03)	.31 (.03)	.47 (.03)	.10 (.02)

Table 5

Regions whose activity related parametrically to increasing vividness ratings for the emotional items.

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
Parametric relation not influenced by valence or arousal						
Cingulate cortex	Posterior cingulate gyrus	23	6, −60, 12	6, −57, 14	11	.001
Frontal Lobe	Inferior frontal gyrus	45	56, 26, 12	55, 25, 10	17	.001
		45	50, 26, 2	50, 25, 0	12	.001
	Medial frontal gyrus	10	10, 42, −12	10, 40, −12	78	.001
	Middle frontal gyrus	8	44, 20, 48	44, 22, 43	25	.001
		6	48, 6, 54	48, 8, 49	11	<.001
	Orbitofrontal gyrus	11	10, 38, −18	10, 36, −17	21	<.001
	Precentral gyrus	4	−36, −20, 52	−35, −17, 49	22	<.001
		4/6	48, −18, 46	48, −15, 43	20	.001
	Superior frontal gyrus	8/9	14, 48, 48	14, 49, 42	201	<.001
		10	−8, 64, 0	−8, 62, −3	82	<.001
		9	−14, 58, 30	−14, 58, 25	8	.001
		10	−20, 50, 0	−20, 48, −2	40	.001
Parietal Lobe	Angular gyrus	39	−46, −74, 36	−45, −70, 37	76	<.001
Temporal lobe	Amygdala		34, −2, −14	34, −3, −12	11	.001
	Fusiform gyrus	19	24, −64, −10	24, −62, −5	9	.001

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
		20	−58, −10, −32	−57, −11, −26	9	.001
	Middle temporal gyrus	20	56, −44, −12	55, −43, −8	10	.001
	Parahippo-campal gyrus	37	34, −40, −14	34, −40, −10	13	.001
	Superior temporal gyrus	39	40, −60, 28	40, −57, 29	16	<.001
		39	−58, −64, 26	−57, −61, 27	18	.001
Parametric relation influenced by valence (negative > positive)						
Cingulate cortex	Cingulate gyrus	23	4, −18, 34	4, −16, 32	31	<.001
Frontal lobe	Inferior frontal gyrus	47	−36, 28, −6	−36, 27, −6	11	<.001
	Medial frontal gyrus	6	4, −22, 64	4, −18, 60	49	<.001
	Precentral gyrus	4	38, −26, 64	38, −22, 60	48	<.001
		4	−32, −32, 62	−32, −28, 58	17	<.001
	Globus Pallidus		28, −18, 0	28, −17, 1	14	<.001
Parietal lobe	Inferior parietal lobule	40	−52, −62, 48	−51, −58, 47	9	.001
	Postcentral gyrus	5	12, −48, 70	12, −43, 67	17	<.001
Putamen			28, 0, 4	28, 0, 4	28	<.001
Temporal lobe	Superior temporal gyrus	22	52, −20, 0	52, −20, 1	18	.001

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
		41	44, −42, 14	44, −40, 15	15	<.001
		22	56, −10, 6	55, −10, 6	23	.001
Parametric relation influenced by arousal (high > low)						
Caudate			10, 6, 16	10, 7, 14	39	<.001
Cingulate cortex	Anterior cingulate gyrus	24	2, 26, −8	2, 25, −8	31	<.001
	Posterior cingulate gyrus	30	−8, −52, 22	−8, −50, 23	13	<.001
Frontal lobe	Medial frontal gyrus	10	−4, 70, 12	−4, 68, 7	32	.001
		9	−6, 46, 26	−6, 46, 22	23	.001
	Middle frontal gyrus	8	30, 30, 50	30, 31, 45	73	<.001
		6	26, −10, 46	26, −8, 43	18	<.001
		11	−22, 28, −12	−22, 27, −11	16	<.001
		9	34, 14, 38	34, 15, 34	12	.001
		10	−30, 58, 26	−30, 57, 21	8	.001
	Superior frontal gyrus	11	38, 46, −16	38, 44, −15	11	.001
		8	−24, 24, 50	−24, 26, 45	14	.001
		10	20, 70, 16	20, 69, 11	9	.001
Insula		13	−40, 18, 10	−40, 18, 8	30	.001
Temporal lobe	Fusiform gyrus	37	−36, −38, −14	−35, −37, −10	17	<.001
	Middle temporal gyrus	21	−64, −10, −6	−64, −10, −5	15	<.001
		39	−34, −56, 26	−34, −53, 27	12	<.001

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
Parametric relation influenced by arousal (low > high)						
Cingulate cortex	Posterior cingulate gyrus	30	−30, −74, 10	−30, −71, 12	212	<.001
Frontal lobe	Precentral gyrus	4	46, −16, 52	46, −13, 49	83	<.001
Occipital Lobe	Lingual gyrus	17	18, −88, −8	18, −86, −2	50	<.001
	Cuneus	17	−22, −96, −8	−22, −93, −2	32	<.001
	Middle occipital gyrus	19	32, −86, 6	32, −83, 10	102	<.001
		18	30, −82, −14	30, −80, −8	175	<.001
		19	−44, −86, 8	−44, −83, 12	10	.001
Parietal Lobe	Superior parietal lobule	7	−28, −58, 48	−28, −54, 47	16	<.001
Temporal lobe	Parahippo-campal gyrus	36	44, −36, −12	44, −35, −8	8	.001
	Fusiform gyrus	19	−24, −56, −16	−24, −55, −11	20	.001
	Middle temporal gyrus	37	50, −68, 4	50, −66, 7	9	.001

Table 6

Regions whose activity related parametrically with the number of episodic details accurately remembered. Gray shading indicates those regions that were revealed at a more liberal threshold.

