

Annual Review of Psychology

Retrieval of Emotional Events from Memory

Elizabeth A. Kensinger and Jaclyn H. Ford

Department of Psychology, Boston College, Chestnut Hill, Massachusetts 02467, USA;
email: elizabeth.kensinger@bc.edu, jaclyn.ford@bc.edu

Annu. Rev. Psychol. 2020. 71:251–72

First published as a Review in Advance on
July 5, 2019

The *Annual Review of Psychology* is online at
psych.annualreviews.org

<https://doi.org/10.1146/annurev-psych-010419-051123>

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Keywords

memory, emotion, retrieval, valence, retrieval goals, memory function

Abstract

The enhancing effects of emotion on memory have been well documented; emotional events are often more frequently and more vividly remembered than their neutral counterparts. Much of the prior research has emphasized the effects of emotion on encoding processes and the downstream effects of these changes at the time of retrieval. In the current review, we focus specifically on how emotional valence influences retrieval processes, examining how emotion influences the experience of remembering an event at the time of retrieval (retrieval as an end point) as well as how emotion alters the way in which remembering the event affects the underlying memory representation and subsequent retrievals (retrieval as a starting point). We suggest ways in which emotion may augment or interfere with the selective enhancement of particular memory details, using both online and offline processes, and discuss how these effects of emotion may contribute to memory distortions in affective disorders.

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INTRODUCTION

Memory enables us to bring past moments into the present, to relive events and revisit locations, and to reframe conversations and reimagine consequences. As William Faulkner [2012 (1951), p. 73] stated in *Requiem for a Nun*, “The past is never dead. It’s not even past.” The past experiences we are most readily able to bring into the present are those that evoked strong emotions at the time they occurred. Mundane experiences—the food eaten for lunch, the scenery on a drive home—slip quickly from mind, while emotionally intense experiences are more likely to remain part of our mnemonic repertoire.

William James (1890, p. 670) forecast the effect of emotion on memory when he stated, “An impression may be so exciting emotionally as almost to leave a scar upon the cerebral tissues.” Extensive research in the twentieth century provided empirical data to support his conjecture: When an event triggers physiological arousal—a feeling of excitation or agitation often accompanied by a change in heart rate or sweating—a cascade of processes begins, enabling the event to be stored in memory. These early-acting effects of emotional arousal have been well demonstrated, with converging evidence revealed in animal models (reviewed in McGaugh 2000) and humans (reviewed in Phelps 2004). This body of research underscored a key feature that sets emotional memories apart from other memories: their durability. While not all details of emotional events are retained accurately (e.g., Hirst et al. 2015), it is less likely that individuals will forget about the occurrence of a highly emotional event relative to a less emotional one.

Another hallmark feature of emotional memories is their richness at the time of retrieval. Individuals often feel that they have brought an emotional event to mind so vividly that they are reexperiencing or reliving portions of that past event. This feeling is a defining characteristic of “flashbulb memories” (Brown & Kulik 1977), the extremely vivid memories that individuals retain for highly consequential public events. The rich subjective vividness associated with the retrieval of an emotional event has been replicated in many laboratory studies (reviewed in Holland &

Kensinger 2010, Kensinger & Schacter 2016): Even when not all of the details are accurate, the memories feel vivid. This selective enhancement of subjective vividness is especially true in studies that have examined retrieval of negative events (e.g., Cooper et al. 2019). Although this evidence suggests an importance to the way that emotional events are brought to mind at the moment of retrieval, the twentieth century saw relatively little research focused on pinpointing the mechanisms that distinguish retrieval of emotional events from retrieval of other experiences. Fortunately, researchers have now started to examine these mechanisms (see Buchanan 2007 for review), highlighting the importance of interactions among the amygdala (e.g., Daselaar et al. 2008, Murty et al. 2010), hippocampus (Daselaar et al. 2008, Ford et al. 2014), and sensory regions (Bowen et al. 2018) in the retrieval of emotional events.

