

# Beyond Fear

## Emotional Memory Mechanisms in the Human Brain

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**ABSTRACT**—*Neurobiological accounts of emotional memory have been derived largely from animal models investigating the encoding and retention of memories for events that signal threat. This literature has implicated the amygdala, a structure in the brain's temporal lobe, in the learning and consolidation of fear memories. Its role in fear conditioning has been confirmed, but the human amygdala also interacts with cortical regions to mediate other aspects of emotional memory. These include the encoding and consolidation of pleasant and unpleasant arousing events into long-term memory, the narrowing of focus on central emotional information, the retrieval of prior emotional events and contexts, and the subjective experience of recollection and emotional intensity during retrieval. Along with other mechanisms that do not involve the amygdala, these functions ensure that significant life events leave a lasting impression in memory.*

**KEYWORDS**—*affect; anxiety; traumatic memory; medial temporal lobe; fear conditioning*

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How we remember emotional episodes from the past has captivated scholarly interest for centuries, from philosophical accounts of the relationship between the passions and mental faculties to psychoanalytic views on the emotional unconscious. When recalling events from one's personal history, not only do emotions figure prominently in the content of the memory, but one also feels differently during the act of emotional recollection than during the recall of a mundane fact. Emotions therefore contribute to both the selective retention and the subjective experience of memory. Rapaport (1950) argued that "memory laws based on logical 'meaning' and 'organization' of the memory material refer only to special cases of memory organization; the more general theory of memory is the theory based on 'emotional organization' of memories" (p. 268). In other words, theorizing how cognitive processes influence memory in the absence of

emotion is to consider only a limited set of circumstances in which memory is normally engaged. A current major goal is to understand the psychological and neural mechanisms by which emotions exert their influence over learning and memory processes in the brain.

Animal studies have used training procedures based on classical conditioning principles to elucidate how the brain forms and retains memories for cues and contexts that predict aversive or rewarding outcomes. For example, when presented with a tone that reliably predicts the delivery of a foot shock, rats will readily acquire fear responses to the tone and other features of the environment. Fear-conditioning models have emphasized a key role of the amygdala, a subcortical structure in the medial temporal lobe of the brain. The amygdala integrates sensory information about threats across subcortical and cortical routes of processing and orchestrates integrated defensive reactions by controlling autonomic and motor output centers (Fig. 1). The amygdala's internal processing and its interactions with the frontal lobes and hippocampus, another structure in the temporal lobe, are important in the acquisition and subsequent suppression (extinction) of fear associations to cues and environmental contexts, and these findings have been confirmed in humans (LaBar and LeDoux, 2006).

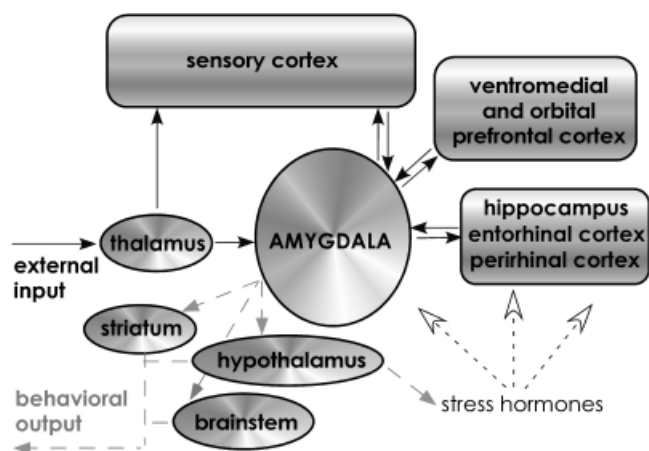
There are lingering questions over whether the neural circuitry revealed by conditioning studies extends to the domain of human emotion beyond situations involving imminent primary reinforcers. What can such an evolutionarily old structure like the amygdala contribute to emotional forms of human memory? Surprising answers to this question continue to emerge as more functions of the amygdala and its cortical interactions are revealed by neuroimaging and by neuropsychological and pharmacological research.

