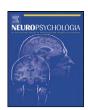
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Amygdala activity at encoding corresponds with memory vividness and with memory for select episodic details

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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.

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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 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

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erroneously but confidently identify a perpetrator (e.g., Charles, Mather, & Carstensen, 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, Delgado, & Phelps, 2004; Sharot, Martorella, Delgado, & Phelps, 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 (Brainerd, Stein, Silveira, Rohenkohl, & Reyna, 2008; Dougal & Rotello, 2007; Gallo, Foster,

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& Johnson, 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, Henson, Rugg, & Dolan, 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, LaBar, & Cabeza, 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, Strange, & Dolan, 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, Garoff-Eaton, & Schacter, 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; Mather, 2007). 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 about an emotional item. 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 about an emotional item. 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 (Anderson, Yamaguchi, Grabski, & Lacka, 2006; Kensinger & Corkin, 2004), 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., Hamann & Mao, 2002; Kensinger & Schacter, 2008), 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.

1. Methods

1.1. 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, Ward, Mendelson, Mock, & Erbaugh, 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).

1.2. Materials

Stimuli comprised photo objects used in prior investigations of emotional memory (objects taken from those used in Waring & Kensinger, 2009; 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 Schmidt et al., in press; Waring & Kensinger, 2009), 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

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