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
Parametric relation not influenced by valence or arousal						
Cingulate cortex	Anterior cingulate gyrus		−10, 28, 8	−10, 27, 6	11	.001
	Cingulate gyrus	24	−14, −10, 46	−14, −8, 43	8	.002
Frontal lobe	Inferior frontal gyrus	47	36, 30, −6	36, 29, −6	8	.005
	Medial frontal gyrus	10	16, 40, −12	16, 38, −12	8	.003
	Middle frontal gyrus	8	50, 14, 44	50, 16, 40	27	.002
	Superior frontal gyrus	11	14, 54, −16	14, 52, −16	8	.003
Temporal lobe	Posterior hippocampus		26, −36, −6	26, −35, −3	10	.004
Parametric relation influenced by valence (positive > negative)						
Caudate			24, −8, 20	24, −7, 19	8	.001
Cingulate cortex	Anterior cingulate gyrus	25	6, 34, −6	6, 33, −7	15	<.001
		32	−14, −14, 34	−14, −12, 32	13	.001
	Cingulate gyrus	24	20, −24, 22	20, −22, 21	9	.001
Parametric relation influenced by valence (negative > positive)						

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
Caudate			−40, −52,10	−40, −50,12	13	<.001
Cingulate cortex	Anterior cingulate gyrus	32	−8, 8, 42	−8, 10, 38	8	.001
	Cingulate gyrus	31	18, −40, 44	18, −37, 42	26	<.001
		31	26, −26, 38	26, −23, 36	11	<.001
Insula		13	−36, 10, 20	−36, 11, 18	17	.001
Occipital lobe	Cuneus	18	16, −72, 18	16, −69, 20	10	.001
		23	−14, −76, 8	8, −40, 50	20	<.001
	Inferior occipital gyrus	19	38, −84, −6	−14, −73,11	22	<.001
	Lingual gyrus	18	18, −86, −20	18, −84,−13	27	.001
	Middle occipital gyrus	19	−36, −88, 2	−36, −75, 6	21	.001
	Superior occipital gyrus	19	−42, −80, 24	−42, −76,26	70	<.001
		18	−52, −54, −18	−51,−53,−12	23	<.001
Parietal lobe	Inferior parietal lobe	40	34, −48, 40	34, −45, 49	12	.001
	Precuneus	18	−22, −78, 18	−22,−75, 20	14	.001
Putamen			28, −6, 0	28, −6, 0	10	.001
Temporal lobe	Fusiform gyrus	37	−46, −66, −14	−46, −65, −9	12	.001
		37	50, −64, −18	50,−63, −12	13	.001

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
	Inferior temporal gyrus	37	−44, −66, −4	−44, −64, 0	16	.001
	Middle temporal gyrus	39	24, −96, 12	24, −92, 16	56	<.001
		39	−36, −72, 28	38, −82, −1	46	<.001
	Parahippo-campal gyrus	30	−22, −46, 0	−22, −45, 2	48	<.001
Parametric relation influenced by arousal (high > low)						
Frontal lobe	Middle frontal gyrus	10	−36, 64, 10	−36, 62, 6	11	.001
Occipital lobe	Lingual gyrus	18	6, −82, −8	6, −80, −3	11	.001
Temporal lobe	Superior temporal gyrus	39	−36, −62, 30	−36, −59,31	33	<.001
Parametric relation influenced by arousal (low > high)						
Cerebellum			30, −50, −20	30, −49,−14	45	<.001
			−18, −44, −28	−18,−44,−21	11	<.001
Cingulate cortex	Anterior cingulate gyrus	32	−14, 32, 28	−14, 32, 24	102	<.001
	Cingulate gyrus	32	−6, 10, 40	−26, 8, 9	11	.001
	Posterior cingulate gyrus	30	4, −64, 6	4, −62, 9	9	.001
		23	−6, −40, 22	−6, −38, 22	10	<.001

Brain Region	Gyrus	Approx. Brodmann area	MNI coordinates (x, y, z)	TAL coordinates (x, y, z)	Cluster size	p-value
Frontal lobe	Inferior frontal gyrus	47	32, 36, −2	32, 35, −3	23	.001
	Medial frontal gyrus	6	−18, −20, 52	−18, −17,49	12	<.001
	Middle frontal gyrus	9	30, 34, 30	30, 34, 26	67	<.001
		11	−28, 42, −4	−28, 41, −5	42	<.001
Insula		13	−42, 8, 16	−42, 8, 14	29	<.001
		13	−32, 22, 16	−32, 22, 14	29	.001
		13	44, 8, 2	44, 8, 1	35	<.001
Parietal lobe	Precuneus	31	−22, −76, 24	−22,−73, 26	21	.001
Putamen			−26, 8, 10	−26, 8, 9	13	.001
Temporal lobe	Middle temporal gyrus	21	−38, 2, −38	−38, 0, −32	16	<.001
	Parahippo-campal gyrus	19	40, −50, −6	40, −49, −3	17	<.001
		36	22, −42, −14	22, −41,−10	21	<.001
		36	−14, −40, 0	−14, −39, 2	15	.001
	Superior temporal gyrus	38	−44, 8, −12	−44, 7, −10	21	.001
		42	−68, −32, 14	−67, −30,14	11	.001
		38	42, 14, −32	42, 12, −28	9	.001