### AROUSAL-MEDIATED MEMORY CONSOLIDATION

McGaugh's (2004) *memory modulation hypothesis* posits that, following an emotionally arousing experience, the amygdala engages adrenergic and cortisol stress-hormone systems that interact to promote memory storage in the cortex. Accumulating evidence supports this hypothesis in studies of human emotional

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**Fig. 1.** The central role of the amygdala in emotional learning and memory as initially derived from animal models of fear conditioning. The amygdala integrates sensory information from subcortical and cortical processing pathways (solid black arrows) and orchestrates coordinated emotional responses to salient events (dashed grey arrows). Inputs from the frontal and temporal lobes (right side) exert contextual control over emotional behavior. Many of the input projections from the cortex are reciprocal, which provides a means for amygdala-dependent emotional processing to influence memory and other cognitive functions. In parallel, activation of stress-hormone systems facilitates storage of newly acquired information via feedback mechanisms from the periphery onto central receptor sites. Subcortical structures are indicated with ovals; cortical structures are indicated with boxes.

memory. For example, people with amygdala damage are impaired in remembering details of the emotionally arousing portion of a story learned several weeks earlier, despite having normal memory for the nonemotional portions of the story (Cahill, Babinsky, Markowitsch, & McGaugh, 1995). When healthy adults are administered a drug (propranolol) that antagonizes the adrenergic system prior to learning the story, they exhibit the same selective emotional-memory deficits as the amygdala-damaged patients (Cahill, Prins, Weber, & McGaugh, 1994), implicating a converging mechanism. Although these findings are typically interpreted as reflecting enhanced memory consolidation by emotional arousal, alternative interpretations—such as effects on attention at encoding that enhance both short- and long-term memory—are possible. In order to specifically implicate consolidation, the emotion effects must be augmented after a delay, as consolidation is defined as a time-dependent selective transfer of new information into long-term storage.

Phelps et al. (1998) presented a list of emotionally arousing and neutral words to amygdala-damaged patients, and recall was tested immediately and following a 1-hour delay. Control subjects showed different forgetting curves for the material over the delay interval, with a decline in memory for the neutral words but a relative increase in memory for the arousing words over time. In contrast, the patients forgot both classes of words at the same rate. Because the effect of emotion on memory was boosted over the delay in control subjects and the patient deficit was exacerbated following this delay, the results specifically implicate a

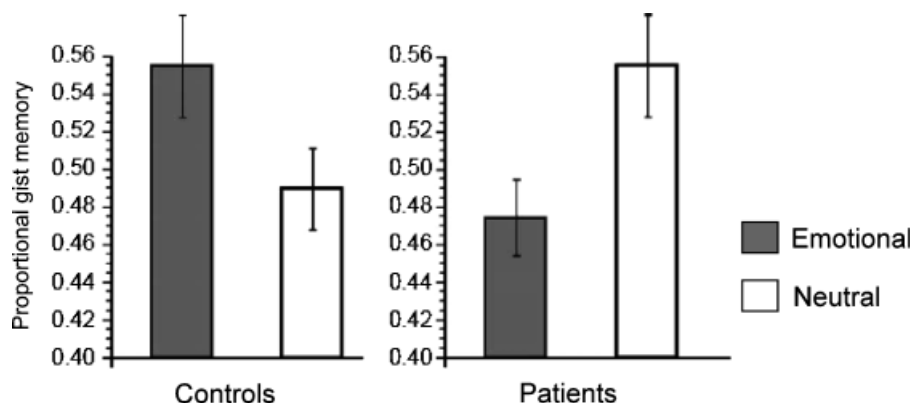
role for the amygdala in arousal-mediated memory consolidation.

But how does the amygdala influence memory circuits in the brain to achieve this retention boost? Dolcos, LaBar, and Cabeza (2004) showed participants pleasant, unpleasant, and neutral pictures while they underwent functional magnetic resonance imaging (fMRI), and participants recalled the pictures after scanning was completed. For each participant, brain activity during encoding was segregated into responses to pictures that were subsequently remembered versus those that were forgotten. Comparison of these activation patterns yields a neural marker for the successful encoding of items into long-term memory: the *Difference in memory (Dm) effect*. The Dm effect in the amygdala and other temporal lobe structures was larger for the emotionally arousing pictures than for the neutral pictures. In addition, the emotional Dm effects were highly correlated across different regions of the temporal lobe, indicating that the amygdala and other temporal lobe structures are functionally coupled during the successful encoding of emotional memories. What makes these fMRI analyses so intriguing is that they provide a glimpse into the momentary neural interactions that predict whether an item a participant is currently viewing will be remembered or forgotten on a subsequent memory test. Whether this fMRI activity is subject to pharmacological alterations that affect stress-hormone systems is an active topic of inquiry.

