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Reconciling Opposing Effects of Emotion on Relational Memory: Behavioral, Eye-Tracking, and Brain Imaging Investigations

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The effects of emotion on memory are wide-ranging and powerful, but they are not uniform. Although there is agreement that emotion enhances memory for individual items, how it influences memory for the associated contextual details (relational memory, RM) remains debated. The prevalent view suggests that emotion impairs RM, but there is also evidence that emotion enhances RM. To reconcile these diverging results, we carried out three studies incorporating the following features: (1) testing RM with increased specificity, distinguishing between *subjective* (recollection based) and *objective* (item–context match) RM accuracy, (2) accounting for emotion–attention interactions via eye-tracking and task manipulation, and (3) using stimuli with integrated item–context content. Challenging the prevalent view, we identified both enhancing and impairing effects. First, emotion enhanced subjective RM, separately and when confirmed by accurate objective RM. Second, emotion impaired objective RM through attention capturing, but it enhanced RM accuracy when attentional effects were statistically accounted for using eye-tracking data. Third, emotion also enhanced RM when participants were cued to focus on contextual details during encoding, likely by increasing item–context binding. Finally, functional magnetic resonance imaging data recorded from a subset of participants showed that emotional enhancement of RM was associated with increased activity in the medial temporal lobe (MTL) and ventrolateral prefrontal cortex, along with increased intra-MTL and ventrolateral prefrontal cortex–MTL functional connectivity. Overall, these findings reconcile evidence regarding opposing effects of emotion on RM and point to possible training interventions to increase RM specificity in healthy functioning, posttraumatic stress disorder, and aging, by promoting item–context binding and diminishing memory decontextualization.

Public Significance Statement
This research demonstrates the importance of a novel way of conceptualizing and measuring associative memory and of accounting for effects of attention in emotion–memory interactions. Our findings challenge the status quo view that emotion impairs relational memory and clarify the conditions in which emotion enhances memory for contextual details associated with distressing stimuli. These results provide strong premises for game-changing approaches in the quest for identifying ways to improve learning and well-being when facing stressors in healthy functioning, as well as to alleviate emotion and memory deficits in emotional disorders and reduce memory declines observed in healthy and clinical aging.

Keywords: arousal, associative memory, contextual memory, recollection, functional magnetic resonance imaging

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Paul C. Bogdan and Florin Dolcos share first authorship. None of the present core research ideas or findings have been previously published. Some of the findings have been included in conference presentations (with abstracts and/or titles published in the associated programs), as follows: (a) the 2022 annual meeting of the Cognitive Neuroscience Society, (b) the 2022 annual meeting of the Memory Disorders Research Society, (c) the 2023 annual meeting of the International Society for Behavioral Neuroscience, and (d) the 2024 annual meeting of the Cognitive Neuroscience Society in a symposium chaired by Florin Dolcos.

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Emotions influence many aspects of our lives, and perhaps their most consequential and far-reaching effects are those related to their impact on memory. For example, emotion–memory interactions determine what situations individuals may pursue or avoid and what experiences they will think/ruminate about. Involuntary retrieval of negative information is at the root of many clinical conditions, such as posttraumatic stress disorder (PTSD), depression, and anxiety (Desmedt et al., 2015; Stramaccia et al., 2021; Sutherland & Bryant, 2007). However, open questions remain, particularly about how emotion influences different aspects of memory. In particular, although it is widely accepted that emotion enhances item memory, its effects on relational memory (RM) are less clear (F. Dolcos et al., 2017; Mather & Sutherland, 2011; Yonelinas & Ritchey, 2015). Some studies report enhancing effects (Madan et al., 2019, 2020), others report impairing effects (Bisby & Burgess, 2014; F. Dolcos et al., 2017; Petrucci & Palombo, 2021), and yet others find no effects (Pereira et al., 2021a; Symeonidou & Kuhlmann, 2022). The main goal of the present research was to reconcile evidence regarding the impact of emotion on RM in a series of behavioral, eye-tracking, and brain imaging investigations, incorporating the following design features: (a) increased specificity in testing RM, (b) accounting for emotion–attention interactions, and (c) using stimuli with integrated item–context content.

Emotion–Memory Interactions: Behavioral Effects

The beneficial impact of emotion on memory for personal events (episodic memory) has been consistently demonstrated during the last few decades (F. Dolcos et al., 2017; LaBar & Cabeza, 2006; Murty et al., 2011). Consistent with anecdotal and scientific evidence that emotion enhances memory, we and others have shown that this memory-enhancing effect of emotion is linked to *arousal*, although *valence*-related differences (positive vs. negative) have also been identified (F. Dolcos & Cabeza, 2002; F. Dolcos et al., 2004a; Kensinger, 2004, 2009; Kensinger & Corkin, 2004; Kensinger & Schacter, 2006; Mickley & Kensinger, 2008). This emotional memory enhancement effect has been attributed to modulatory influences occurring during encoding and early stages of consolidation, although there is also evidence implicating retrieval processes (F. Dolcos et al., 2004a, 2004b, 2005; McGaugh, 2004; Roozendaal & McGaugh, 2011). Processing of emotional information is prioritized by attention and also interacts with working and semantic memory processes—for example, emotional experiences stick longer to our mind and benefit from deeper semantic processing (F. Dolcos et al., 2004a; Dunsmoor et al., 2022; Mather & Sutherland, 2011; Öhman et al., 2001). Given that all these aspects boost memory, it is not surprising that they also contribute to further memory enhancements when augmented by emotion. Notably, there is also evidence that emotional memory is susceptible to modulation by the engagement of emotion control strategies that can up- or downregulate the impact of emotion on perception and memory (Dillon et al., 2007; F. Dolcos, Katsumi, Bogdan, et al., 2020; Y. Katsumi & Dolcos, 2020; S. H. Kim & Hamann, 2012).

Additional evidence regarding emotion–memory interactions provides more nuance to the general enhancing effects mentioned above, such as regarding the impact of emotion on memory for central versus peripheral aspects of events (Kensinger et al., 2007; Riggs et al., 2011; Touryan et al., 2007). Consistent with the idea that emotion captures attention (Öhman et al., 2001; Pessoa, 2005; Vuilleumier et al., 2001), there is evidence of enhanced memory for details that are central to emotional stimuli/items (item memory) at the expense of memory for peripheral details or for the associated contextual details (RM). This and related research typically use pairs of item–context pictures shown side by side or one picture on top of the other and reveals enhanced memory for the emotional items alone but reduced memory for emotional–neutral pairs relative to neutral–neutral pairs (Bisby & Burgess, 2014; Bisby et al., 2016, 2018; Caplan et al., 2019; Madan et al., 2017). However, such designs may be susceptible to memory interference due to attention, given that negative stimuli can downregulate processing of nearby information. This explanation for emotional impairment of RM

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remains debated, and some studies claim that attention does not fully account for reduced associative memory in emotional situations (Bisby et al., 2018). Nonetheless, the idea is consistent with the arousal-biased competition theory, positing enhanced perception for emotional items, which have privileged access to processing resources, but impaired memory for the associated contextual details, whose processing is less prioritized (Mather & Sutherland, 2011). Accordingly, it too predicts enhanced memory for emotional items, which have privileged access to processing resources, but impaired memory for the associated contextual details, whose processing is less prioritized.

Importantly, in extreme circumstances, this biased processing of emotional information is also purportedly responsible for symptoms of memory *de*contextualization caused by trauma (Al Abed et al., 2020; Bisby et al., 2020). The extreme emotional arousal of traumatic events leads to powerful, but gist-based, memories (F. Dolcos et al., 2013; Hayes et al., 2011) for the highly distressing central details (e.g., the weapon of an assailant) that are accompanied by poor recollection of related contextual details (e.g., the face of the assailant using the weapon). This memory *de*contextualization, or rupture between memories for central components (item memory) and memory for the associated contextual details (RM), is posited to explain intrusive recollection of memories for traumatic events outside of their initial context. Such memories can be triggered by seemingly neutral cues (e.g., the noise of a backfiring car can trigger memories of a highly distressing combat event in war veterans; Bisby & Burgess, 2017; Brewin et al., 2010; Desmedt et al., 2015). Due to their intrusive nature, these recollections are the cause of dysfunctions and difficulties in reintegration upon returning to civilian life (Shor et al., 2022; Worthen & Ahern, 2014).

Despite accumulating evidence supporting this view, there is also evidence that emotion enhances RM, but the circumstances in which emotion enhances or impairs RM are an issue of ongoing debate (Bisby & Burgess, 2017; F. Dolcos et al., 2017). Across three studies involving behavioral (Studies 1–3) and brain imaging data (Study 3), the present research aimed to reconcile diverging evidence on emotional RM, by considering the following design features: (a) increased specificity in testing RM, distinguishing between and linking *subjective* and *objective* RM accuracy, (b) accounting for emotion–attention interactions via eye-tracking and task manipulation, and (c) using stimuli with integrated item–context content. Regarding *RM specificity*, unlike the evidence mentioned above, several studies using item–context composite images during encoding found that emotion enhances RM tested for the item–background pairs (Madan et al., 2020; Mickley Steinmetz et al., 2016; Ventura-Bort, F. Dolcos, et al., 2020; Ventura-Bort, Wendt, et al., 2020). As discussed below, the level of integration between item and context may also influence the impact of emotion on RM, but factors other than the nature of stimuli may also influence the impact of emotion on RM. One such factor is the type of retrieval task, which may influence the specificity of retrieval when testing RM—for instance, evidence suggests that emotion enhances cued recall, but not cued recognition (F. Dolcos & Cabeza, 2002; F. Dolcos et al., 2004a; Madan et al., 2020; see also Mickley Steinmetz et al., 2016; Oyarzún & Packard, 2012). This highlights the importance of testing specificity in determining whether emotion enhances or impairs RM.

Aside from the studies that tested the impact of emotion using typical RM paradigms, there is also evidence from studies of item memory that is consistent with the idea that emotion enhances RM. For instance, studies by Dolcos and collaborators using free and cued recall during retrieval (F. Dolcos & Cabeza, 2002; F. Dolcos et al., 2004b) found enhanced memory for emotional pictures relative to neutral ones. Although, technically, these tasks tested memory for emotional and neutral items, again, it was the specificity of details (provided in writing) that were used to determine whether the pictures were correctly recalled or not (e.g., green snake on tree, open mouth, facing viewer). Importantly, emotional pictures were recalled with increased specificity, even though they were equated with the neutral ones in terms of complexity and the richness of specific details available. Similarly, studies testing cued recognition of emotional and neutral items with increased specificity also point to increased RM by emotion (F. Dolcos et al., 2005; Phelps & Sharot, 2008; Ritchey et al., 2008; Sharot et al., 2004). Namely, unlike the studies mentioned above where RM was impaired by emotion (reviewed in Bisby & Burgess, 2017), which involved simpler old/new decisions during the recognition of emotional and neutral items, such studies used the Remember/Know (R/K) task, which emerged from the pioneering work by the late Endel Tulving distinguishing between Recollection and Familiarity (Tulving, 1985). In this task, recollection-based responses (*R*) indicate that participants both recognize the item as old and remember specific contextual details (what, when, where) from encoding (see the Methods section). In contrast, familiarity-based responses (*K*) indicate that the participants recognize that they saw particular stimuli during encoding but cannot retrieve any specific contextual associations, as implied by definitions of RM (see research on the dual process model; Cohen et al., 1997; Moscovitch et al., 2006; Renoult et al., 2019; Yonelinas, 2001). Again, this highlights the importance of specificity when measuring aspects of RM to determine whether emotion enhances or impairs it.

This evidence also points to the need to distinguish between *subjective* and *objective* forms of RM. Specifically, Remember responses reflect RM, as they require connections between an item and other pieces of information, but it is a *subjective* measure of RM because it is not clear what specific contextual details participants remember. This is because the contextual details that participants use to make the *R*-based responses are not available to the experimenters. On the contrary, the studies discussed earlier, asking participants to identify the item–context pairs, measure *objective RM* because they assess participants' ability to distinguish between original and recombined item–context pairs (Bisby & Burgess, 2017; Madan et al., 2020; Mao et al., 2017; Mickley Steinmetz et al., 2016; Ventura-Bort, Dolcos, et al., 2020; Ventura-Bort, Wendt, et al., 2020). Based on this dissociation, a pattern of findings emerges in the literature, in which emotion enhances subjective RM but impairs objective RM. However, this idea has not been systematically tested (but see the study by Rimmele et al., 2011), and thus the present research assessed the impact of emotion on both subjective and objective RM.

Importantly, this conceptualization of recollection and RM does not fundamentally diverge from typical perspectives on these topics. Traditionally, RM has been defined as measuring connections between two or more pieces of information, so that the activation of one informational node leads to the activation of the corresponding associated node(s) (Eichenbaum et al., 1992). This concept is intimately tied to the idea of recollection, which is generally thought of as the retrieval of the *experience of* encountering a given stimulus (Tulving, 1985). In other words, recollection entails not just recognizing that a stimulus was previously encountered but also retrieving specific contextual associations regarding when/where the stimulus was previously encountered (Cohen et al., 1997). Hence, the present framing is precisely consistent with the early literature introducing these notions, along with contemporary studies that have likewise conceptualized recollection in terms of retrieving contextual RM (e.g., Butterworth et al., 2023; Dimsdale-Zucker et al., 2022; F. Dolcos et al., 2005; Frithsen et al., 2019; Sadeh et al., 2018; Wais et al., 2010; Yonelinas et al., 2010).

It should be noted that there can be various degrees of subjectivity associated with the R/K task, in the emotional memory literature. For instance, Sharot et al. (2004) reported a purely subjective enhancement effect of emotion on recollection because it enhanced the "feeling of recollection," wherein participants reported higher rates of *R*-based responses to emotional stimuli. However, in that study emotion did not actually enhance the accuracy of *R*-based responses. Here, similar to other reports (e.g., F. Dolcos et al., 2005), we focused on accurate *R* versus *K* responses, consistent with the way this task is typically used in the memory literature. Yet, as argued above, subjectivity is still present because the associated details that inform participants' decisions (albeit accurate) are not available to the experimenter. It is also possible that the said associations may not exactly match the participants' experience from encoding, even if they inform accurate *R*-based responses. The subjectivity can be further reduced if participants are also able to accurately produce the relational details that informed their *R*-based decisions. However, we argue that a certain level of subjectivity still remains, given the nature of the task asking participants to distinguish between *K* and *R* responses, based on whether they just have the feeling of familiarity with memory probes or they can also retrieve specific associated details (including about their own subjective reaction to the stimuli during encoding), which could then also be assessed more objectively with follow-up assessments. Given these, we use the term "subjective RM" in a relative (yet, informative) way, in the context of complementing the R/K task with a more objective task assessing RM based on identifying item–context matches. As discussed below, this relative dichotomic combination of tasks captures more comprehensively the richness of RM than any of the two approaches alone. Future studies should further investigate the link between the impact of emotion on memory performance in R/K tasks with varying degrees of subjectivity and accuracy in tasks assessing objective RM.

Measuring subjective and objective RM together permits a more comprehensive assessment of RM and better captures the complexity of episodic memory. Specifically, testing subjective RM, with the R/K test, captures how processing an item can be accompanied by the activation of connected informational representations, which is a defining feature of RM (Eichenbaum et al., 1992). As detailed in the Methods section, the present study also adapted the R/K to capture RM aspects that the traditional R/K tasks do not, by presenting participants with only portions of an image (instead of whole pictures) and encouraging them to retrieve associated contextual details from encoding (including other elements of the picture). One limitation of the R/K test for investigating RM is that Remember responses do not solely reflect retrieval of associations but also depend on item memory, as suggested by evidence of correlations between item memory accuracy and R-based responses (Dobbins et al., 2000; Dunn, 2004). Nevertheless, when used together with an objective measure of RM, as employed here, the R/K test allows for a more complete assessment of emotion's effects on RM. This design also permits the investigation of possible links between these two measures of RM (e.g., to see if accuracy in the subjective RM is confirmed by objective RM accuracy). Hence, measuring both subjective and objective RM captures more fully the complexity of episodic memory, thus compensating for their individual limitations.

