



Reprint of: fMRI studies of successful emotional memory encoding: A quantitative meta-analysis[☆]

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ABSTRACT

Over the past decade, fMRI techniques have been increasingly used to interrogate the neural correlates of successful emotional memory encoding. These investigations have typically aimed to either characterize the contributions of the amygdala and medial temporal lobe (MTL) memory system, replicating results in animals, or delineate the neural correlates of specific behavioral phenomena. It has remained difficult, however, to synthesize these findings into a systems neuroscience account of how networks across the whole-brain support the enhancing effects of emotion on memory encoding. To this end, the present study employed a meta-analytic approach using activation likelihood estimates to assess the anatomical specificity and reliability of event-related fMRI activations related to successful memory encoding for emotional versus neutral information. The meta-analysis revealed consistent clusters within bilateral amygdala, anterior hippocampus, anterior and posterior parahippocampal gyrus, the ventral visual stream, left lateral prefrontal cortex and right ventral parietal cortex. The results within the amygdala and MTL support a wealth of findings from the animal literature linking these regions to arousal-mediated memory effects. The consistency of findings in cortical targets, including the visual, prefrontal, and parietal cortices, underscores the importance of generating hypotheses regarding their participation in emotional memory formation. In particular, we propose that the amygdala interacts with these structures to promote enhancements in perceptual processing, semantic elaboration, and attention, which serve to benefit subsequent memory for emotional material. These findings may motivate future research on emotional modulation of widespread neural systems and the implications of this modulation for cognition.

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Emotion influences multiple aspects of cognition, and the impact of emotion on memory processes has been particularly well studied. Emotion is known to modulate both non-declarative and declarative forms of memory (see LaBar & Cabeza, 2006 for a review). In particular, declarative memories for emotionally salient information tend to be enhanced relative to their neutral counterparts, marked by both improved memory accuracy for emotional information (Burke, Heuer, & Reisberg, 1992; Cahill et al., 1996;

Dolcos, LaBar, & Cabeza, 2004a; Dolcos, LaBar, & Cabeza, 2004b; LaBar & Phelps, 1998) as well as increased vividness of these memories (Dolcos, LaBar, & Cabeza, 2005; Ochsner, 2000; Sharot, Delgado, & Phelps, 2004; Sharot & Yonelinas, 2008). These enhancements are thought to arise from the beneficial influence of emotion on the initial encoding of a memory trace (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Dolcos et al., 2004a; Kensinger & Corkin, 2004) and its consolidation, or strengthening, over time (Hamann, Ely, Grafton, & Kilts, 1999; Kleinsmith & Kaplan, 1963; LaBar & Phelps, 1998; Ritchey, Dolcos, & Cabeza, 2008).

At the behavioral level, emotion has robust but complex effects on declarative memory. Memory enhancements can be driven by either the intensity of the stimulus' valence (how emotionally positive or negative it is) or its induced emotional arousal (see Kensinger, 2004 for a review). Arousal has an inverted-U relationship with memory, in that moderate levels of arousal lead to memory enhancements whereas very high levels lead to impairments (Liang, McGaugh, & Yao, 1990; Roozendaal, Nguyen, Power, & McGaugh, 1999). The impact of emotion on memory may also

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change depending on which features of the memorandum are tested. For example, it has been suggested that emotion differentially impacts the gist versus details of a memory (Burke et al., 1992; Heuer & Reisberg, 1992; Kensinger, Garoff-Eaton, & Schacter, 2006; Kensinger, Garoff-Eaton, & Schacter, 2007b). The influence of emotion on detailed memory may be further modulated by whether details are central versus peripheral to the emotionally salient features of the stimulus, leading to memory enhancements or impairments, respectively (Christianson & Loftus, 1991; Kensinger, Garoff-Eaton, & Schacter, 2007a; Loftus, 1979). Thus emotion influences memory encoding in a complex manner. For these reasons, further investigation into the cognitive and neural mechanisms that support these processes is warranted.

At the neural level, a wealth of evidence supports the participation of the amygdala and medial temporal lobes (MTL) in promoting emotional memory enhancements in both animals (McGaugh, 2004) and humans (Kensinger, 2004; LaBar & Cabeza, 2006) for reviews. Recently, human neuroimaging has afforded the opportunity to examine memory processes across the entire brain; thus, there is now emerging evidence regarding the distributed neural systems that support emotional memory encoding. These neuroimaging studies have largely focused on the enhancing effects of emotion on declarative memory formation. The present meta-analysis seeks to quantitatively integrate these results, with an emphasis on how transient activations during encoding predict enhanced memory for emotional information.