## FOCUSING OF EMOTIONAL MEMORIES

One account of the emotional-story findings discussed earlier is that the amygdala (and adrenergic engagement) normally focuses attention on material presented during the emotional segments of the story, which in turn foregrounds in memory this central thematic information (called *gist*) at the expense of background peripheral details. Adolphs, Tranel, and Buchanan (2005) tested this hypothesis by presenting amygdala-damaged patients with target items embedded in a series of either emotional or neutral pictures (Fig. 2). Gist and peripheral-detail memory were then tested for the targets as a function of the emotional-encoding manipulation. A narrowing of memory focus on gist information was found for the emotional-encoding condition in the control subjects but not in the patients. It is not yet clear whether central focusing occurs during the initial learning of the material or is a consequence of consolidation or retrieval, since the brain damage could have affected any one of these memory stages.

Focusing of memory on central information during emotional situations occurs in various real-world scenarios. In eyewitness testimony, memory is often focused on the weapons present at a crime scene at the expense of peripheral information such as the clothing worn by accomplices. In posttraumatic stress disorder (PTSD), patients sometimes report tunnel vision in their traumatic flashbacks, such that the memory contains a central event (e.g., detonating of a bomb) without contextual details. It will be



**Fig. 2.** Emotional focusing on central (gist) information in memory in normal controls as compared with patients with amygdala damage. Participants viewed target pictures embedded in neutral or emotional audiovisual story contexts. Recognition memory for central (gist) information and peripheral details in the target pictures was assessed after a 24-hour delay. (Memory for gist information is depicted as a proportion of the total memory score.) When target pictures were embedded in emotional contexts, control subjects (left) recognized more central than peripheral information, but patients with amygdala damage (right) recognized more peripheral than central information. The opposite pattern was found for target pictures embedded in neutral contexts. Adapted from “Amygdala Damage Impairs Emotional Memory for Gist But Not Details of Complex Stimuli,” by R. Adolphs, D. Tranel, & T.W. Buchanan, 2005, *Nature Neuroscience*, 8, p. 514. Copyright 2005, Nature Publishing Group. Adapted with permission.

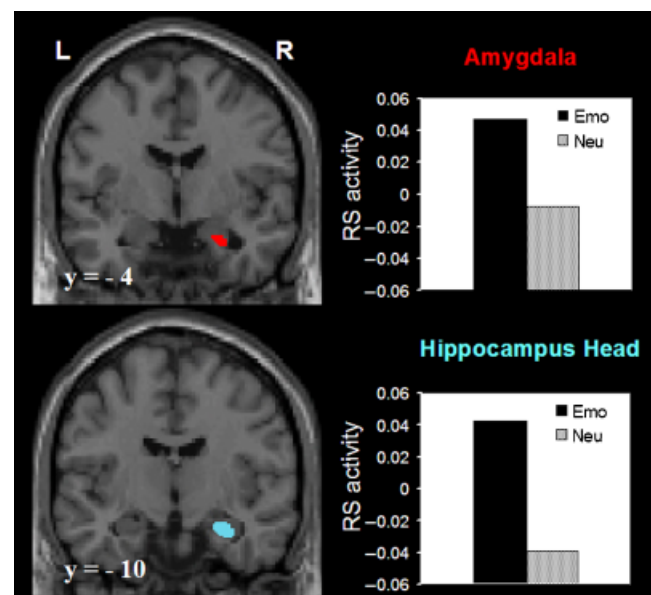
important to characterize with neuroimaging techniques the brain regions that focus memory under these circumstances.