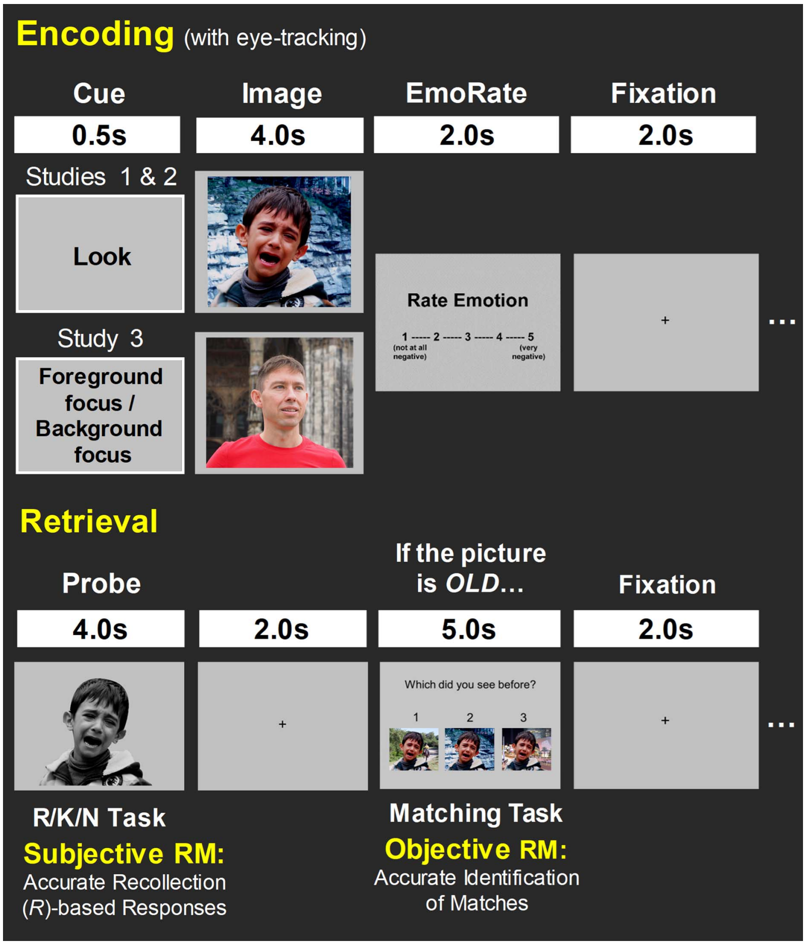
The R/K test allows a more specific assessment of emotion's effects on memory retrieval. That is, unlike the typical old/new recognition tasks that capture only general item memory, the R/K task specifically distinguishes between memory for items accompanied by subjective RM (i.e., recollection/*R*-based responses) from memory for items without RM (i.e., familiarity/*K*-based responses; Yonelinas, 1994, 2001; Yonelinas et al., 2010). This is particularly the case for the present study's implementation of the R/K task (see Figure 1 and the Methods section), and this dissociation can be investigated at both behavioral and brain imaging levels. Although previous research has not yet systematically examined emotion's impacts on subjective and objective RM together, the study by Rimmele et al. (2011) deserves to be noted, as it employed the R/K task and also measured objective RM. This study showed that emotion yielded higher rates of Remember responses, which were followed by increased rates of objective RM misses. However, the study did not account for attention nor employ integrated stimuli, which bear relevance for understanding the differential effects of arousal on various aspects of episodic memory.

Regarding the *role of attention*, although impaired RM by emotion may be attributable to the attention-capturing effects of emotion, studies supporting the prevalent view did not record or manipulate participants' eye movements to investigate this possibility. Indeed, emotional information tends to capture attention (Öhman et al., 2001), which in turn can lead to enhanced memory for central aspects at the expense of memory for peripheral/contextual details (Kensinger et al., 2007; J. S. Kim et al., 2013; Riggs et al., 2011; Steinmetz & Kensinger, 2013). This suggests an indirect effect of emotion, which can disrupt RM via increasing fixation on specific emotional aspects of the stimuli, as suggested above. Hence, it is important to assess such effects using eye-tracking and task manipulations that can enhance or reduce the impact of attention-related effects—for example, by instructing participants which aspects of the stimuli to attend (item/foreground vs. context/background; F. Dolcos et al., 2022; F. Dolcos, Katsumi, Shen, et al., 2020). However, such manipulations of experimental conditions or instructions have not been used in conjunction with measures of visual attention to distinguish between attention-related and other factors influencing RM. With this focus, it is also important to distinguish between objective and subjective RM, given the evidence showing that negative emotion's impact on the latter, as measured in free recall tests, is independent of attention (Talmi et al., 2007). Therefore, another main goal of the present research was to clarify the impact of emotion on objective RM specifically by measuring and accounting for the effects of attention.

Finally, regarding *stimulus integration*, consistent with the idea that emotion can bind together central and contextual details of events into unified representations (Chiu et al., 2013), studies reporting an enhancing effect of emotion on RM have often used integrated stimuli. Aside from using stimuli with semantically and perceptually connected elements (e.g., realistic foreground–background pairings; Madan et al., 2020; Mickley Steinmetz et al., 2016; Ventura-Bort,

Figure 1

Diagram of the Encoding and Retrieval Tasks



Note. During encoding, participants viewed emotional and neutral images and then rated their reactions to them. Studies 1 and 2 (free viewing) did not involve any cueing about where to focus attention, whereas in Study 3 participants were cued to focus either on (foreground focus) or away from (background focus) the emotional content of stimuli. In all studies, the foreground was either negative or neutral, whereas the background was always neutral, and participants were not informed that their memory would be tested (incidental learning). During retrieval, for all studies, subjective RM was first tested, and then for all images initially shown during encoding, objective RM was also tested. Notably, the recollection-based responses in the R/K task reflect subjective RM, because participants are asked to make them only if they can remember specific contextual details associated with the items viewed during encoding. This is different from previous RM studies, in which participants made less specific old/new responses to items. Moreover, unlike previous studies, the present design also allowed probing the link between subjective and objective RM (i.e., to test if subjective RM accuracy is confirmed by objective RM accuracy). Functional magnetic resonance imaging data were also recorded during encoding in Study 3. RM = relational memory; R/K/N = Remember/Know/New. Adapted with permission from "The Impact of Focused Attention on Emotional Experience: A Functional MRI Investigation," by F. Dolcos, Y. Katsumi, C. Shen, P. Bogdan, S. Jun, R. Larsen, W. Heller, K. Freeman Bost, & S. Dolcos, 2020, *Cognitive, Affective, & Behavioral Neuroscience*, *20*, pp. 1011–1026 (https://doi.org/10.3758/s13415-020-00816-2), Copyright 2020 by Springer Nature, and "The Impact of Focused Attention on Subsequent Emotional Recollection: A Functional MRI Investigation," by F. Dolcos, Y. Katsumi, P. C. Bogdan, C. Shen, S. Jun, S. Buetti, A. Lleras, K. F. Bost, M. Weymar, S. Dolcos, 2020, *Neuropsychologia*, *138*(10), p. 3 (https://doi.org/10.1016/j.neuropsychologia.2020.107338), Copyright 2020 by Elsevier. See the online article for the color version of this figure.

Dolcos, et al., 2020; Ventura-Bort, Wendt, et al., 2020), integration can also be promoted through instructions that facilitate binding (e.g., instructing participants to imagine that an object is part of a background scene; Bogdan, Dolcos, Federmeier, et al., 2023; Ventura-Bort et al., 2016). Indeed, semantic relatedness among aspects of the memoranda is relevant to RM, and emotional stimuli tend to have increased semantic cohesiveness compared with neutral stimuli (Badham et al., 2012; Barnacle et al., 2021; Caplan et al., 2019; Phelps et al., 1997). Moreover, emotional–neutral pairs, as a whole, are less semantically related than neutral–neutral pairs, which may explain impaired RM for the emotion–neutral pairs and can confound the impact of emotion on RM if the semantic item–context integration is not controlled for (Barnacle et al., 2021). This is consistent with theoretical work, such as the object-based framework by Mather (2007), which posits that emotion enhances memory for information perceived to be part of the same object. This framework is based, in part, on evidence of how specific features of emotional stimuli, such as their color or location, are better retrieved than features of neutral stimuli (D'Argembeau & Van der Linden, 2004; Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003). Because the realistic nature and ecological validity of stimuli are essential aspects to consider, we developed composite pictorial stimuli with distinguishable but integrated item–context features.

Neural Correlates of Emotion–Memory Interactions

Neuroscientific data are invaluable for understanding the effects of emotion on memory and can inform cognitive interpretations of behavioral data. During the last few decades, overwhelming evidence has been accumulated regarding the neural correlates associated with the impact of emotion on episodic memory. Using task-related functional magnetic resonance imaging (fMRI), we and others have shown that the memory-enhancing effect of emotion is linked to the engagement of neural mechanisms involving interplays among cortical and subcortical brain regions (F. Dolcos et al., 2004b; Murty et al., 2011; Sharot et al., 2004). An influential hypothesis in the field—the "modulation hypothesis"—highlights the contribution of medial temporal lobe (MTL) structures involved in emotion processing (amygdala, AMY) and memory (hippocampus, HC, and the associated parahippocampal cortices, PHC), linking the memory enhancement by emotion to modulatory influences of AMY on HC activity, during encoding and early stages of consolidation (McGaugh, 2004). Aside from this direct mechanism, involving cortical and subcortical MTL structures, evidence also points to a mediated mechanism, involving indirect influences through cortical structures associated with various aspects of processing that contribute to the memory-enhancing effect of emotion (F. Dolcos et al., 2017; LaBar & Cabeza, 2006). Specifically, linked to their role in semantic memory, working memory, and attention, evidence points to a role of ventral and dorsal lateral prefrontal cortices (vlPFC, dlPFC), as well as parietal cortical areas, respectively.

The MTL mechanisms mentioned above also contribute to enhanced subjective RM by emotion, which is associated with agonistic/synergistic AMY–HC interactions (F. Dolcos et al., 2005; F. Dolcos, Katsumi, Bogdan, et al., 2020; Sharot et al., 2004). However, impaired RM by emotion is associated with antagonistic AMY–HC interactions, as shown by evidence that AMY activation during encoding predicts lower RM accuracy and reduced HC activity (Bisby & Burgess, 2017; Bisby et al., 2016). These findings are consistent with the emotional binding account by Yonelinas and Ritchey (2015), who posit that enhanced item memory by emotion is linked to interactions between the AMY and other MTL regions associated with memory for items (perirhinal cortex [PRC]), whereas reduced persistence of emotional RM is linked to reduced HC involvement during item–context binding. This interpretation is consistent with the attentional account mentioned above regarding the opposing effects of emotion on item memory versus RM, whereby focusing on emotional aspects facilitates item–emotion binding, at the expense of item–context binding. Relatedly, narrower attention predicts decreased HC activation (Voss et al., 2017), which may explain why some studies show impaired HC activity by emotion (for elaboration on this reasoning, see Voss et al., 2017). However, no previous study has investigated the role of MTL regions in the impact of emotion on subjective versus objective RM and on the link between them or accounted for attentional effects. Finally, outside the MTL, prefrontal cortex (PFC) areas also play a role in emotional modulation of memory, and their involvement is typically linked to top–down effects (F. Dolcos et al., 2017; Etkin et al., 2011). For instance, activity in both vlPFC and dlPFC regions during encoding predicts enhanced emotional memory (F. Dolcos et al., 2004a; Murty et al., 2011; Schümann & Sommer, 2018). Moreover, the involvement of the vlPFC in recollection (Ranganath et al., 2003) identifies this region as a particular target in the investigation of subjective RM, but no previous study has investigated its role in the impact of emotion on subjective versus objective RM and the link between them.

The Present Research

To address the open questions highlighted above, the present research measured and manipulated attention-related effects during encoding of composite pictorial stimuli with integrated item–context content. Additionally, the retrieval tasks allowed for increased specificity in measuring the impact of emotion on subjective RM, objective RM, and the link between them (Figure 1). In separate studies, participants were either asked during encoding to freely view composite emotional and neutral pictures (Studies 1 and 2) or were cued by an instruction screen to focus on foreground (FG) or background (BG) aspects of the images (Study 3). After viewing each image, participants rated their emotional experience on a 5-point scale (1 = *not at all negative*; 5 = *very negative*). During encoding, Studies 1 and 2 recorded eye-tracking data to account for eye movements, and Study 3 also recorded fMRI data. Each study used the same retrieval procedures with a retention interval of 3–7 days. During retrieval, participants first completed a Remember/Know test for memory of the emotional and neutral foregrounds, which probed item memory and *subjective* RM. Then, similar to previous RM studies, participants were also asked to identify the exact item–context combinations that they saw during encoding, based on being shown the original and recombined versions of all old composite pictures (*objective* RM).

Unlike previous studies, this combined task allowed for the specific assessment of subjective and objective RM, both separately and linking them. Regarding the latter, the present design specifically allowed us to test the possibility that emotion does not just enhance the likelihood of subjective RM (F. Dolcos, Katsumi, Bogdan, et al., 2020) but also increases the likelihood of accurate subjective and objective RM together. Given that emotion enhances item memory, to examine its effects on subjective RM specifically, analyses focused on R versus K comparisons and also incorporated measurements from an objective RM test. The latter was measured right after via a forced-choice recognition test by asking participants to identify the item–context combinations that they saw during encoding (Figure 1). The assessment of attentional effects, linked to both natural scanning paths of visual pictorial stimuli and to cued manipulations of attentional focus (on or away from the emotional content of images), allowed us to account for effects of attention (both statistically and through task manipulation) in the impact of emotion on RM. Finally, recording fMRI data allowed investigation of the associated MTL and PFC mechanisms, with the expectation that enhanced RM by emotion would be associated with agonistic/synergistic engagement of AMY and HC, with possible additional top–down influences from the PFC.

Study 1

In Study 1, we tested the pattern emerging in the literature mentioned above, whereby emotion enhances subjective RM but impairs objective RM. As mentioned above, this hypothesis has not been systematically tested in the literature. This was done here by directly comparing these effects within the same sample of participants. Importantly, increased comprehensiveness in measuring RM also allowed us to test the possibility that emotion does not just enhance the accuracy of subjective RM (F. Dolcos, Katsumi, Bogdan, et al., 2020) but also increases the likelihood of being confirmed by accurate objective RM. To test this prediction, analyses compared the effect of emotion on recollection-based (item memory with RM) versus familiarity-based (item memory without RM) accuracy. Along with investigating this novel area, this study is also the first to statistically account for attention-related effects in measuring objective RM, based on recording eye-tracking data.

Method

Participants

Twenty-nine in-person participants recruited from a local university (62% female, 38% male; $M_{\text{age}} = 19.7$, $SD_{\text{age}} = 1.30$; 31% White, 38% Asian, 21% Hispanic, 10% Black) completed the encoding and retrieval tasks for this study (no exclusions). Information regarding the participants' sexes was collected by simply asking participants to state their sex. Ethnicity was assessed by asking participants to select from among five options, "Asian or Pacific Islander," "Black," "First Nations origin," "Hispanic," or "White, not of Hispanic origin"; for each option, a brief description was provided. Similar procedures were used for Study 2, with slight differences noted (see example below), and Study 3 used identical procedures to those from Study 1. For instance, for Study 2 (replication study), participants were provided with the following response options assessing gender: "Male," "Female," "Other," or "Prefer not to say." The sample size was motivated by related studies on emotional RM (e.g., Dunsmoor et al., 2019; Madan et al., 2020), and replication of the findings was tested in Study 2, involving a larger sample. All participants provided informed consent under a protocol approved by the institutional review board (IRB) and received course credit. Below, we report the variables we collected via our tasks; see also Supplemental Material 1—Questionnaires, which details a list of questionnaires collected to assess individual differences, although these are not analyzed here. The present studies were not preregistered.

Procedure

Encoding Task. As illustrated in Figure 1, composite images (60 negative and 30 neutral) were presented one at a time, and participants were instructed to look at each of them naturally and then rate their emotional response to each picture. No specific instructions about how to scan the pictures were provided. Composite images were created by overlaying negative or neutral FG components upon visually complex neutral BGs (the proportions of FG and BG areas were about 50%/50%), with FGs and BGs carefully selected so that the two components formed an integrated image. The FG and BG components were extracted from freely available online sources and affective picture databases, including the International Affective Picture System (Lang et al., 1997), Geneva Affective Picture Database (Dan-Glauser & Scherer, 2011), Military Affective Picture System (Goodman et al., 2016), Nencki Affective Picture System (Marchewka et al., 2014), and Emotional Picture Set (Wessa et al., 2010). A validation study ($N = 19$) showed that the negative and neutral composite images were matched for FG location (i.e., top, bottom, left, right, middle), complexity, brightness, contrast, human presence, and animal presence (all ps > .05) and confirmed (using 9-point Likert scales) that the emotional images were negatively valenced ($M_{\text{Valence}} = 2.46$, $SD_{\text{Valence}} = 0.79$) and arousing ($M_{\text{Arousal}} = 4.95$, $SD_{\text{Arousal}} = 1.05$), while neutral images were appropriately neutral ($M_{\text{Valence}} = 4.79$, $SD_{\text{Valence}} = 0.48$) and nonarousing ($M_{\text{Arousal}} = 2.17$, $SD_{\text{Arousal}} = 0.46$); the two conditions showed significant differences in both arousal and valence (both ps < .001).