1. The critical role of the amygdala and MTL memory system

Within the behavioral neuroscience literature, the amygdala has been critically implicated in the acquisition of information about the spatial location, nature and intensity of threat signals in the environment using conditioning paradigms such as avoidance learning (Davis & Whalen, 2001). Other structures in the MTL, including the hippocampus and parahippocampal gyrus, have been more generally linked with declarative memories (Eichenbaum, Yonelinas, & Ranganath, 2007). The memory modulation hypothesis proposes that amygdalar projections to the MTL declarative memory system are critical for consolidating memories for emotionally arousing events (McGaugh, 2004). Within avoidance learning paradigms, pharmacological interventions affecting either the amygdala or MTL are capable of enhancing or mitigating enhancements in emotional memory, even when they occur during the post-acquisition consolidation period (Hatfield & McGaugh, 1999). It has been proposed that these effects are dependent on interactions between the amygdala and MTL, in which amygdalar inputs target the MTL during the formation of declarative memories, although these interactions may additionally be supported by bi-directional connections between the amygdala and MTL (Pape & Pare, 2010).

The amygdala has been repeatedly implicated in emotional memory encoding and consolidation in humans as well. In humans, individuals with damage to the amygdala are impaired relative to controls in declarative memory for arousing versus neutral stimuli (Adolphs, Cahill, Schul, & Babinsky, 1997; Cahill, Babinsky, Markowitsch, & McGaugh, 1995; Phelps et al., 1998). Consistent with these findings, in healthy subjects amygdala activity during encoding correlates with one's ability to retrieve emotional but not neutral memories (Cahill et al., 1996; Hamann et al., 1999). Early PET and fMRI studies were limited to blocked-design analyses, which provide limited information about the neural systems underlying emotional memory encoding. Because these analyses tested across-subject effects that predicted individual differences in emotional memory, they may be confounded with general dif-

ferences in the perceptual properties of emotional memoranda, in encoding orientation, or in participants' reactivity to emotional stimuli. Over the past decade, event-related fMRI has been utilized to identify encoding success activity (ESA) for emotional memoranda by using subsequent memory paradigms (as reviewed by Paller & Wagner, 2002). These paradigms explicitly test the difference between encoding activity time-locked to stimulus onset for subsequently remembered (hits) and forgotten (misses) items by back-sorting fMRI data according to participants' behavioral performance during later memory retrieval. Thus, these analyses better provide a measure of transient changes in brain activity that predicts successful memory encoding on an item-by-item basis. Using this technique, the amygdala has been repeatedly shown to exhibit greater ESA for emotional than neutral memory (LaBar & Cabeza, 2006).

The relationship between the amygdala and MTL structures has also been investigated in humans. In parallel with animal studies indicating that co-activation of the hippocampus and amygdala is critical to emotional memory formation, neuroimaging results have also shown enhanced functional connectivity between the amygdala and memory-related regions during encoding of emotional information (Dolcos et al., 2004b; Hamann et al., 1999; Kensinger & Corkin, 2004; Kilpatrick & Cahill, 2003; Murty et al., 2009; Ritchey et al., 2008; St Jacques, Dolcos, & Cabeza, 2009). The localization of these findings has varied across papers, with some enhancements linked to the hippocampal formation (Dolcos et al., 2004b; Hamann et al., 1999; Kensinger & Corkin, 2004; Murty et al., 2009; St Jacques et al., 2009) and others to the surrounding cortical MTL, including entorhinal and perirhinal cortices in anterior MTL (Dolcos et al., 2004b; Hamann et al., 1999; Ritchey et al., 2008) and parahippocampal cortex in posterior MTL (Kilpatrick & Cahill, 2003). Critically, a neuroimaging study investigating emotional memory encoding in patients with MTL lesions demonstrated that reciprocal connections between the amygdala and MTL were necessary to produce emotional memory enhancements (Richardson, Strange, & Dolan, 2004). Although these findings stem from fMRI data from the encoding period, they have often been interpreted as reflecting the initiation of consolidation processes that unfold over time (Hamann et al., 1999; Ritchey et al., 2008), in line with the modulation hypothesis (McGaugh, 2004). Beyond this evidence for MTL-amygdala interactions, findings regarding the MTL memory system's specific role in emotional memory have been more varied. In one study, ESA within the anterior hippocampus and entorhinal cortex was reported to be greater for emotional than neutral stimuli (Dolcos et al., 2004b), but other studies have reported that this memory-related activity is shared equally across emotional and neutral stimuli (Cahill et al., 1996; Hamann et al., 1999; Kensinger & Corkin, 2004).

2. Beyond the amygdala and MTL: emotional memory effects across the brain

The majority of fMRI studies regarding the neural correlates of emotional memory formation have focused on interactions between the amygdala and MTL memory system. However, emotion is known to affect many facets of cognition. The amygdala itself is highly interconnected with the rest of the brain (Young, 1993), modulating processing networks which may, in turn, guide memory formation. For example, retrograde tracing studies have revealed direct feedback pathways from the amygdala to the ventral visual pathway (Amaral, Behniea, & Kelly, 2003). This anatomical relationship between emotional and visual processing is bolstered by a wealth of data detailing emotional enhancements on activation in visual areas and perceptual encoding (Dolan & Vuilleumier, 2003; Vuilleumier & Pourtois, 2007).

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