#### BEYOND THE MEMORY MODULATION HYPOTHESIS: RETRIEVAL OF EMOTIONAL EXPERIENCES

McGaugh’s memory modulation hypothesis concerns consolidation mechanisms and does not postulate a critical role for the amygdala during the retrieval of emotional experiences. However, recent fMRI studies in humans suggest that this classic view of amygdala function may be incomplete. Smith, Henson, Dolan, and Rugg (2004) found greater activation in the amygdala and other structures when individuals accurately recognized neutral objects that were previously encoded in emotional picture contexts (both pleasant and unpleasant) relative to those encoded in neutral picture contexts. This pattern occurred despite the fact that only the neutral objects were presented during the recognition test. Thus, the amygdala participates in reinstating emotional contextual information during retrieval and/or links emotional changes signaled by other brain regions to specific retrieval cues.

Dolcos, LaBar, and Cabeza (2005) conducted an fMRI study of recognition memory 1 year after participants had been exposed to positive, negative or neutral pictures. For each participant, brain activity was segregated into responses to pictures that were accurately remembered versus those that were forgotten. Comparison of these activation patterns serves as a neural marker for the successful retrieval of items from long-term memory. In the amygdala and other temporal lobe regions, activity was enhanced for the successful retrieval of the emotional pictures (both positive and negative) relative to the neutral ones (Fig. 3).

This activity was correlated more strongly across the temporal lobe regions for the emotional pictures than it was for the neutral



**Fig. 3.** Contribution of the amygdala and hippocampus to successful retrieval of emotionally arousing pictures 1 year after encoding. Retrieval success (RS) is defined as a difference in blood-oxygen-level-dependent signal change for pictures that were successfully remembered versus those that were forgotten. In the right amygdala and head (forward) region of the hippocampus, RS activity was larger for emotional (Emo) compared to neutral (Neu) pictures. L = left hemisphere, R = right hemisphere. Reproduced from “Remembering One Year Later: Role of the Amygdala and the Medial Temporal Lobe Memory System in Retrieving Emotional Memories,” by F. Dolcos, K.S. LaBar, & R. Cabeza, 2005, *Proceedings of the National Academy of Sciences, USA*, 102, p. 2629. Copyright 2005, National Academy of Sciences. Reproduced with permission.

ones, implicating a tighter functional connectivity during successful emotional item retrieval than during neutral item retrieval.

fMRI studies of autobiographical memory confirm the engagement of similar brain areas during retrieval. For instance, Greenberg et al. (2005) showed that the retrieval of pleasant autobiographical memories in response to personally tailored cue words elicited activation of the amygdala, hippocampus, and frontal lobes. Activity in these regions was also more highly correlated during autobiographical retrieval than during the retrieval of general semantic knowledge. The findings indicate that the amygdala was functionally incorporated into a fronto-temporal memory network but only when experiences from the personal past were being retrieved.

An issue that is commonly raised with retrieval studies is whether the activation patterns reflect retrieval processes per se or whether instead they reflect the formation of new memories for the retrieval episodes. Although retrieval of prior events recapitulates activity in some brain areas that were active during the initial encoding of the events, the brain regions discussed here may make unique contributions to encoding and retrieval. For instance, amygdala activity signals successful retrieval of both emotional items and contexts, but during encoding its activity more strongly predicts emotional item memory (Kensinger and Schacter, 2006). Moreover, in the Dolcos et al. (2004, 2005) studies, the temporal lobe regions exhibited some hemispheric asymmetry as a function of memory stage within participants: Whereas the encoding effects were localized mainly in the left hemisphere, the retrieval effects were localized mainly in the right hemisphere. As discussed further below, the amygdala and hippocampus make selective contributions to some retrieval processes but not others, which would not be predicted according to an encoding-of-retrieval account.

Nonetheless, important questions regarding the amygdala's contribution to retrieval processes remain. For instance, does the amygdala engage neurohormonal systems to reconsolidate emotional events in memory when they are retrieved? The issue of memory reconsolidation is currently receiving intense scrutiny. If memories are always reconsolidated upon retrieval, then interventions that block the reconsolidation process may reduce the details available in subsequent retrievals of the same memory, including their emotional salience. For the treatment of PTSD and other affective disorders, blocking reconsolidation of specific memories would have immense clinical value but, at the same time, would raise ethical concerns.