Eye Tracking. During encoding for the in-person studies, eye positions and movements were recorded from each participant's right eye using the EyeLink 1000 system at a sampling rate of 1,000 Hz (SR Research, ON, Canada). A pseudorandom 9-point calibration was performed at the beginning of the experimental session and after every other experimental block. The monitor's diagonal measured 21″, corresponding to 43° of visual angle at the participant's viewing distance of 58 cm. Fixations and saccades were determined using a displacement threshold of 0.1°, a velocity threshold of 35°/s, and an acceleration threshold of $9{,}500°/s^2$ (SR Research). Gaze analyses focused on the proportion of fixations within the FG or BG components.

Retrieval Task. Six days following encoding, participants completed the surprise retrieval tasks illustrated in Figure 1. This multiday retention interval was employed to avoid possible ceiling effects and because emotion's impact on memory increases over time (F. Dolcos et al., 2013; Kleinsmith & Kaplan, 1963; Ritchey et al., 2008). In each trial, participants were first shown a FG component in grayscale (the original 90 images from encoding plus 45 foils: 30 negative and 15 neutral) and instructed to perform the Remember/Know/New task (Geraci et al., 2009; Tulving, 1985), by (a) choosing Remember (R) if they identified the FG as old and could also recollect specific contextual details from encoding, such as information about the BG and/or information about their thoughts and/or feelings when initially encountering the stimuli, (b) choosing Know (K) if they knew that the FG was old but could not retrieve any specific contextual details as the image simply felt just familiar to them, or (c) choosing New (*N*) if they had no memory for the FG images. For Remember and Know responses, examples were provided of how people may experience such memories outside the laboratory, like encountering someone and remembering that they are a classmate (Remember) or instead just knowing that they have met before but without remembering any contextual details (Know). For Remember responses, although it is difficult to know the specific recollected details that informed their decisions (hence the subjective nature of the task), Remember responses nonetheless reflect the ability to retrieve contextual associations from encoding. Given that the task presents participants only with the FG component of the stimuli and encourages them to try and retrieve associated contextual details (including from the pictures' background), it is also more likely than in the traditional R/K studies using the whole pictures as cues (e.g., F. Dolcos et al., 2005) that these contextual details are related to the BG component of the composite pictures (i.e., FG–BG associations). This is consistent with earlier evidence on the types of contextual details retrieved during recollection, showing that the visual and spatial information is commonly retrieved following encoding screens where multiple stimuli are shown near one another (Perfect et al., 1996). Hence, subjective confirmed by objective RM refers to the fact that accuracy in the objective RM test confirms the accuracy of the subjective RM responses, but not necessarily the exact details that informed the accurate recollection-based responses. Overall, using a combination of tasks that assess both subjective and objective memory associations, and the link between them, allowed us to capture more completely the richness of episodic memory and to measure the impact of emotion on RM. This approach can also mimic the retrieval of memories for real-life events, where reflecting on recollected memories can be complemented by confirmation of their accuracy based on objective sources (photos/footage of events). Identifying the exact contextual details (perceptual or otherwise) that informed the Remember responses was beyond the goals of the present design and is a question for further research.

Following the R/K responses, participants rated their level of confidence using a 3-point scale (not illustrated in Figure 1 and not analyzed here). Then, objective RM was tested for all old items (regardless of the R/K accuracy) using a three-alternative forced-choice task (Figure 1). Participants were shown the FG components overlaid upon three different BGs from the encoding session (one identical and two recombined) and instructed to select the correct match and then reported their confidence again (also not analyzed here). Notably, the two foil BG options were designed to be equally integrated (semantically and visually) with the FG component for both emotional and neutral conditions.

Data Analysis

Item memory was assessed in terms of raw and corrected recognition scores for the R/K test (hit−false alarm rates), calculated separately for the emotional and neutral conditions, with a focus on the *R*-based responses, reflecting subjective RM. Objective RM was assessed as accuracy in the three-alternative forced-choice task. Subjective confirmed by objective RM was assessed as the proportion of old items associated with both Remember responses in the R/K test and accurate FG–BG matches in the objective RM test (i.e., RHit–Hit). Memory scores were submitted to paired *t* tests comparing the emotion and neutral conditions and two-way repeated measures analyses of variance (ANOVAs) with picture type (Emotional vs. Neutral) and memory (Remember vs. Know) as factors.

The gaze analyses first used paired *t* tests to compare the proportion of fixations in the BG between the emotional and neutral conditions. The effect of picture type on gaze was also assessed using a multilevel linear regression (R-style equation):

$$\text{BG Gaze} \sim 1 + \text{Picture Type} + (\text{Picture Type}|\text{Participant}). \quad (1)$$

Next, a multilevel logistic regression was used to investigate the effect of picture type on objective RM while controlling for gaze:

$$\begin{aligned}\text{Objective RM} \sim 1 &+ \text{Picture Type} + \text{BG Gaze}\\ &+ (\text{Picture Type} + \text{BG Gaze}|\text{Participant}). \quad (2)\end{aligned}$$

Based on the coefficients from these two regressions, an attention-related indirect effect of emotion on objective RM was also measured (Picture Type → BG Gaze → Objective RM), and the significance of the mediation was assessed using Monte Carlo simulations (described by Selig & Preacher, 2008). The focus was on the effects of gaze on objective RM because it was here that we expected possible diverging effects mediated by attention. On the contrary, examining subjective RM while accounting for gaze contributes less to this specific aim. However, for completeness, a similar regression was also performed predicting subjective RM as a function of emotion and BG gaze (see Supplemental Material 2—Additional Eye-Tracking Results).

Software and Modeling Details

Multilevel regressions were tested using R (R Core Team, 2013) and the *lme4* package (Bates et al., 2015). The models included random intercepts and random slopes for each predictor, grouped by participant, and modeled the full variance–covariance structure among these random effects. This strategy is consistent with recommendations and evidence that simpler models, such as ones with only random intercepts, inflate the Type I error rate of predictor coefficient significance (Barr et al., 2013; Meteyard & Davies, 2020).

The statistical assumptions of the *t* tests, ANOVAs, and multilevel regressions were evaluated (e.g., the normality of residuals) and revealed that these assumptions were violated in some cases. However, previous studies have shown that the violations we saw are generally of no concern, as long as there are no highly influential outliers (Knief & Forstmeier, 2021; Lumley et al., 2002). This was confirmed to indeed be the case (analyzed variables $|Z| < 2.5$ for every study in the article). Hence, consistent with the suggestion by Knief and Forstmeier (2021) that researchers lean toward parametric tests, even if normality assumptions are violated (e.g., because they permit clearer comparison between articles), parametric tests were used for the results reported below. Nonetheless, to guarantee the robustness of the findings, the analyses were also tested using nonparametric procedures: the Wilcoxon signed-rank test, the Friedman test, and a bootstrapping approach for testing significance in the multilevel regressions. These analyses showed that every significant result of a parametric test remained significant when tested using a nonparametric test (ps $< .05$).

Results

Emotion Enhances Subjective Relational Memory Confirmed by Objective Relational Memory

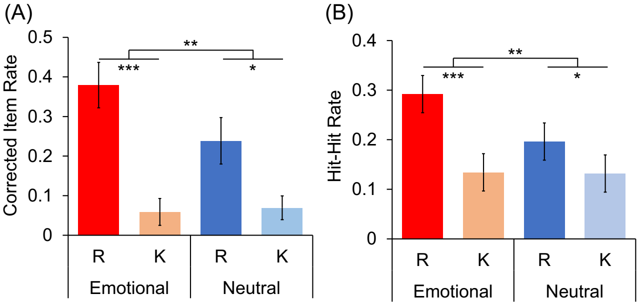
First, this study replicated the typical evidence of enhanced item memory by emotion, and, because this effect was driven by recollection (R-based responses; Table 1 and Figure 2A), it also replicated findings of enhanced subjective RM by emotion (F. Dolcos et al., 2005; Rimmele et al., 2011; Sharot et al., 2004). This was evidenced by a two-way ANOVA yielding a significant main effect of emotion, $F(1, 28) = 15.1$, $p < .001$, $\eta_p^2 = .35$, and Emotion × Memory interaction, $F(1, 28) = 8.12$, $p = .008$, $\eta_p^2 = .22$, along with post hoc tests identifying greater R-based memory for emotional than for neutral items, $t(28) = 3.95$, $p < .001$, $d = 0.73$. Importantly, this study also confirms our overarching hypothesis by providing evidence of enhanced subjective RM accuracy confirmed by objective RM accuracy by emotion (Emo RHit–Hit > Neu RHit–Hit; Figure 2B and Table 1), which was likewise driven by R-based responses. This was evidenced by another two-way ANOVA showing a significant main effect of Emotion, $F(1, 28) = 10.5$, $p = .003$, $\eta_p^2 = .27$, and a significant Emotion × Memory interaction, $F(1, 28) = 8.67$, $p = .006$, $\eta_p^2 = .24$, along with post hoc tests showing greater rates of RHit–Hit for emotional than for neutral images, $t(28) = 4.00$, $p < .001$, $d = 0.74$. These findings show that when RM is conceptualized in terms of both subjective and objective responses, emotion enhances RM even if attention is not accounted for.

Emotion Enhances Objective Relational Memory When Statistically Accounting for Attention

When testing objective RM separately, there was no memory enhancement by emotion, $t(28) = 0.88$, $p = .39$, $d = 0.16$ (Table 1). These results parallel previous studies identifying null effects of arousal on contextual memory (Pereira et al., 2021a; Symeonidou & Kuhlmann, 2022). However, this analysis did not yet account for the attention-capturing effect of emotion using eye tracking. Instead, when eye-tracking data were incorporated, both impairing and enhancing effects of emotion on objective RM were identified. Namely, images with negative FG were associated with significantly fewer fixations within the BG areas compared with the images with neutral FG, $t(28) = -8.52$, $p < .001$, $d = -1.58$ (Figure 3A). In turn, consistent with an attention-capturing effect of emotion leading to reduced processing of contextual/BG details, this had an impairing effect on objective RM accuracy, as illustrated by the mediation model ($a \times b = -0.11$ [−0.20, −0.04], $p < .001$; Figure 3B and 3C). Importantly, aside from this indirect effect, a significant direct enhancing effect of emotion on RM was also identified, when gaze was statistically controlled for via a multilevel regression (Figures 3B and 3C). See also Supplemental Material 2 (Additional Eye-Tracking Results) for the findings from a similar regression predicting subjective RM as a function of emotion and BG gaze. These findings (replicated in Study 2) show the importance of accounting for attention in examining the impact of emotion on RM.

Figure 2

Enhanced Subjective Relational Memory and Subjective Confirmed by Objective Relational Memory



Note. (A) Emotional images yielded higher rates of accurate recollection-based responses (subjective relational memory) and (B) higher rates of subjective confirmed by accurate objective relational memory (RHit–Hit). R = Remember; K = Know. See the online article for the color version of this figure.
* $p < .05$. ** $p < .01$. *** $p < .001$.

Discussion

Together, these findings highlight the importance of both using complementary measures of RM to capture the richness of RM

Table 1

Retrieval Results for Study 1

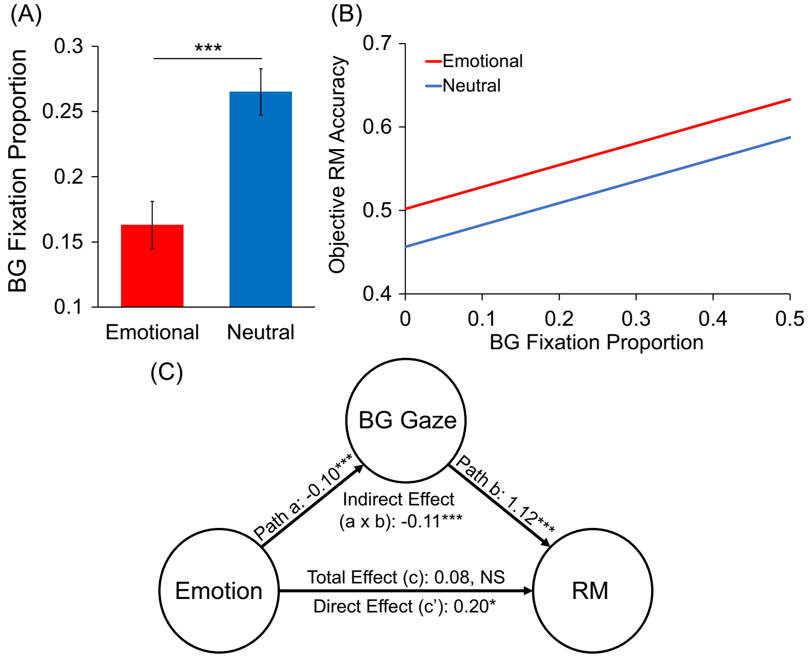
	Remember/Know			
Picture type	RHit	KHit	R-FA	K-FA
Emotional	.48 [.40, .56]	.26 [.20, .32]	.10 [.04, .15]	.20 [.14, .25]
Neutral	.35 [.27, .44]	.25 [.20, .31]	.12 [.03, .20]	.18 [.12, .25]

	R/K and objective RM		Objective RM
Picture type	RHit–Hit	KHit–Hit	(RM) hit
Emotional	.29 [.23, .36]	.13 [.10, .17]	.54 [.51, .58]
Neutral	.20 [.15, .24]	.13 [.10, .17]	.53 [.49, .56]

Note. The Remember/Know (R/K) columns indicate the response rates for old images correctly identified as old (uncorrected hit rate) and new/foil images incorrectly identified as old (false alarms). The "R/K and objective RM" column indicates the proportion of old trials where participants responded R or K and also made a correct objective RM response. The RHit–Hit rate represents subjective confirmed by objective RM. The objective RM results correspond to the objective RM accuracy, calculated separately. R-FA = remember-false alarms; K-FA = know-false alarms; RM = relational memory.

Figure 3

Enhanced Objective Relational Memory by Emotion When Statistically Accounting for Attention



Note. (A) The emotional images were associated with fewer fixations within the neutral BG areas. (B and C) The proportion of fixations in the BG areas significantly predicted subsequent RM accuracy, but, once gaze-related differences between the emotional and neutral conditions were controlled, a direct enhancing effect of emotion on RM accuracy emerged, alongside an indirect impairing effect. The results here are based on a multilevel regression. See also Supplemental Figure S1, which illustrates the results of fitting a separate logistic regression for each participant. BG = background; RM = relational memory; NS = not statistically significant. See the online article for the color version of this figure.
* $p < .05$. *** $p < .001$.

with increased specificity and controlling for attentional effects in studying the impact of emotion on memory. These allowed us to provide reconciling evidence concerning opposing effects of emotion on RM and showed that, indeed, depending on how emotional RM is conceptualized and measured, enhancing or impairing (or null) effects can be identified. The results also point to a distinction between subjective and objective RM, given earlier evidence that the emotion's effects on the former do not hinge on attentional mechanisms (Talmi et al., 2007). However, given the relatively limited sample size of the present study ($N = 29$), a replication study (Study 2) was conducted, targeting the same emotional memory effects and recording eye-tracking data to account for effects of attention.

Study 2

This study aimed to replicate the primary results of Study 1. First, the study aimed to replicate the identified enhancing effects of emotion on subjective RM and the enhancing effects on subjective confirmed by objective RM. Second, the study aimed to replicate the two effects seen linked to objective RM—namely, the impairing indirect effect of emotion mediated by attention along with the enhancing direct effect of emotion. Because of COVID-19 restrictions, this study was conducted online and used webcam-based eye tracking (Papoutsaki et al., 2016). Previous studies, including from our group, have demonstrated the efficacy of webcam-based eye tracking and its ability to replicate findings identified via traditional, infrared eye tracking (Bogdan, Dolcos, Buetti, et al., 2023; Schneegans et al., 2021; Semmelmann & Weigelt, 2018; Yang & Krajbich, 2021).

Method

Participants

Seventy-seven participants were recruited from the local university (60% female, 38% male, 2% other; $M_{\text{age}} = 19.4$; $SD_{\text{age}} = 1.22$) and completed both the encoding and retrieval tasks for this online study. The demographics information corresponds to participants' genders, measured by providing participants with four options: “Male,” “Female,” “Other,” or “Prefer not to say.” Ethnicity was not recorded due to a technical error in transitioning from in-person to online data collection. Data from 13 participants were excluded because of below chance memory accuracy (false alarm rate ≥ item hit rate or RM accuracy <33.4%) or low response rates (no response in 20% or more trials), yielding a final sample of

64 participants. Importantly, the findings do not meaningfully change if all data sets are included (all significant effects remain $p < .05$). This sample size was motivated by power analyses done using the Study 1 data. Based on the Study 1 ANOVAs and the Emotion × Memory interaction effect, power analyses using G*Power (Faul et al., 2009) show that the sample size of 64 has high power (99%, $\alpha = .05$) to detect significant emotional enhancement of subjective confirmed by objective RM. Additionally, based on Study 1 multilevel regressions, power analyses using the *simr* R package (Green & MacLeod, 2016) show that the sample size also has sufficient power (90%, $\alpha = .05$) to detect a significant effect of emotion on objective RM; *simr* is a Monte Carlo tool designed for power analysis of multilevel regressions. Participants provided informed consent under a protocol approved by the IRB and received course credit for participation. Like in Study 1, questionnaires were also collected (see Supplemental Material 1—Questionnaires), but those data are not analyzed here.

Procedure

The task design was identical to Study 1, except for transitioning the study into an online environment. This involved slightly shortening the retention interval (3–5 days), to account for lower engagement typically seen in online studies, and using participants' webcams for eye tracking. The latter was done with the *WebGazer.js* package (Papoutsaki et al., 2016), which predicts gaze location in real time and saves the location coordinates: one coordinate (x, y) per webcam refresh (25–40 Hz, depending on participants' webcams). Participants were instructed to stay as still as possible and to keep their faces relatively close to their laptop webcam and screen, so that their faces spanned roughly 50% of the height of their webcam's video capture range (an example image was provided to help participants position their faces). Analyses were the same as in Study 1 but with a change to accommodate the webcam-based eye-tracking data. Unlike Study 1 (measuring the proportion of FG/BG fixations), Study 2 measured the proportion of time spent within the FG/BG areas because the webcam-based gaze data are too noisy to model fixations. Further details on the webcam-based eye-tracking procedures are provided in our earlier methodological report comparing in-person and online eye tracking (Bogdan, Dolcos, Buetti, et al., 2023).

Results

Each significant result from Study 1 was replicated. Specifically, emotion enhanced subjective RM, as increased item memory for emotional stimuli, $t(63) = 9.57$, $p < .001$, $d = 1.21$, was driven by recollection (*R*-based responses; Table 2 and Figure 4A). This was evidenced by a two-way ANOVA yielding a significant Emotion × Memory interaction, $F(1, 63) = 26.2$, $p < .001$, $\eta_p^2 = .29$, and associated post hocs. Likewise, emotion enhanced subjective RM accuracy confirmed by objective RM accuracy by emotion, Emo RHit–Hit > Neu RHit–Hit; $t(63) = 7.66$, $p < .001$, $d = 0.97$ (Table 2 and Figure 4B). This effect was also driven by R-based responses, as evidenced again by a two-way ANOVA showing a significant Emotion × Memory interaction, $F(1, 63) = 25.2$, $p < .001$, $\eta_p^2 = .29$, and associated post hocs. Finally, as described below, the multilevel regression replicated the dual enhancing (direct) and impairing (indirect) effects of emotion on objective RM (Figure 4C).

This study also showed similar eye-tracking and objective RM results to those from Study 1. Namely, images with negative FG were associated with significantly less gaze within the BG areas compared with the images with neutral FG, $M_{\text{emo}} = .41$ [.37, .45], $M_{\text{neu}} = .44$ [.41, .47]; $t(63) = -4.3$, $p < .001$, $d = -0.54$. This attention-capturing effect of emotion, in turn, yielded a significant indirect impairing effect on RM accuracy ($a \times b = -0.013$ [−0.024, −0.004]; Figure 4C). Finally, alongside this indirect impairing effect, there was also a significant enhancing direct effect ($\beta = 0.19$, $p = .002$). In sum, these results reiterate the points made by Study 1: Depending on how emotional RM is conceptualized and measured, impairing or enhancing effects can be identified. This speaks to the value of measuring RM with increased specificity and accounting for emotion's attentional effects on memory.

Discussion

Study 2 replicated each significant result from Study 1, including the attention-related findings, which were identified via webcam-based

Table 2
Retrieval Results for Study 2

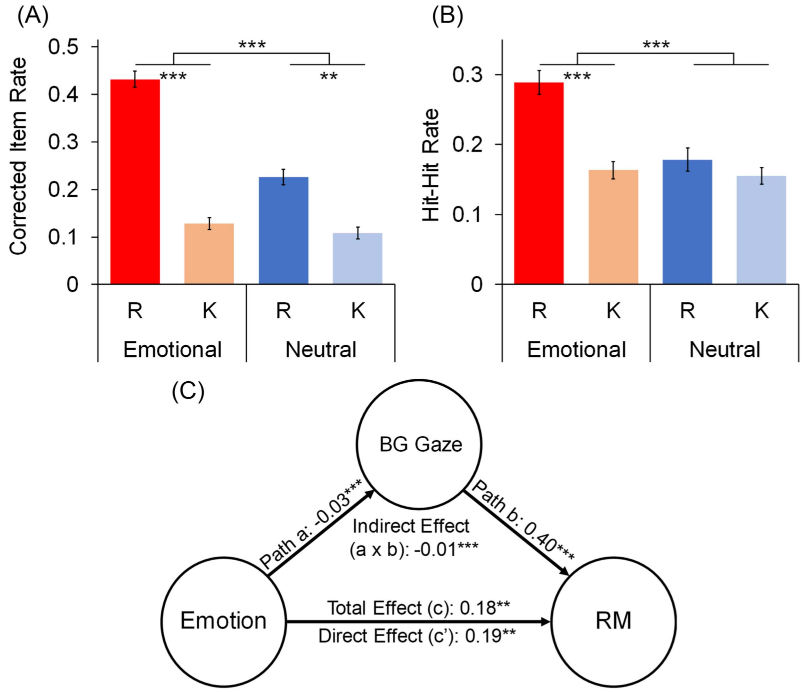
	Remember/Know			
Picture type	RHit	KHit	R-FA	K-FA
Emotional	.49 [.44, .53]	.31 [.27, .35]	.06 [.04, .08]	.18 [.15, .21]
Neutral	.29 [.25, .33]	.32 [.28, .35]	.07 [.04, .10]	.21 [.17, .25]

	R/K and objective RM		Objective RM
Picture type	RHit–Hit	KHit–Hit	(RM) Hit
Emotional	.29 [.26, .32]	.16 [.14, .19]	.54 [.51, .57]
Neutral	.18 [.15, .21]	.15 [.13, .18]	.50 [.47, .53]

Note. The Remember/Know (R/K) columns indicate the response rates for old images correctly identified as old (uncorrected hit rate) and new/foil images incorrectly identified as old (false alarms). The "R/K and objective RM" column indicates the proportion of old trials where participants responded R or K and also made a correct objective RM response. The RHit–Hit rate represents subjective confirmed by objective RM. The objective RM results correspond to the objective RM accuracy, calculated separately. R-FA = remember-false alarms; K-FA = know-false alarms; RM = relational memory.

Figure 4

Study 2 Replication of the Study 1 Results



Note. (A) Emotional images yielded higher rates of accurate recollection-based responses (subjective RM). (B) Emotional images also yielded higher rates of subjective confirmed by accurate objective RM (RHit–Hit). (C) The proportion of fixations in the BG significantly predicted subsequent RM accuracy. Modeling the effects of emotion on attention and memory via a multilevel regression shows a significant enhancing (direct) effect and a significant impairing (indirect) effect. R = Remember; K = Know; BG = background; RM = relational memory. See the online article for the color version of this figure.
** $p < .01$. *** $p < .001$.

eye tracking. These findings were extended in Study 3, which investigated the same effects, but the study accounted for emotion's impact on attention via task manipulation rather than through regressions using gaze as a predictor. Study 3 also involved the collection of fMRI data in a subset of participants.

Study 3

This study used the same composite stimuli and basic task design as in Studies 1 and 2, measuring both subjective and objective RM and the link between them. However, rather than accounting for emotion's impacts on attention via eye-tracking measurement and statistical control, this study accounted for emotion–attention biases by instructing participants on how to attend to the composite images, hence accounting for effects of attention through task manipulation. Participants were cued before the presentation of each image to either focus on the FG or BG aspects of the stimuli, and analyses compared the emotional versus neutral conditions by also including the attentional focus instruction as a factor. From an emotion regulation standpoint, this manipulation is equivalent to engaging focused attention (FA), which is a type of attentional deployment emotion regulation strategy that can up- or downregulate participants' emotional responses (F. Dolcos et al., 2022). Therefore, we expected that this explicit manipulation of attentional focus would enhance/diminish the experienced emotion and its modulation of subsequent memory (F. Dolcos et al., 2022). Accordingly, we expected that focusing on emotional aspects of stimuli (FG focus) would maximize the enhanced subjective RM for emotional stimuli and the likelihood of also being confirmed by accurate objective RM, hence replicating the findings from Studies 1 and 2. We also expected that focusing away from the emotional aspects (BG focus) would diminish the purported attention-capturing effect of emotion and that this prioritization of processing contextual details would lead to enhanced objective RM.

Functional MRI data were collected during encoding from a subset of participants to investigate the MTL and PFC mechanisms linked to the two main novel behavioral effects: (1) enhanced subjective confirmed by objective RM (RHit–Hit) for emotional stimuli, which was maximized when focusing on the emotional aspects of stimuli (EmoFG condition), and (2) enhanced objective RM by emotion, which was maximized when focusing on the contextual details of emotional stimuli (EmoBG condition). For (1), the focus was on the role of MTL regions identified as being involved in enhanced subjective RM when upregulating processing of emotional information, which included amygdalar, hippocampal, and anterior PHC areas (F. Dolcos, Katsumi, Bogdan, et al., 2020).

We expected that subregions of these areas would also be associated with enhanced subjective confirmed by objective RM (RHit–Hit) for emotional stimuli. For (2), the focus was on the role of MTL regions found to show enhanced activity when upregulating processing of nonemotional, contextual information, which included posterior PHC (aka., PHC proper) areas (F. Dolcos, Katsumi, Shen, et al., 2020). We expected that subregions of these areas would also be associated with enhanced objective RM when focusing on the contextual details of emotional stimuli, aside from being associated with enhanced perceptual processing of contextual information (R. Epstein & Kanwisher, 1998).

Beyond just this work, memory research in general has demonstrated that subjective RM and objective RM are linked to MTL involvement, including hippocampal effects specifically (Eichenbaum et al., 1992; Eldridge et al., 2000; Manns et al., 2003; Mayes et al., 2007), and earlier studies on emotional modulation of recollection have likewise reported MTL/hippocampal involvement (F. Dolcos et al., 2005; Phelps & Sharot, 2008). Given these previous results, we expected to identify significant MTL effects linked to the present dependent variables associated with the highest level of memory performance for the two main behavioral effects mentioned above. Finally, outside of the MTL, the focus was on regions of the lateral PFC (vlPFC and dlPFC), which are broadly involved in affective, attentional, and mnemonic processing (F. Dolcos, Katsumi, Moore, et al., 2020; Murty et al., 2011; Ranganath et al., 2003) and thus are targets of particular interest in emotion–attention–memory interactions. We expected that the PFC’s involvement in enhanced RM by emotion would be consistent with a top–down role in modulating the MTL activity associated with the two behavioral effects mentioned above.

Method

Participants

Fifty-four in-person participants recruited from the local university and surrounding area ($M_{\text{age}} = 26.2$, $SD_{\text{age}} = 7.8$; 67% female, 33% male; 61% White, 17% Asian, 13% Hispanic, 9% Black) participated in this study. Sex and ethnicity were recorded using procedures identical to Study 1. Power analyses, based on the Study 1 results and using the same procedures as for Study 2, suggest that this sample has high power (99%, $\alpha = .05$) to detect significant emotional enhancement of subjective confirmed by objective RM, and the sample has sufficient power (80%, $\alpha = .05$) to detect a significant effect of emotion on objective RM. A subsample of this study’s participants ($N = 24$; $M_{\text{age}} = 34.0$, $SD_{\text{age}} = 4.8$; all female; 88% White, 8% Hispanic; 4% Black), recruited from a larger study on mother–child dyads (Fiese et al., 2019), also underwent MRI recordings during encoding. Three participants were excluded from all analyses due to outlier emotional ratings (z score greater than 2.5), and two additional participants were excluded from analyses involving the R/K test because they never responded “Remember” for any condition. All participants provided informed consent under a protocol approved by the IRB and received course credit or financial compensation.

Procedure

Participants viewed a series of composite images, with instruction before each image to focus on the image’s FG or BG component and rated their emotional responses to each image (Figure 1). For both the emotional and neutral conditions, half of the images were preceded by a cue to focus on the FG and half by a cue to focus on the BG: 30 negative FG focus (EmoFG) trials, 30 negative BG focus (EmoBG) trials, 15 neutral FG focus (NeuFG) trials, and 15 neutral BG focus (NeuBG) trials. For the subset of participants who completed the fMRI version of the task, the intertrial interval was extended to 9.5 s, to allow the hemodynamic response to return to baseline. Three to seven days ($M = 5.22$, $SD = 1.50$) following encoding, participants completed a surprise retrieval task, identical to that of Studies 1 and 2. Data on participants’ emotional responses in each condition were previously reported by F. Dolcos et al. (2022) for the behavioral participants and F. Dolcos, Katsumi, Shen, et al. (2020) for the fMRI participants. In this study, eye-tracking data were recorded for manipulation-check purposes only, to ensure that participants adhered to the task instructions, but were not reported here. See, instead, F. Dolcos et al. (2022) for these data in the non-fMRI subsample and F. Dolcos, Katsumi, Shen, et al. (2020) for these data in the fMRI subsample.

MRI scanning was conducted via a 3T Siemens MAGNETOM scanner with a 64-channel head coil, at Beckman Institute’s Biomedical Imaging Center of the University of Illinois. After the sagittal localizer and the 3D MPRAGE anatomical images (repetition time [TR] = 2,000 ms; echo time [TE] = 2.25 ms; flip angle = 8°; field of view [FOV] = 230×230 mm^2, matrix size = 256×256 mm^2; slice thickness = 1 mm; volume size = 172 slices; voxel size = $1 \times 1 \times 1$ mm^3), five blocks of full-brain echo-planar imaging functional images were acquired axially with a simultaneous multislice sequence (TR = 1,500 ms, TE = 30 ms; flip angle = 40°; FOV = 230×230 mm^2; matrix size = 144×144 mm^2; slice thickness = 1.6 mm; volume size = 76 slices; multiband acceleration factor = 4, voxel size = $1.6 \times 1.6 \times 1.6$ mm^3; phase encoding anterior to posterior).

Behavioral Data Analysis

Analyses targeted the same memory measures used in Studies 1 and 2, including subjective RM accuracy, objective RM accuracy, and subjective confirmed by objective RM (RHit–Hit). These data were submitted to paired t tests, and repeated measures ANOVAs, with picture type (Emotional vs. Neutral), memory (Remember vs. Know), and attention (FG focus vs. BG focus) as factors.

Functional Magnetic Resonance Imaging Preprocessing

Preprocessing of fMRI data was performed using SPM12 (Wellcome Department of Cognitive Neurology, London, United Kingdom). Functional images were first corrected for acquisition order and realigned to correct for motion artifacts. Next, the high-resolution anatomical image was co-registered to the first functional image for each participant, and functional images were spatially normalized (resampled to 2 mm isotropic voxels) to the Montreal Neurological Institute template. Last, the functional images were spatially smoothed using a 6-mm Gaussian kernel, full width at half maximum.

Blood Oxygenation Level-Dependent Signal Analysis

Analyses of fMRI data were conducted using in-house custom MATLAB scripts, which were developed at Duke University’s

Brain Imaging and Analysis Center and are publicly available online (https://wiki.biac.duke.edu/biac:tools; Denkova et al., 2010; F. Dolcos, 2013; F. Dolcos et al., 2004b, 2008; Iordan & Dolcos, 2017; Iordan et al., 2019; Morey et al., 2009). The fMRI signal was selectively averaged in each participant's data as a function of trial type (Emotional/Neutral, FG/BG focus, RHit–Hit/Miss–Miss, objective RM Hit/Miss) and TR/time point. Selective averaging across trial types was performed after trial-level baselines (i.e., one TR immediately before stimulus onset) were subtracted, hence correcting for potential temporal autocorrelation and low-frequency drifts. The impact of in-scanner motion was further mitigated by removing trials exhibiting large global signal intensity deviations ($SD > 3$). No assumptions about the shape of the hemodynamic response function were made because this allows finer comparisons of the MR signal on a TR-by-TR basis (Denkova et al., 2010; F. Dolcos, 2013; F. Dolcos et al., 2004b, 2008; Iordan & Dolcos, 2017; Iordan et al., 2019; Morey et al., 2009). This is particularly important for investigating brain responses linked to emotion processing and regulation, as they can affect the duration of the blood oxygenation level-dependent (BOLD) response, hence limiting the effectiveness of hemodynamic response function modeling (M. A. Lindquist & Wager, 2007; Waugh et al., 2010, 2014, 2016). The within-participant (first-level analysis) averages were submitted to paired *t* tests (second-level random-effects analysis), using the contrasts detailed below.