### THE SUBJECTIVE EXPERIENCE OF EMOTIONAL REMEMBERING

Most studies attempt to reveal how emotional content alters the strength of memory traces. However, emotional memories are also distinctive in their phenomenological characteristics, including their vividness, one's sense of traveling back in time to

re-experience the contextual details of the memory (called *recollection*), and their physiologic changes that generate feeling states. Researchers have begun to explore how brain activity during retrieval relates to the subjective aspects of emotional remembering in ways that go beyond mere alterations in memory strength. For instance, amygdala and hippocampal activity during autobiographical memory retrieval correlates with subjective ratings of emotional intensity provided by the participants, even when the potentially confounding influence of event recency is controlled (Addis, Moscovitch, Crawley, & McAndrews, 2004; Daselaar et al., in press). When participants attempt to retrieve personal memories from generic cue words (e.g., *picnic*), fMRI activity in the amygdala begins before they have a fully-formed memory in mind (as indicated by a voluntary button press), and this activity predicts subsequent emotional-intensity ratings provided by the participants (Daselaar et al., in press). Therefore, the amygdala may use arousal information based on incomplete memory representations to help select memories during search attempts and to facilitate the retrieval of associated contextual information from other brain regions—which, in turn, leads to greater vividness and reliving as the memory unfolds in the mind.

Several experiments have contrasted the sense of recollection with the sense of *familiarity*, a form of retrieval in which the memory trace has little supporting contextual information. As a commonplace example, feelings of familiarity often occur when individuals are encountered outside of their typical social context. Emotionally arousing events are more likely to be retrieved with a sense of recollection than with a sense of familiarity, and the selective retention advantage for recollected memories has been linked to activity in the amygdala and hippocampus during the retrieval of emotional items and contexts (e.g., Dolcos et al., 2005). This line of work is catapulting the neurobiology of emotional memory into the realm of subjective aspects of recall, promising to unveil how the feelings that arise during personal life reflections are mediated neurally.

### OTHER EMOTIONAL MEMORY MECHANISMS

The cortical interactions and hormonal engagement by the amygdala are not the only means by which emotional experiences are remembered. Kensinger and Corkin (2004) found that another region of the frontal lobes interacts with the hippocampus to boost memory for less-arousing emotional stimuli and that this effect bypasses the amygdala. Valence-based effects in the absence of high arousal are thought to reflect semantic relatedness and other organizational benefits of emotion. For example, words that share emotional valence tend to be more semantically related than a random selection of neutral words, and this shared valence yields retention advantages. Amygdala-damaged patients can use semantic knowledge and other organizational strategies to improve memory for emotional material

under some circumstances—an important compensatory avenue in the face of impaired amygdala function.

### CONCLUSIONS AND FUTURE DIRECTIONS

More than just the brain's watchdog for detecting impending threat, the amygdala is now known to regulate various aspects of emotional learning and memory by interacting, both directly and indirectly, with memory-related regions of the frontal and temporal lobes. The effects of emotion appear at multiple stages of memory processing, and the same brain regions may make unique contributions at each of these stages. Traditional accounts of amygdala function as a facilitator of memory consolidation are being extended by contemporary approaches to include aspects of memory retrieval and the subjective experiences that occur during autobiographical recollection. Although this review highlighted emotional influences on long-term declarative memory, other memory systems are receiving increased attention, including working memory and procedural learning. Individual differences in emotional memory are being investigated at multiple levels of analysis—from the study of age and sex differences in brain activation to genetic variation of neurotransmitter receptors expressed in the relevant neural circuitry. Finally, while beneficial in many respects, emotion can impair memory under some conditions, including prolonged or intense stress, task-irrelevant emotional distraction, and anxiety and mood disorders. Studying these adverse consequences and identifying how emotion-regulation strategies and pharmacologic interventions ameliorate them will promote a fuller understanding of the emotional organization of memory.

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#### Recommended Reading

LaBar, K.S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, 7, 54–64.

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