Analyses of brain activation targeted two main contrasts, which both measured subsequent memory effects, or difference due to memory (Dm) effects (Paller et al., 1987; Paller & Wagner, 2002). The two contrasts mapped onto two behavioral effects of interest mentioned above: (1) enhanced subjective confirmed by objective RM (RHit–Hit) for emotional stimuli, which was found to be maximized when focusing on the emotional aspects of stimuli (EmoFG condition), and (2) enhanced objective RM by emotion, which was found to be maximized when focusing on the contextual details of emotional stimuli (EmoBG condition). The present analyses supplement earlier reports focusing on subjective RM alone (F. Dolcos, Katsumi, Bogdan, et al., 2020) or on general attentional effects regardless of objective RM (F. Dolcos, Katsumi, Shen, et al., 2020). Thus, across previous reports and here, the fMRI results cover subjective and objective RM both separately and together, paralleling the behavioral analytic strategy. The first effect was examined using an EmoFG RHit–Hit > Emo Miss–Miss contrast, for which participants each contributed 9.1 trials, on average, to EmoFG RHit–Hit and 9.6 trials, on average, to Emo Miss–Miss (i.e., emotion trials where participants both erroneously responded "New" in the R/K tests and selected the incorrect FG–BG pair). The right-hand side of the contrast, Emo Miss–Miss, combined data from the EmoFG and EmoBG conditions, to ensure that there were sufficient trials, as the EmoFG Miss–Miss condition alone yielded just 2.5 trials per participant, on average, due to the EmoFG condition upregulating memory. The second effect was examined using an EmoBG (RM) Hit > (RM) Miss contrast, for which participants contributed, on average, 15.6 trials to the EmoBG Hit condition and 14.4 trials to the EmoBG Miss condition. The significance of activation clusters was assessed using a cluster-based significance threshold (see below), and outcomes of these contrasts identifying patterns of brain activations also served as seed clusters used for functional connectivity analyses, as described below.

Investigations of responses in both MTL and PFC regions involved voxel-wise analyses of the BOLD signal, but identification of MTL activity was further guided by an anatomical region of interest (ROI) approach. Namely, to specifically identify MTL locations from neighboring areas, we used an MTL anatomical mask, which was manually traced based on published guidelines (Moore et al., 2014). Then, we further guided our investigation by earlier findings mentioned above regarding the role of MTL regions that were (a) identified as being involved in enhanced subjective RM when upregulating processing of emotional information, which included amygdalar, hippocampal, and anterior PHC areas (F. Dolcos, Katsumi, Bogdan, et al., 2020), or (b) found to show enhanced activity when upregulating processing of nonemotional, contextual information, which included posterior PHC areas (F. Dolcos, Katsumi, Shen, et al., 2020). The main focus was on clusters from each contrast that overlapped with these earlier results, but we also provide details on significant MTL effects outside of those overlapping with our earlier findings. For the PFC, voxel-wise analyses were performed without using any guiding anatomical ROIs.

Functional Connectivity Analysis

Nondirectional functional connectivity analyses were performed to investigate possible agonistic/synergistic effects within the MTL and top–down influences from PFC on MTL activity. These analyses used three independent seeds from the MTL (L AMY: −18, −8, −14; R AMY: 18, −4, −18; L HC: −22, −8, −26) and one from the PFC (L vlPFC: −44, 28, 16) regions, targeting MTL–MTL and PFC–MTL interactions. In the MTL, the focus was on examining modulatory influences of the AMY on activity in memory-related regions (McGaugh, 2004), consistent with the behavioral effect of interest—that is, increased subjective RM confirmed by accurate objective RM for emotional stimuli. For this, bilateral AMY seeds were identified based on the activation clusters derived from the EmoFG RHit–Hit > Emo Miss–Miss contrast described above, and both AMY seeds also overlapped with our earlier findings on subjective RM (F. Dolcos, Katsumi, Bogdan, et al., 2020). Similarly, we explored possible modulatory influences on other MTL areas linked to enhanced objective RM by emotion, which was maximized when focusing on the contextual details of emotional stimuli. For this, a left HC seed was identified based on the EmoBG (RM) Hit > EmoBG (RM) Miss contrast. Finally, aside from these MTL seeds, a left vlPFC seed was also identified based on the overlap in activity between the two Dm contrasts mentioned above and was used to investigate possible top–down modulatory influences from PFC on MTL activity. In all these analyses, each seed was used independently for voxel-wise analyses of MTL–MTL and PFC–MTL functional connectivity.

Measurement of functional connectivity effects used a two-level approach, much like the analysis of BOLD signals. For the first-level analysis of each participant, trial-by-trial correlations were measured for each condition of interest (EmoFG RHit–Hit and EmoBG [RM] Hit). Among the trials of a given condition, correlations were measured between the signal extracted from a given seed (averaged across all seed voxels) and the signal associated with each MTL voxel. For example, EmoFG RHit–Hit functional connectivity corresponds to trial-by-trial correlations among the signal extracted from seed voxels and MTL voxels, both from EmoFG RHit–Hit trials. For a given participant and condition, this procedure generates a voxel-wise map of connectivity between a given seed and each MTL voxel. Then, the first-level correlations were Fisher z transformed and submitted to one-sample t tests (second-level analysis), which yielded voxel-wise t maps. Next, paralleling the analysis of BOLD response, group-level random-effects t tests were also performed for both conditions of interest: EmoFG RHit–Hit > Emo Miss–Miss and EmoBG (RM) Hit > EmoBG (RM) Miss. This approach has been validated by previous research (F. Dolcos et al., 2006; Iordan & Dolcos, 2017) and is similar to a β-series correlation (Rissman et al., 2004) but uses the BOLD signals rather than β values.

To assess statistical significance, a primary (voxel-level) intensity threshold of $p < .005$ (uncorrected) was used, and the necessary cluster extent thresholds to correct for multiple comparisons at $p < .05$ were determined using the "Slotnick method" (https://osf.io/3wf7b/; Slotnick, 2017a, 2017b). This version was last updated on April 24, 2019. The Slotnick technique estimates a cluster-level threshold corrected for multiple comparisons via Monte Carlo simulations. For each iteration, a three-dimensional brain volume is modeled by sampling from a normal distribution, which is smoothed by the specified full-width half maximum estimated from the data. A voxel-wise intensity threshold ($p < .005$) is applied to the data, and the sizes of the resulting clusters are recorded. After 1,000 iterations, the probability associated with each cluster size is calculated to determine a cluster size cutoff at $p < .05$. The Slotnick method (Slotnick, 2017a, 2017b) has been widely used in the literature, and of particular relevance for the present report are studies investigating the neural mechanisms associated with emotion processing and episodic memory, similar to the present study (e.g., Beaty et al., 2020; Bowen et al., 2020; Ford et al., 2022; Fortier et al., 2023; Jakobi et al., 2022; Suzuki et al., 2023; Thakral et al., 2020; Thakral et al., 2022). For the MTL regions, we had specific hypotheses based on evidence about their involvement in memory and memory modulation by emotion (McGaugh, 2004; Voss et al., 2017; Yonelinas & Ritchey, 2015). Hence, for these analyses, we conducted the Monte Carlo simulation using a full MTL anatomical mask (covering roughly 7% of all brain voxels), which was manually traced based on published guidelines (F. Dolcos et al., 2004b; Moore et al., 2014). The use of hypothesis-driven region-of-interest approaches where correction for multiple comparisons is implemented within a restricted search space remains common in MTL research (e.g., Barker et al., 2022; Grob et al., 2023; Liu et al., 2021; Pedersen et al., 2018; Tu & Diana, 2021). Notably, the use of a full MTL mask is a more conservative approach than analyzing just a subset of the MTL regions that often correct at a sub-MTL level within specific regions—for example, solely the HC or the AMY (Barker et al., 2022; Liu et al., 2021; Pedersen et al., 2018). Based on this approach, an extent threshold of 20 voxels was identified for the MTL regions. The extent threshold was also calculated at the whole-brain level, which yielded a threshold of 46 contiguous voxels.

For reference, the tables also indicate whether identified clusters are significant under a stricter threshold, calculated using Analysis of Functional NeuroImages (AFNI) 3dClustSim (35 voxels for the MTL and 127 voxels for the whole brain). Like Slotnick's cluster_extent_beta, AFNI 3dClustSim is a Monte Carlo method that measures cluster size thresholds based on simulated null data sets. However, unlike the Slotnick method, which calculates p values with respect to every cluster across the simulated null data set, the AFNI script calculates p values based on only the largest cluster size linked to each data set. Because the AFNI method calculates the cumulative probability of cluster sizes (p values) with respect to the largest cluster seen in each simulated data set, its cluster extent thresholds are corrected at a more conservative family-wise error level. To provide a further perspective on the robustness of the MTL effects, given family-wise-error correction, complementary ROI-based multivariate analyses were also conducted (see Supplemental Material 4). These analyses explored the effect of subsequent memory using emerging machine-learning strategies that can enhance statistical sensitivity when applied to sample sizes like ours (Bogdan, Iordan, et al., 2023).

Results

Emotion Upregulation Maximizes Enhanced Subjective Relational Memory Confirmed by Objective Relational Memory

First, this study replicated the enhanced subjective RM (R-based responses) by emotion, and this effect was the highest when focusing on the FG areas of emotional pictures (EmoFG-R condition; Table 3 and Figure 5A). This was demonstrated by a two-way ANOVA using emotion and attention as factors, which showed significant main effects of emotion, $F(1, 48) = 58.1$, $p < .001$, $\eta_p^2 = .55$, and attention, $F(1, 48) = 153.0$, $p < .001$, $\eta_p^2 = .76$, as well as by a three-way ANOVA also including memory as a factor, which yielded a significant Emotion × Attention × Memory interaction, $F(1, 48) = 6.86$, $p = .011$, $\eta_p^2 = .13$. Moreover, emotion also enhanced subjective RM confirmed by objective RM (RHit–Hit), which was again most prominent when focusing on the emotional aspects of stimuli (EmoFG-R condition; Table 3 and Figure 5A). A two-way ANOVA on Hit–Hit rates revealed significant main effects of emotion, $F(1, 48) = 41.1$, $p < .001$, $\eta_p^2 = .46$, and attention, $F(1, 48) = 55.2$, $p < .001$, $\eta_p^2 = .53$, and a three-way ANOVA that included memory as a factor further confirmed that this enhancement was driven by the R-based responses. The three-way ANOVA identified significant Emotion × Memory, $F(1, 48) = 15.2$, $p < .001$, $\eta_p^2 = .24$, and Attention × Memory, $F(1, 48) = 20.0$, $p < .001$, $\eta_p^2 = .29$, interactions, and post hoc analyses showed that the EmoFG condition yielded the highest rates of accurate subjective RM confirmed by objective RM accuracy (Table 3 and Figure 5B). Overall, these findings further clarify the impact of emotion on RM and replicate the enhancing effect of emotion on subjective confirmed by accurate objective RM, through voluntary modulation of the attentional focus.

Emotion Enhances Objective RM When Accounting for Attention With Task Manipulation

Emotion also enhanced objective RM accuracy when measured separately, and this effect was maximized when focusing on contextual details of the emotional pictures (EmoBG condition; Figure 6 and Table 3). Supporting these observations, a two-way ANOVA ($N = 51$) targeting the effects of emotion and attention on objective RM accuracy revealed a significant main effect of emotion, $F(1, 50) = 4.61$, $p = .036$, $\eta_p^2 = .08$, which was driven by the EmoBG condition, EmoBG > EmoFG; $t(50) = 2.06$, $p = .045$, $d = 0.29$ (Figure 6); the same ANOVA also yielded a significant main effect of attention, $F(1, 50) = 4.78$, $p = .033$, $\eta_p^2 = .09$. These results add further evidence reconciling opposing effects of emotion

Table 3

Retrieval Results for Study 3

	Remember/Know			
Condition	RHit	KHit	R-FA	K-FA
EmoFG	.52 [.46, .59]	.30 [.25, .35]	.06 [.04, .08]	.20 [.16, .24]
EmoBG	.26 [.21, .31]	.31 [.27, .35]		
NeuFG	.34 [.27, .40]	.36 [.30, .42]	.06 [.03, .08]	.22 [.18, .26]
NeuBG	.13 [.10, .16]	.27 [.23, .32]		

	R/K and objective RM		Objective RM
Condition	RHit–Hit	KHit–Hit	(RM) Hit
EmoFG	.27 [.24, .32]	.16 [.13, .19]	.50 [.46, .53]
EmoBG	.15 [.13, .19]	.16 [.14, .19]	.53 [.50, .56]
NeuFG	.17 [.13, .21]	.16 [.13, .20]	.47 [.43, .51]
NeuBG	.06 [.04, .08]	.14 [.11, .17]	.50 [.46, .54]

Note The retrieval results are organized as in Study 1, with the only notable difference being that Study 3 introduced the foreground focus (FG) versus background focus (BG) manipulation during encoding. Note that because false alarm (FA) rates could not be specific to the FG or BG trials, the same FA scores were used to calculate the corrected scores for FG and BG conditions. R-FA = remember-false alarms; K-FA = know-false alarms; R/K = Remember/Know; RM = relational memory; EmoFG = emotional foreground focus; EmoBG = emotional background focus; NeuFG = neutral foreground focus; NeuBG = neutral background focus.

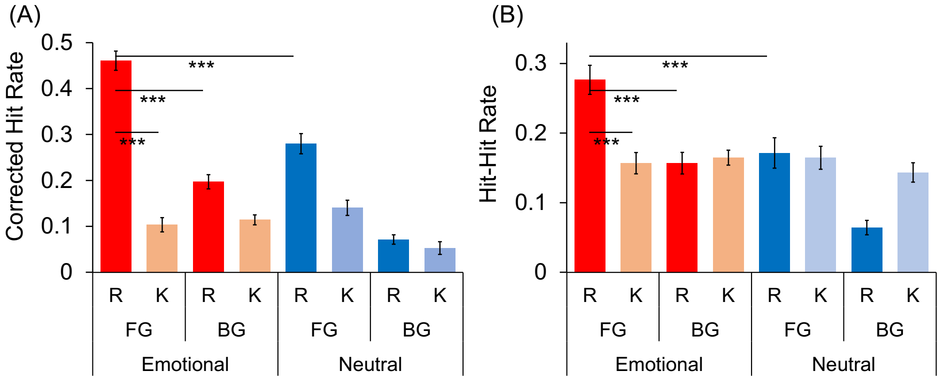
on RM, by showing that voluntary downregulation of emotion processing and prioritization of processing contextual details enhances objective emotional RM.

Neural Correlates of Enhanced Subjective Confirmed by Objective Relational Memory When Focusing on Emotion

As expected, analyses revealed significant MTL activation patterns that predicted emotional subjective confirmed by objective RM. These results include clusters in the bilateral AMY (Table 4 and Figure 7, left side panel), which notably overlap with the MTL areas predicting accurate subjective RM alone (F. Dolcos, Katsumi, Bogdan, et al., 2020). Moreover, the follow-up ROI-based analyses using multivariate techniques and family-wise-error correction provided additional evidence for its role in subjective RM (see Supplemental Material 4). Beyond the AMY, a posterior hippocampal cluster predicting subjective confirmed by objective RM, when focusing on emotional (FG) aspects of stimuli, was also identified (Table 4 and Figure 7, right side panel). A PRC cluster (15 voxels), overlapping with earlier findings on emotion's influence on subjective RM (F. Dolcos, Katsumi, Bogdan, et al., 2020), also emerged, but it did *not* cross the significance threshold (20 voxels). In the PFC, these analyses identified significant activation clusters in both dlPFC and vlPFC areas (Table 4).

Figure 5

Enhanced Subjective Relational Memory and Subjective Confirmed by Objective Relational Memory Was Maximized by Emotion Upregulation

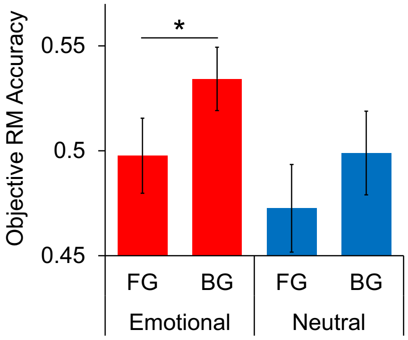


Note. Focusing on emotion (emotional foreground focus condition) yielded (A) the highest rates of accurate *R*-based responses (subjective relational memory) and (B) the highest rates of subjective confirmed by accurate objective relational memory (RHit–Hit). R = Remember; K = Know; FG = foreground; BG = background. See the online article for the color version of this figure.

*** $p < .001$.

Figure 6

Enhanced Objective Relational Memory by Emotion When Accounting for Attention With Task Manipulation



Note. Emotion enhanced objective RM accuracy, which was the highest when the processing of contextual details was prioritized (emotional background focus condition). RM = relational memory; FG = foreground; BG = background. See the online article for the color version of this figure.
* $p < .05$.

Analyses of functional connectivity showed that subsequent subjective confirmed by objective RM was also predicted by significant functional coupling between the AMY and memory-related MTL areas and between PFC and MTL regions (Table 5). The former connectivity patterns (MTL–MTL) included significant coupling between seed voxels from bilateral AMY, which were identified by the activation analyses reposted above, and hippocampal areas (Table 5). The latter functional connectivity patterns (PFC–MTL) included significant coupling between seed voxels from the left vlPFC and both emotion and memory-related MTL areas (Table 5). Overall, these patterns are consistent with synergistic interactions among MTL areas and between PFC and MTL regions predicting enhanced subjective confirmed by objective RM, when focusing on emotional aspects of pictures.

Table 4

Medial Temporal Lobe and Prefrontal Cortex Correlates of Enhanced Subjective Confirmed by Objective Relational Memory When Focusing on Emotion

Brain region	Side	BA	MNI coordinate *x*	*y*	*z*	*t*	Cluster size
MTL clusters							
Amygdala	L		−18	−8	−14	3.57	21
Amygdala	R		20	−2	−22	3.75	26
Hippocampus tail	R		22	−36	6	4.32	28
PFC clusters							
Superior frontal cortex	L	6	−16	34	56	5.02	186[a]
Middle frontal cortex	L	46	−44	32	18	4.64	591[a]
Inferior frontal cortex	L	45	−52	20	4	4.55	
Inferior frontal cortex	R	44	62	22	14	5.38	140[a]

Note. Peak coordinates of clusters showing a significant difference due to memory effects for the emotional foreground focus RHit–Hit trials. BA = Brodmann area; MNI = Montreal Neurological Institute; MTL = medial temporal lobe; PFC = prefrontal cortex; L = left; R = right.
[a] Indicates clusters that are also significant at the more conservative threshold (see the Methods section).

Neural Correlates of Enhanced Objective Emotional Relational Memory When Focusing on Context

Analyses targeting the neural correlates of this behavioral effect revealed a cluster of activation in the left head of the HC that predicted subsequent objective RM when focusing on contextual details of emotional pictures (Table 6 and Figure 8). Consistent with our expectations, there was also a posterior PHC/parahippocampal place area (PPA; R. Epstein & Kanwisher, 1998) cluster showing a similar subsequent memory/Dm effect (14 voxels). Although this latter cluster did not reach the extent threshold for significance (20 voxels), it overlapped with the PPA area involved in the perceptual processing of contextual information when focusing on the background details of emotional pictures (F. Dolcos, Katsumi, Shen, et al., 2020). Furthermore, the follow-up ROI-based multivariate analyses identified posterior PHC activation as predicting subsequent objective RM (see Supplemental Material 4). In the PFC, similar to findings on subjective confirmed by objective RM, significant activations were identified in both dlPFC and vlPFC clusters predicting enhanced subsequent objective emotional RM (Table 6).

Similar to the connectivity results described above, analyses using the anterior HC and PFC seeds showing enhanced activity predicting objective emotional RM when focusing on contextual details also identified evidence of HC–MTL and PFC–MTL cross-talk linked to this behavioral effect (Table 7). Specifically, the anterior hippocampal seeds showed significant coupling with emotion- and memory-related MTL regions. The same was also the case for the PFC–MTL connectivity patterns, which also point to dissociable modulatory influences from the left PFC seed, showing overlapping Dm effects for the two targeted behavioral effects, on activity in emotion- and memory-related MTL regions (Table 7 and Figure 9). Similar to the findings on subjective confirmed by objective RM, these patterns are consistent with synergistic interactions among these regions.

Converging and Dissociable Prefrontal Cortex Modulation of Medial Temporal Lobe Activity Linked to Enhanced Relational Memory by Emotion

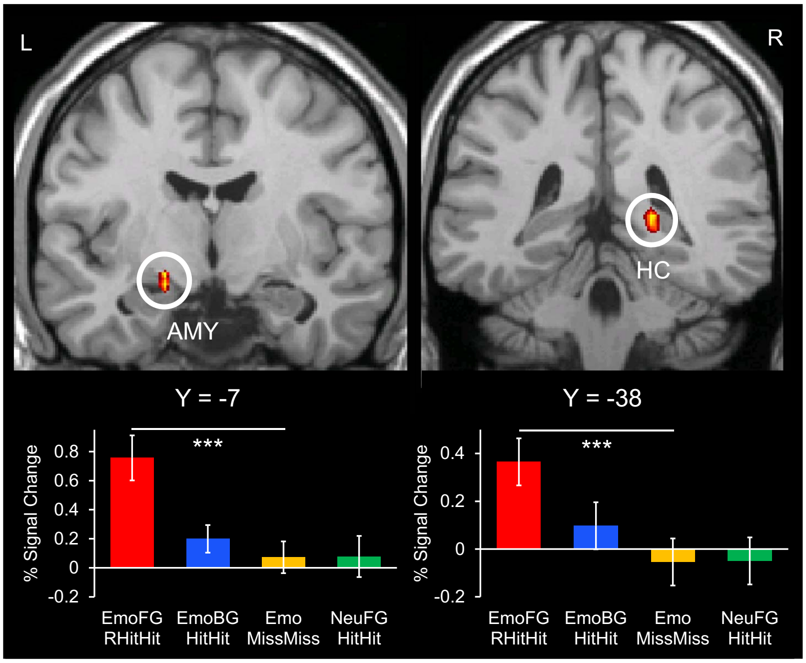
Interestingly, analyses investigating the MTL and PFC correlates of the two targeted behavioral effects identified a common area in the left vlPFC that showed Dm effects for both subjective confirmed by objective RM and the objective emotional RM (Figure 9, top panels). Moreover, connectivity analyses using this conjunction cluster as a seed identified evidence of converging and dissociable connectivity with MTL regions, linked to the two behavioral effects (compare Tables 5 and 7). For instance, both effects were associated with significant vlPFC–AMY coupling but with dissociable AMY clusters. Overall, these connectivity findings are consistent with vlPFC modulation of MTL activity linked to enhanced RM by emotion.

Discussion

Studies 1, 2, and 3 demonstrated that emotion enhances RM if measured with increased specificity and more comprehensively and

Figure 7

Amygdalar and Hippocampal Activations Associated With Enhanced Subjective Confirmed by Objective Relational Memory, When Focusing on Emotion



Note. Illustrated are clusters showing a significant difference due to memory effects for the EmoFG RHit–Hit trials in the left posterior amygdala (AMY) and right posterior hippocampus (HC). The bar graphs display the functional magnetic resonance imaging signals associated with different conditions, extracted from the areas highlighted by the white circles, at the peak time point following the picture onset. L = left; R = right; EmoFG = emotional foreground focus; EmoBG = emotional background focus; NeuFG = neutral foreground focus. See the online article for the color version of this figure.

if emotion–attention interactions are accounted for (statistically or by task manipulation). Whereas the first two studies accomplished this via multilevel modeling, using eye-tracking data, Study 3 diminished innate attention-capturing tendencies in emotion–attention interactions by instructing participants to engage with the images in specific ways. Indeed, Study 3 showed that by instructing participants to focus away from the emotional content and on the nonemotional background of pictures, it is possible to diminish the emotional response while enhancing processing of and memory for contextual details. The manipulation aspect of the present study carries implications from an emotion regulation standpoint, as it shows that it is possible to prevent potential decontextualization of distressing memories via attentional control (see the General Discussion section). The fMRI data revealed MTL and PFC mechanisms linked to the two main behavioral findings: (1) enhanced subjective confirmed by objective RM for emotional stimuli, which was maximized when focusing on the emotional aspects of pictures, and (2) enhanced objective RM by emotion, which was maximized when focusing on the contextual details of emotional pictures. In both cases, we found evidence of MTL and PFC activity and of MTL–MTL and PFC–MTL coupling associated with emotional RM, linked to the specificity of defining and measuring RM and to the task manipulation involving up- or downregulation of emotion processing.

Transparency and Openness

The analytic code and study materials relevant to all three studies of the present report have been uploaded to a public repository (https://osf.io/fr5d2/; Bogdan et al., 2024), and future additions will be made upon further clarifying sharing-related matters with the local IRB office. Adhering to the journal's Transparency and Openness Promotion guidelines, we report all measurements and design elements, we properly cite the methods used, and our reporting meets the APA standards. We also report that the present studies, analyses, and sample sizes were not preregistered and that our article also includes a direct replication.

General Discussion

This research addressed open issues and reconciled discrepant evidence regarding the impact of emotion on RM, by capitalizing on three unique design features: (a) measuring RM with increased specificity, (b) accounting for emotion–attention effects, and (c) using integrated stimuli. Results from Study 1 showed that (a) emotion enhances subjective confirmed by objective RM (RHit–Hit) and that (b) emotion can elicit opposing effects on objective RM, depending on whether attention effects are accounted for or not with eye-tracking data. Study 2 replicated these initial results with

Table 5

Significant Medial Temporal Lobe–Medial Temporal Lobe and Prefrontal Cortex–Medial Temporal Lobe Functional Coupling Associated With Subjective Confirmed by Objective Relational Memory When Focusing on Emotion

			MNI coordinate				
Brain region	Side	BA	*x*	*y*	*z*	*t*	Cluster size
L amygdala							
Amygdala	R		20	0	−16	6.48	118[a]
Hippocampus head	R		32	−18	−16	4.45	32
R amygdala							
Amygdala	L		−20	−2	−16	8.86	228[a]
Hippocampus head	L		−20	−16	−14	3.95	
Hippocampus head	R		30	−12	−20	5.14	188[a]
Hippocampus body	R		30	−22	−14	5.04	
Posterior PHC	R	35	22	−28	−20	4.43	45[a]
L vlPFC							
Amygdala	L		−24	0	−16	5.12	39[a]
Amygdala	R		24	0	−14	4.52	29
Perirhinal cortex	R	20	42	−14	−40	5.60	42[a]
Hippocampus head	L		−34	−14	−16	5.67	23
Posterior PHC	L	35	−28	−30	−22	4.96	22
Posterior PHC/PPA	L	36	−28	−42	−6	5.39	53[a]
Posterior PHC/PPA	R	35	24	−34	−12	4.68	142[a]
Hippocampus tail	R		28	−44	−6	4.83	

Note. Peak coordinates of medial temporal lobe (MTL) clusters from connectivity analyses of EmoFG RHit–Hit trials. The results are organized by the seed used for each connectivity analysis (R amygdala, L amygdala, and L vlPFC). Voxel-wise connectivity was assessed between each seed and MTL voxels. The table refers to the parahippocampal place area (PPA) as the posterior subregion of the posterior parahippocampal cortex (PHC; R. Epstein & Kanwisher, 1998). BA = Brodmann area; MNI = Montreal Neurological Institute; vlPFC = ventrolateral prefrontal cortex; L = left; R = right.

[a] Indicates clusters that are also significant at the more conservative threshold (see the Method section).

a larger sample size. Study 3 provides further evidence for these patterns using a task that directly manipulated the attentional focus. Results showed that (a) enhanced subjective confirmed by objective RM for emotional stimuli was maximized when focusing on the emotional aspects of stimuli (EmoFG condition) and (b) that enhanced objective RM by emotion was maximized when focusing on the contextual details of emotional stimuli (EmoBG condition). The fMRI analyses revealed that (a) both behavioral effects were predicted by enhanced MTL activation and significant MTL–MTL coupling. Regarding the activation patterns, Dm effects emerged across the AMY and HC, extending our earlier results regarding their role in subjective RM only. In addition, connectivity patterns were seen between these regions and PHC areas, extending our earlier results regarding the upregulation of the PPA when processing contextual information. Outside the MTL, (b) a common area in the left vlPFC showed Dm effects for both behavioral effects, and (c) functional coupling between this area and MTL regions was tied to both forms of RM. Below, we discuss these results in detail.

Table 6

Medial Temporal Lobe and Prefrontal Cortex Correlates of Enhanced Objective Emotional Relational Memory When Focusing on Contextual Information

			MNI coordinate				
Brain region	Side	BA	*x*	*y*	*z*	*t*	Cluster size
MTL clusters							
Hippocampus head	L		−22	−6	−26	4.02	32
PFC clusters							
Middle frontal cortex	L	8	−36	38	36	6.28	65
Inferior frontal cortex	L	45	−40	28	14	4.97	76
Inferior frontal cortex	L	10	−40	46	−6	4.77	69

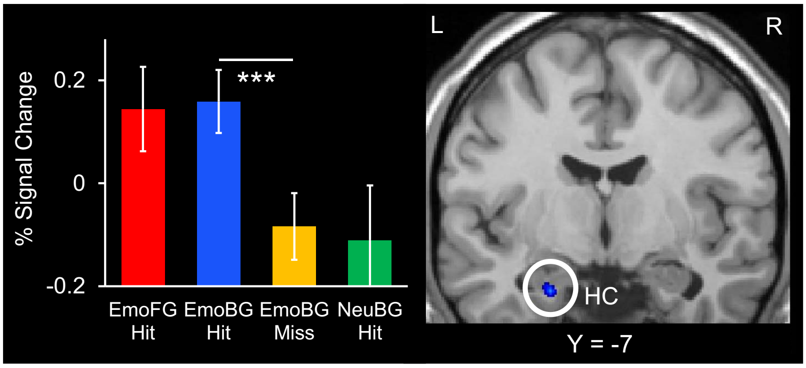
Note. BA = Brodmann area; MNI = Montreal Neurological Institute; MTL = medial temporal lobe; L = left; PFC = prefrontal cortex.

Behavioral Results

The present approach, highlighting the importance of measuring RM with increased specificity and of controlling for effects of attention (statistically and by task manipulation), allowed us to provide reconciling evidence concerning opposing effects of emotion on RM. The research here specifically used the R/K task to test subjective RM. To be clear, the R/K test alone does not provide a pure measure of RM, given that Remember responses correlate with item memory (Dobbins et al., 2000; Dunn, 2004). However, the present employment of the R/K test alongside an objective measure of RM, wherein participants match pairs of items and the associated background, allows for a more specific and complete assessment of the emotion's effects on associative processes. Enhanced subjective confirmed by objective RM (RHit–Hit) by emotion extends evidence regarding the enhancing effects of emotion on subjective RM, as illustrated by research distinguishing between recollection- and familiarity-based responses (F. Dolcos et al., 2005; Kensinger, 2009;

Figure 8

Hippocampal Activation Predicts Enhanced Objective Emotional Relational Memory When Focusing on Contexts



Note. Illustrated are clusters showing a significant difference due to memory (Dm) effect for the EmoBG Hit in the left anterior hippocampus (HC). The bar graphs display the functional magnetic resonance imaging signals associated with different conditions, extracted from the shown cluster at the peak time point following picture onset. L = left; R = right; EmoFG = emotional foreground focus; EmoBG = emotional background focus; NeuBG = neutral background focus. See the online article for the color version of this figure.

Kensinger & Corkin, 2003; Ochsner, 2000; Rimmele et al., 2011; Ventura-Bort et al., 2021). The conceptualization of recollection-based retrieval as subjective RM is consistent with traditional (Eichenbaum et al., 1992) and contemporary views regarding these notions (e.g., Butterworth et al., 2023; Dimsdale-Zucker et al., 2022; F. Dolcos et al., 2005; Frithsen et al., 2019; Sadeh et al., 2018; Wais et al., 2010; Yonelinas et al., 2010), as well as with anecdotal evidence so powerfully captured by Proust's literary work emphasizing the vividness and richness of memories that can be remembered and relived in incredible details when triggered with the right cues (Proust, 1913). Not surprisingly, oftentimes, such memories are emotionally charged.

Increased specificity in measuring RM may also explain differences from previous research pointing to opposing effects of emotion on item memory versus memory for the associated contextual details (Bisby & Burgess, 2014, 2017; Bisby et al., 2016). Those studies

Table 7

Significant Medial Temporal Lobe–Medial Temporal Lobe and Prefrontal Cortex–Medial Temporal Lobe Functional Coupling Associated With Objective Emotional Relational Memory When Focusing on Contextual Information

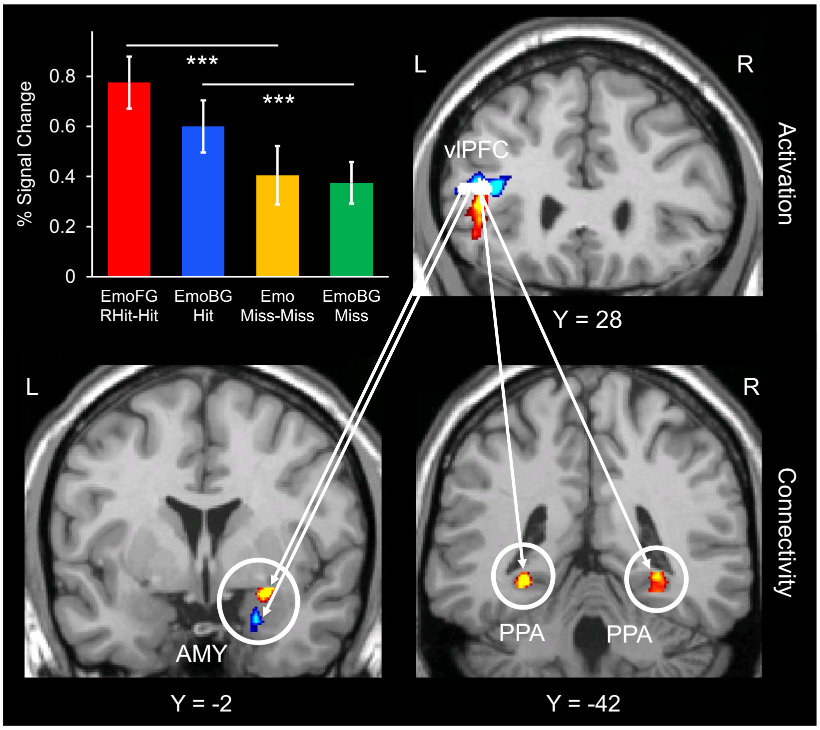
			MNI coordinate				
Brain region	Side	BA	*x*	*y*	*z*	*t*	Cluster size
L hippocampus head							
Amygdala/EC	L	28	−24	0	−30	5.12	280[a,b]
Posterior PHC	L	35	−28	−26	−20	4.31	98[a,b]
Amygdala	R		24	−2	−18	5.43	296[b]
Entorhinal cortex	R	28	24	4	−34	5.97	
Hippocampus body	R		34	−20	−20	5.46	160[b]
Posterior PHC/PPA	R	36	34	−32	−16	3.87	
L vlPFC	L	36	−28	−36	−14	5.16	107[b]
Amygdala	L		−26	−6	−22	4.06	138[b]
Hippocampus head	L		−26	−14	−20	5.25	
Amygdala	R		24	−6	−22	3.88	86[b]
Posterior PHC/PPA	L	36	−26	−32	−12	6.67	164[b]
Posterior PHC	R	36	38	−34	−20	4.58	51[b]
Hippocampus tail	L		36	−24	−8	4.67	63[b]

Note. Peak coordinates of MTL clusters from connectivity analyses of the emotional background focus Hit trials. The results are organized by the two seeds used for the connectivity analyses (L hippocampus head and L vlPFC). Voxel-wise connectivity was assessed between these seeds and the MTL voxels. BA = Brodmann area; MNI = Montreal Neurological Institute; EC = entorhinal cortex; L = left; R = right; PHC = parahippocampal cortex; PPA = parahippocampal place area; vlPFC = ventrolateral prefrontal cortex.

[a] Indicates voxels from the cluster elicited by the HC seed's connectivity with itself, which expands into neighboring MTL regions; the reported voxels do not include HC voxels, which were anatomically masked out. [b] Indicates clusters that are also significant at the more conservative threshold (see the Method section).

Figure 9

Evidence of Prefrontal Cortex Modulation of Medial Temporal Lobe Activity Linked to Enhanced Relational Memory by Emotion



Note. (Top) The white area indicates the overlap between the red cluster showing a difference due to memory effect (Dm) for enhanced subjective confirmed by objective relational memory (RM) when focusing on emotional aspects of pictures (EmoFG RHit–Hit > Emo Miss-Miss) and the blue cluster showing a Dm effect for enhanced objective emotional RM when focusing on the contextual details of pictures (EmoBG [RM] Hit > EmoBG [RM] Miss). (Bottom) The two brain images illustrate areas showing significant coupling with the white vlPFC seed cluster: Red indicates connectivity linked to EmoFG RHit–Hit (AMY and PPA), and blue indicates connectivity linked to EmoBG (RM) Hit (AMY). L = left; R = right; vlPFC = Ventrolateral Prefrontal Cortex; AMY = amygdala; PPA = parahippocampal place area; EmoFG = emotional foreground focus; EmoBG = emotional background focus. See the online article for the color version of this figure.

assessed the accuracy of item memory using simpler old/new responses, instead of using the R/K paradigm, and thus could not link measures of subjective and objective RM. Some studies measured both subjective and objective RM using the so-called judgment-of-memory approach (Madan et al., 2017). In their tasks, participants encoded pairs of stimuli, and then during retrieval, they first judged whether they believed (subjectively) that they could retrieve the associated items based on being cued with one of the pair’s items. Then, participants also attempted to identify (objectively) what the original pair consisted of. However, the differences in results from the present studies could be related to possible differences in the type of subjective details that drive the accuracy of subjective RM (and its confirmation by accurate RM) in the R/K paradigm employed here versus the judgment-of-memory tasks used by Madan et al. (2017). In addition, factors beyond the retrieval procedures may be at play, as Madan et al. (2017) tested RM for pairs of unrelated items, contrasting our use of integrated stimuli, which is another possible explanation for the diverging results. At any rate, such conceptual and methodological differences illustrate how the specific retrieval procedures employed can influence whether enhancing, impairing, or null effects of emotion on RM emerge, which should be further clarified by future research.

The present study also extends research by Rimmele et al. (2011), who likewise tested memory using a task that included both an R/K test and an objective RM item–context matching test. However, their study only tested objective RM in item memory Hit trials (R or K responses), whereas our study tested objective RM for every old image regardless of participants’ R/K responses. They found that emotion impaired objective RM following Remember responses, but it had no significant effect on objective RM following Know responses. Thus, these earlier results point to possible modulation by emotion of the link between subjective and objective RM. To further clarify this, our studies also tested objective RM for every image and included separate analyses of objective RM, not conditional on R/K responses. Hence, the present design is better suited for pinpointing the effects of emotion on objective RM, both together with and separately from subjective RM. Overall, our more extensive analyses, along with a design that also accounted for emotion–attention interactions, recorded fMRI, and included features to upregulate emotion's effects (e.g., a longer retention interval and integrated stimuli), provide a more complete perspective of the emotion's effects on memory and the associated neural correlates. Notably, the present experimental design also opens the possibility of investigating other possible combinations of behavioral patterns. For instance, it would be interesting to investigate the eye gaze pattern and/or the related brain activity for the successful subjective RM but failed objective RM (i.e., for the RHit–Miss trials). Similarly, clarification of such patterns for failed subjective RM but successfully "recovered" memories when tested objectively (i.e., for the Miss–Hit trials) would also be interesting. However, answering these questions was not part of the main goal of the present research and should be the focus of future research.

Turning to the importance of accounting for the effects of attention, Studies 1 and 2 accomplished this statistically via multilevel modeling and incorporation of eye-tracking data, and Study 3 manipulated the attentional focus by instructing participants to engage with the images in specific ways. By incorporating eye-tracking data, Study 1 distinguished between an indirect, impairing effect (mediated by attention) and a direct, enhancing effect of emotion on objective RM. Importantly, these findings were replicated by Study 2. The attention-capturing properties of emotional stimuli are well documented (reviewed by Carretié, 2014; F. Dolcos, Katsumi, Moore, et al., 2020; Öhman, 2005; Pourtois & Vuilleumier, 2006), and earlier memory studies have also investigated the interplay between emotion, attention, and memory for central versus peripheral scene information (J. S. Kim et al., 2013; Riggs et al., 2011; Steinmetz & Kensinger, 2013). In these studies, participants viewed screens containing both negative (central) and neutral (peripheral) information while recording eye tracking. These studies typically find enhanced memory for central details, possibly linked to a capturing effect of emotion, at the expense of memory for peripheral information. Interestingly, the emotional enhancement of memory for central information persisted even when attention-capturing effects were statistically controlled for. However, these designs do not measure RM per se, as they typically assess separately the memory for central and peripheral details. The present research extends this approach into the domain of emotional RM, and unlike the research on central versus peripheral memory, patterns related to emotional RM fundamentally change once attention effects are controlled for. Here, the magnitude of attentional effects is strikingly large, enough to mask a significant direct effect. Thus, emotional memory research should not treat the possibility of attentional biases as a mild caveat but rather as a major factor that can determine whether enhancing or impairing effects are found (for further discussion, see Herweg, Solomon, & Kahana, 2020; Voss et al., 2017). Aside from methodological aspects, there are also theoretical implications regarding emotional trade-offs in memory (Kensinger et al., 2007; Mather & Sutherland, 2011), and overall our results show that depending on how emotional RM is conceptualized and measured, null, impairing, or enhancing effects can be identified.

As shown in Study 3, the effects of attention can also be investigated through task manipulations. On the one hand, instructing participants to focus on the emotional content maximizes enhanced subjective emotional RM and the likelihood of being confirmed by accurate objective RM. On the contrary, focusing away from the emotional content and on the nonemotional background of pictures diminished the emotional response and enhanced perceptual processing and memory for contextual details. Our investigation provided initial evidence regarding the importance of voluntary attentional focus in clarifying the impact of emotion on RM. A previous study using a design similar to those mentioned above measuring trade-offs in the impact of emotion on memory for central versus peripheral information (J. S. Kim et al., 2013; Riggs et al., 2011; Steinmetz & Kensinger, 2013) reported the disappearance of the central/peripheral trade-off when participants were instructed to process the pictures in a way that would allow them to guide an artist in accurately reproducing their content based on the participants' descriptions of the pictures (see Experiment 4 by Kensinger et al., 2007). However, as mentioned above, those designs do not measure RM per se, as the memory for central and peripheral details is assessed separately. Moreover, even though it encouraged detailed processing of perceptual details, that task did not involve emotion regulation. Here, by instructing participants to specifically focus on the contextual details of emotional stimuli during encoding, their emotional responses are reduced (F. Dolcos, Katsumi, Shen, et al., 2020), and we found evidence of enhanced RM by emotion, which was reflected in increased accuracy in correctly matching the emotional items to their associated scene backgrounds (Figure 6).

One key emerging question is how the present findings can be reconciled with earlier literature, which has found that emotion impairs objective RM and argued that the impairment does not hinge on attention. The work by Bisby et al. (2018) is one such example. This earlier research attempted to account for attention by examining RM when negative and neutral stimuli were presented sequentially rather than side by side and found emotional impairment. However, their studies also showed that emotional impairment was more subtle when negative and neutral stimuli were shown sequentially, which supports the idea that attentional effects may be at play. It is also worth noting that negative arousal can narrow attention even when negative stimuli are not directly present, such as in studies involving loud stress-inducing noises or electric shocks (Hockey, 1970; Mendl, 1999). The present research, which measures gaze or directly manipulates the attentional focus, may more fully control emotion–attention effects on memory encoding. Hence, our findings on negative stimuli impairing RM, in part, via attention are compatible with this earlier research.

The present attentional manipulation has important practical implications from an emotion regulation perspective. Specifically, *FA* is an emotion regulation strategy, wherein individuals adjust their attentional focus to upregulate or downregulate their emotional responses. Our earlier reports using the present design and samples showed that voluntarily focusing on the BG component of emotional images leads to downregulation of experienced emotional responses associated with picture processing, as measured by changes in emotional ratings. These earlier reports (F. Dolcos et al., 2022; F. Dolcos, Katsumi, Shen, et al., 2020) leveraged the rating and eye-tracking data from Study 3 data that were not analyzed here. Adding to these results, our present findings illustrate how controlling the attentional focus also influences memory formation and suggest that these dual effects—reduced experienced emotion and increased objective RM—are connected. Specifically, voluntary attentional focus on background diminishes the natural involuntary attention-capturing effect of emotion and reduces the amount of emotional information processed. This both dampens the emotional response and opens the door for increased processing and encoding of contextual information, which in turn leads to enhanced item–context binding and heightened RM.

Because our study focused on capturing more comprehensively the richness and specificity of RM, rather than on source memory—a related concept that is also often studied in the context of emotional memory (Chiu et al., 2013)—our findings may be particularly meaningful for understanding clinical disorders, such as PTSD. Whereas the way source memory is typically tested concerns limited associations with an item's properties (e.g., the color of words or the frame color of pictures), typical RM tasks capture richer associations (e.g., between objects/faces and background scenes). Therefore, they may be more appropriate for understanding involuntary retrieval of memories for distressing events, which is a defining feature of maladaptive emotional processing in PTSD. Uncontrolled spontaneous recollection of traumatic memories in PTSD, outside of the context in which distressing events occurred, is thought to reflect memory *de*contextualization. This is because the link between an emotional stimulus and the associated contextual information is degraded or ruptured, such that these relations lose specificity and the emotional content is more readily activated by nonspecific cues (Bisby et al., 2020; F. Dolcos, 2013). It is also possible that strengthening the binding between a distressing event and its context may also increase the likelihood of retrieving memories of the event, if one repeatedly encounters the original encoding context of the distressing event. Future studies should also investigate whether engaging FA during repeated exposure to contexts previously associated with distressing events promotes the formation of new associations for those contexts, so that over time they will be perceived as safe. Potentially diminished retrieval of distressing memories as a result of such new safe associations for originally problematic contexts also has practical and clinical implications and deserves further consideration by researchers and clinicians. Investigating these topics, much like in the present research, will require further tasks probing RM comprehensively and with high specificity.

Beyond encoding, the present findings complement evidence regarding the effectiveness of FA in modulating the emotional responses to retrieved memories, as internal stimuli (e.g., Denkova et al., 2015; Iordan et al., 2019), which can also promote memory *re*contextualization. These combined findings have important practical implications because they point to potentially game-changing innovations for emotion regulation, such as training these types of attentional focus strategies to use when encountering challenging emotional stimuli (external or internal), to increase resilience and reduce distress (e.g., S. Dolcos et al., 2021). Hence, the present results add to the multifaceted practical relevance of this approach to regulating emotional responses and memories.

On a similar note, aging is associated with RM impairments (Bastin et al., 2014; F. Dolcos et al., 2017; Etchamendy et al., 2012), and the present results speak to possible attention-based strategies to facilitate encoding and enhance the specificity of RM. Age-related memory decline is partially rooted in the effect of aging on attention (Chan et al., 2011; Lee et al., 2018; Zheng et al., 2018), and providing older adults with instructions on how to scan images helps mitigate drops in memory performance (Shih et al., 2012). The present findings suggest that such attentional strategies may assist with encoding different types of memories. Neural evidence adds to these claims. Older adults with youthful episodic memory function show more distinct stimulus representations during encoding in regions linked to higher order visual processing, including the parahippocampal and fusiform gyri (Katsumi et al., 2021). In contrast, age-related decline is linked to dampened processing in posterior brain areas and functional networks linked to attention (Davis et al., 2008; Lee et al., 2018; Zheng et al., 2018). Hence, the attentional control aspects of the present design may be a promising area for the development of compensatory strategies to boost memory in older adults (see also work on episodic specificity induction, which is another strategy to enhance retrieval; Madore et al., 2014).

Regarding our final design feature, the present results shed further light on the use of integrated, ecologically valid stimuli, in memory research. This is another difference from earlier research showing emotional item enhancement and RM impairment (Bisby & Burgess, 2014; Bisby et al., 2018), which may explain the differences in findings, and hence warrants further clarification. Some previous emotional memory research has likewise employed integrated stimuli, such as the study by Steinmetz and Kensinger (2013). However, the said study investigated emotion's impact on memory for central versus peripheral information, separately, as opposed to their association. Unlike that study, testing memory for the BG component separately, we tested memory for FG–BG associations. Similarly, some studies have used integrated stimuli and tested RM (Madan et al., 2020; Mickley Steinmetz et al., 2016), but these earlier designs showed that the RM enhancement only applied to retrieval via free recall (e.g., participants cued with emotional objects were better able to generate verbal descriptions of their background). Given that arousal's enhancements of memory are more prominent in recall-based designs, in general (Chang et al., 2021), these studies suggest that identifying emotional enhancement of RM requires both presenting integrated stimuli during encoding and testing free recall during retrieval. Instead, the present findings demonstrate that emotional enhancement of RM also applies to recognition, hence broadening the span of emotion's effects. It is also worth noting that none of these earlier studies incorporated the R/K test into their retrieval procedures nor collected eye-tracking data. Our research demonstrates the benefits of combining these different aspects to more comprehensively capture the complexity of RM and carve out the effects of emotion. Integrated stimuli have also seen rising use in emotional memory research beyond image-based designs (e.g., Dev et al., 2021; Makowski et al., 2017), and the present findings add to the evidence that using these types of integrated stimuli can yield results that diverge from those obtained with nonnaturalistic designs. However, to our knowledge, no study has manipulated the level of integration, which should be addressed in future work.

Taken together, the present behavioral findings provide reconciling evidence concerning opposing effects of emotion on RM, by showing that emotion enhances RM if measured with increased specificity and if emotion–attention interactions are accounted for. As discussed in the next section, these findings are complemented by the fMRI results regarding the neural correlates of the two main behavioral effects identified in Study 3. However, an important question still emerges regarding the behavioral findings: What drives the enhancing direct effect of emotion on objective RM (illustrated in Figure 3), which arises once the indirect effects mediated by attention are controlled? Insight may come from evidence regarding the impact of emotion on perception and memory linked to the timing of emotion processing. Evidence shows that emotional information is processed faster than neutral information (reviewed by Öhman, 2005; Vuilleumier, 2005), and this privileged access to processing resources may also explain its enhancing effect on memory (F. Dolcos & Cabeza, 2002). Interestingly, even when perceptual processing is limited by the availability of processing resources (Pessoa, 2005), as shown by tasks where emotional information is presented as a task-irrelevant distraction (Shafer & Dolcos, 2012; Shafer et al., 2012), emotional information still finds a way to enhance memory, and this pervasive effect can emerge with very brief stimulus presentation (250 ms; Shafer & Dolcos, 2012; Shafer et al., 2012). Although the present fMRI data do not speak directly to the neural correlates of this behavioral effect, it is possible that it is linked to the MTL role discussed below, which is part of direct/automatic mechanisms contributing to the memory-enhancing effect of emotion (F. Dolcos et al., 2017; LaBar & Cabeza, 2006; Pessoa & Adolphs, 2010). Further studies are needed on the precise cognitive and neural mechanisms of the direct, possibly automatic effect of emotion on RM identified here, but the present evidence demonstrates that emotion also elicits effects independently of attention.

It is important to recognize that our studies used only negatively valenced emotional stimuli, which may elicit different results than positive stimuli. Research using verbal stimuli as memoranda has repeatedly found differences between the two valences, with heightened memory for associations with positive words relative to associations with negative words (Anderson & Shimamura, 2005; Madan et al., 2019; Zimmerman & Kelley, 2010). Regarding other types of memoranda, the evidence is somewhat less clear, but the literature overall shows a trend wherein studies testing the effects of positive valence are more likely to find enhancing effects on RM (Pierce & Kensinger, 2011; Smith et al., 2004, 2005). Potentially, this valence-based dissociation is linked to attention. Whereas negative arousal narrows attention, positive arousal expands participants' attention and encourages them to explore more diverse pieces of information (see broaden-and-build theory; Fredrickson, 2004; Fredrickson & Branigan, 2005). Hence, opposite to how negative stimuli may indirectly impair RM due to attentional narrowing, positive stimuli may enhance RM via attentional broadening, although this hypothesis is yet to be tested directly. Further research would also benefit from investigation of similar issues related to other types of memory associations, such as temporal, which is another emerging area regarding the impact of emotion on RM (Bogdan, Dolcos, Federmeier, et al., 2023; Palombo et al., 2021; Petrucci & Palombo, 2021). For further discussion on the generalizability of the findings, see also the Constraints on Generality section.

Functional Magnetic Resonance Imaging Results

The patterns of activity and functional connectivity linked to the two main behavioral findings identified in Study 3 are consistent with synergistic interactions between emotion- and memory-related MTL areas and with a top–down role of the left vlPFC in modulating these effects. We found that both enhanced subjective confirmed by objective RM for emotional stimuli (maximized when focusing on the emotional aspects of stimuli) and enhanced objective RM by emotion (maximized when focusing on the contextual details of emotional stimuli) were predicted by enhanced MTL activation and enhanced MTL–MTL interactions during encoding. Moreover, a common area in the left vlPFC showed Dm effects linked to both behavioral effects, and functional coupling between this area and emotion- and memory-related MTL regions was associated with both forms of RM. Regarding the MTL findings, the present patterns of activity and functional connectivity suggest dissociable pathways by which emotion enhances RM, linked to the two behavioral effects. Specifically, whereas the first behavioral effect may involve modulatory influences originating in the AMY on activity in brain regions associated with recollection and RM (HC), through an *emotion-to-memory* route (see Tables 4 and 5), the second behavioral effect may involve modulatory influences among MTL regions involved in processing perceptual contextual information (PHC) and RM encoding (HC), through a *perception-to-memory* route (see Tables 6 and 7); the latter also benefits from AMY's involvement. These conclusions on AMY and PHC activation are also supported by multivariate tests employing family-wise error correction methods (Supplemental Material 4). Although the present analyses did not test for directional influences among regions, these hypotheses are consistent with our activation and connectivity results and speak to earlier evidence testing directionality (Inman et al., 2018; McGaugh et al., 1996; Roozendaal & McGaugh, 1997; Sato et al., 2017).

The findings regarding the emotion-to-memory route expand the modulation hypothesis, wherein the AMY influences processing in other MTL regions via direct projections (Caffé et al., 1987; McGaugh, 2000, 2004; Packard et al., 1994). This broad modulatory account is also motivated by studies using electrical stimulation or pharmacological intervention to demonstrate causal influences of the AMY on hippocampal processing (Inman et al., 2018; McGaugh et al., 1996; Roozendaal & McGaugh, 1997). The present results suggest that upregulating modulation by the AMY also applies to its role in RM, as evidenced by our results on subjective RM confirmed by objective RM. Beyond just memory studies, AMY–HC coupling is also linked to various forms of emotion processing (see meta-analyses by Di et al., 2017). The present findings are at odds with the model by Yonelinas and Ritchey (2015) regarding the impact of emotion on item versus RM, which posits that arousal prompts the AMY to strengthen encoding in MTL regions involved in item memory (PRC), but it causes the HC to disengage from associative binding, leading to faster decay of HC-based associations (see also Bisby & Burgess, 2017; Bisby et al., 2016). As discussed earlier and shown here, this discrepancy can also be related to differences in the way RM is conceptualized and measured.

The results regarding the perception-to-memory route extend previous findings identifying the PPA's involvement in enhanced perceptual processing of contextual details under attentional focus (Aly & Turk-Browne, 2016; F. Dolcos, Katsumi, Bogdan, et al., 2020; Turk-Browne et al., 2013) and are consistent with research showing its involvement in encoding contextual information (Herweg, Sharan, et al., 2020; LaFlamme et al., 2021). The PHC is a large heterogeneous region, and our results were predominantly linked to its posterior segments, which include the PPA, thought to play a specific role in perceiving scenes and encoding contextual information (Aminoff et al., 2007; Diana et al., 2013; R. A. Epstein, 2008; R. Epstein & Kanwisher, 1998). Moreover, our own earlier report showed that focusing on contextual perceptual information upregulates PPA activity (F. Dolcos, Katsumi, Shen, et al., 2020). It should be noted, however, that the PHC proper as a whole also has other functions. The present connectivity findings also extend results from nonemotional memory research showing how HC–PPA synergistic interactions support contextual processing and contextual memory (Herweg, Sharan, et al., 2020; Herweg, Solomon, & Kahana, 2020;

Tullo et al., 2023). Adding to this earlier research, the present results suggest that emotional memory encoding is linked to HC–PPA connectivity, which itself may be upregulated via AMY influences, given our identified AMY–PPA results. Alternatively, emotional upregulation of processing in the PPA and HC may be tied to indirect effects of the AMY, via its upregulation of perceptual processing earlier in the visual stream, as evidenced by psychophysiological interaction and dynamic causal modeling studies (Ousdal et al., 2014; Sato et al., 2017). Overall, although supported by previous research and the present connectivity results, the existence of this route is more speculative compared with the standard emotion-to-memory route, and thus more research is needed to confirm it. For instance, future research could involve manipulations aimed at enhancing perceptual processing leading to enhanced RM—for example, by instructing participants that their memory for contextual/BG details or for item–context/FG-BG associations would be tested and encouraging them to intentionally bind perceptual contextual details with the FG content of stimuli. It is expected that this voluntary upregulation of memory encoding, complementing the voluntary attentional control to focus on contextual/BG details, would promote the formation of FG–BG associations, which will be reflected in increased PHC activity and PHC–HC connectivity. We also expect that these effects would be greater for stimuli with emotional FG, which would further confirm the relevance of this route for understanding the emotion's impact on RM.

Interestingly, both routes involve direct and indirect emotional influences, through amygdalar engagement. For example, for the emotion-to-memory route, the AMY may also influence the HC activity indirectly, via its impact on other regions, such as the PPA, which influences the hippocampal binding (Chun & Phelps, 1999; Eichenbaum et al., 1992; 2007; Herweg, Solomon, & Kahana, 2020; Konkel & Cohen, 2009; Moscovitch et al., 2006; Roozendaal & McGaugh, 2011; Schacter et al., 2017; Yonelinas et al., 2019), and is also susceptible to effects of arousal (Murty et al., 2011). The AMY–PPA connectivity patterns identified here for subjective confirmed by objective RM are consistent with this idea and with evidence of bidirectional connections among these regions (McGaugh, 2002; Phelps & LeDoux, 2005; Stefanacci et al., 1996). Although further research is needed to confirm these purported routes and to clarify how they may map onto different aspects of memory, such research may also benefit from considering functional heterogeneity within the HC's role (Dalton et al., 2022). Consistent with this idea, the present results showed that the subjective confirmed by objective RM contrast identified a cluster in the HC tail, whereas the objective RM contrast identified a cluster in the HC head. One possibility is that these two areas correspond to differential encoding of associative information along the longitudinal axis of the HC, but this speculation needs to be further tested. Overall, the present findings are consistent with a model of dual enhancement of associative memory by emotion, but more research is needed to identify the contribution of the two MTL routes mentioned above.

Turning to the role of non-MTL regions, the present left vlPFC findings are consistent with a common role of this area in both behavioral effects, possibly through top–down influences on MTL activity. Regarding the Dm activity results, some of the vlPFC clusters identified here overlap with earlier results predicting enhanced emotional episodic memory (F. Dolcos et al., 2013; F. Dolcos et al., 2004a; Shafer & Dolcos, 2012), and these findings are also consistent with a role of the left vlPFC in nonemotional subjective RM (Ranganath et al., 2003). The seemingly multifaceted involvement of the vlPFC in memory complements evidence regarding its role in affective processing (Berboth & Morawetz, 2021; F. Dolcos, Katsumi, Shen, et al., 2020; Fusar-Poli et al., 2009; K. A. Lindquist et al., 2016; Murty et al., 2011), along with its involvement in attentional and cognitive control to mitigate emotional distraction (F. Dolcos, Katsumi, Moore, et al., 2020; Iordan et al., 2013; Shafer et al., 2012; Sylvester et al., 2018); for research linking all of these notions, see F. Dolcos et al. (2013) and Engen and Anderson (2018). Regarding the functional connectivity findings, the present results are consistent with evidence of increased vlPFC–AMY connectivity linked to various aspects of emotion processing (Berboth & Morawetz, 2021; Di et al., 2017; F. Dolcos et al., 2006). The idea that the vlPFC plays a top–down attentional control role in the present design is also consistent with causal evidence from transcranial magnetic stimulation and dynamic causal modeling studies, suggesting that the vlPFC modulates amygdalar activity (Kung et al., 2023; Sydnor et al., 2022). The functional connectivity findings are also consistent with evidence of structural and functional heterogeneity of the vlPFC, as well as with its nodal position in various large-scale functional networks (e.g., the salience, ventral attention, and cingulo-opercular networks; Corbetta et al., 2008; Dosenbach et al., 2008; Haber et al., 2022; Seeley, 2019). Hence, it is not surprising that this region can exert top–down modulatory influences that may orchestrate the engagement of MTL regions across multiple Dm contrasts.

It is important to note that our procedure for assessing the cluster extent thresholds was selected for consistency with our earlier reports using the fMRI data set (F. Dolcos, Katsumi, Bogdan, et al., 2020; F. Dolcos, Katsumi, Shen, et al., 2020) and similar studies in the literature that likewise used this approach (e.g., Beaty et al., 2020; Bowen et al., 2020; Duggirala et al., 2022; Thakral et al., 2020, 2022). However, the alternative cluster extent thresholds determined by AFNI's 3dClustSim yielded more conservative estimates, which would render some of our reported results subthreshold, had they been evaluated at $p_{\mathrm{FWE}} < .05$. Nonetheless, the multivariate analyses reported in the Supplemental Materials give weight to the validity of the univariate analyses, particularly for the significant AMY result and the subthreshold PPA findings. Additionally, the connectivity results largely remain significant even at this stricter threshold, and thus the overall conclusions would remain unchanged. The readers are advised that different, albeit valid, methods used to correct for multiple comparisons may result in differences in findings. Related to this point on conservative analyses, future research may also benefit from further leveraging developments in multivariate fMRI analysis, which are more sensitive (although less specific) and can identify meaningful patterns even with very strict family-wise error thresholds (Bogdan, Iordan, et al., 2023; Scheinost et al., 2019; Weaverdyck et al., 2020).

Constraints on Generality

The present results are based on data from (a) samples of undergraduate students from a Western university and (b) other participants from the surrounding area. We expect that the inclusion of both student and nonstudent participants increases the generalizability of the findings. Also pointing to generalizability, available evidence shows that emotional memory effects are similar across cultures (Kwon et al., 2009), and the *Behavioral Neuroscience* literature demonstrates how emotional memory pathways are evolutionarily engrained and widespread (Phelps & LeDoux, 2005). However, the effect sizes of memory patterns may still vary depending on a population's sensitivity to arousing stimuli. Setting aside demographics, questions about generalizability exist on which specific design features are necessary to replicate our findings. For example, our studies used incidental encoding and relatively lengthy retention intervals, as these experimental features upregulate emotion's impact on memory (F. Dolcos et al., 2005; Kensinger et al., 2005; Kleinsmith & Kaplan, 1963; Ritchey et al., 2008). Intentional encoding and/or shorter retention intervals are also common in emotional memory research, and thus further studies are needed to investigate whether our findings generalize across these and other dimensions.

Conclusion

By capitalizing on three key novel design features and integration of behavioral, eye-tracking, and fMRI data, the present research provided evidence reconciling discrepant findings regarding the impact of emotion on RM. Studies 1 and 2 showed that emotion enhances not only item memory and subjective RM alone but also subjective confirmed by objective RM. In addition, these studies showed that emotion enhances objective RM when measured separately and when attention effects are accounted for with eye-tracking data. Study 3 extended these findings by directly manipulating the attentional focus and showed that enhanced subjective confirmed by objective RM for emotional stimuli was maximized when focusing on the emotional aspects of stimuli, whereas enhanced objective RM by emotion was maximized when focusing on the contextual details of emotional stimuli. The fMRI data from Study 3 revealed MTL and PFC mechanisms responsible for these two main behavioral findings, consistent with a model of dual enhancement of associative memory by emotion linked to MTL engagement, orchestrated by left vlPFC influences. Specifically, maximized enhancement of subjective confirmed by objective RM when focusing on emotional aspects of stimuli was predicted by the engagement of an emotion-to-memory MTL route, reflected in increased activation in the AMY and HC along with functional coupling between these regions. In contrast, maximized enhancement of objective RM when focusing on the contextual details of emotional stimuli was predicted by the engagement of a purported perception-to-memory MTL route reflected in heightened HC activation and connectivity with the PPA. Importantly, for both behavioral effects, the left vlPFC arose as relevant in terms of both activation and connectivity with MTL regions, consistent with a top–down modulatory role. By challenging the status quo view that emotion impairs RM, these findings shed light on the neurobehavioral mechanisms of emotion–memory interactions and have practical implications for preventing memory *de*contextualization and promoting *re*contextualization following traumatic events. This research may inform training interventions to enhance memory specificity by preserving intact item–context associations when facing daily stressors, increase well-being in healthy functioning and affective disorders, as well as reduce RM declines in healthy and clinical aging.

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