It is critical to focus on how emotion affects retrieval for two broad reasons. First, the content accessed at retrieval guides our behavior and influences our decision making. Processes that act at the time a memory is formed or stored alter the likelihood of that information to be accessed later, but the weight of a memory in influencing behavior and thought is determined by what is accessed at the time of retrieval. In this review, we focus on consciously accessible retrieval, in complement to the literature that has examined how retrieval of often-fearful memories can guide actions and decisions implicitly (reviewed in Bergstrom 2016, Do Monte et al. 2016). Second, the way content is accessed during the retrieval of emotional memory traces affects well-being. Affective disorders are often accompanied by biases in how emotional events are remembered: Negative content comes to mind too readily or in irrelevant contexts, or it is brought to mind so vividly that the past distracts from the ability to process the present. More generally, while memory for negative events prevents us from repeating mistakes, focusing too much on the negative details of past events at the time of retrieval can impair social relationships (Nolen-Hoeksema et al. 2008), and memory biases may exacerbate anxiety about the future (e.g., Wu et al. 2015). Elucidating memory retrieval processes can therefore be critical both for the advancement of basic science and for translation to the clinic.

In this review, we emphasize that retrieval can be both an end point and a starting point for emotional memories (see **Figure 1**). Retrieval is most commonly depicted as an end point: Retrieval reflects the access to a memory trace that has already been created and stored, and the ability to bring content to mind (i.e., successful retrieval) often curtails additional memory processes. While this characterization of retrieval as an end point is apt, retrieval can also be a starting point: The content accessed affects our actions and decisions in the moment, and the act of retrieval can reshape or reprioritize a memory trace, propagating longer-term effects on thought and behavior (Kornell & Vaughn 2016, Schwabe et al. 2014). Emotional content and affective reactions can

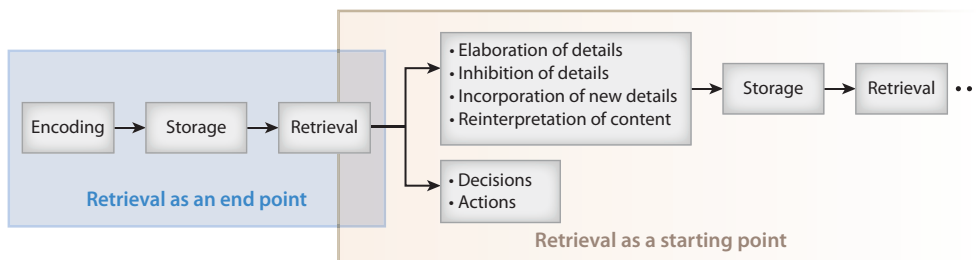


Figure 1

Retrieval is both the outcome of a cascade of episodic memory processes (retrieval as an end point) and a trigger for additional processes that guide behavior and affect how information is maintained in memory over time (retrieval as a starting point).

hold particular weight in guiding decision making (Baumeister et al. 2007, Madan et al. 2014), and it can be particularly adaptive to update or reprioritize memory traces based on new information that suggests their emotional import (Dunsmoor et al. 2015, Kensinger 2015). This makes it especially relevant to think about retrieval as a starting point for emotional memories.

RETRIEVAL AS AN END POINT: EMOTIONAL VALENCE AND RETRIEVAL GOALS AFFECT HOW MEMORY TRACES ARE ACCESSED

What comes to mind at the moment of retrieval can be a consequence of three general factors: the content of the information we seek to retrieve (i.e., the content in the memory trace), the external environment in which we find ourselves (e.g., the retrieval cues available and the context in which we are located), and the internal state that drives our retrieval (e.g., our goal state). There are intricately complex interactions among these spheres of influence (see DuBrow et al. 2017, Holland & Kensinger 2010). While a full explication of those interactions is beyond the scope of this review, we delve into the effects and interactions of two key contributors: the affective valence of the content within the emotional memory trace (i.e., whether the content is unpleasant or pleasant) and the person's goals at the moment that the memory trace is accessed.

Retrieving Memories with Valenced Content

Scholars have frequently reported asymmetries in the way that positive and negative events are experienced (e.g., Ohira et al. 1998, Robinson-Riegler & Winton 1996, Storbeck & Clore 2005). These asymmetries are succinctly captured in Baumeister and colleagues' (2001) review titled "Bad Is Stronger than Good," in which they outline how people tend to notice losses more than gains, feel more impact from negative than positive feedback, and process negative information more thoroughly than positive information. These asymmetries also extend to memory outcomes. For instance, negative events are more likely than positive ones to be associated with vivid recollection (e.g., Dewhurst & Parry 2000, Ochsner 2000). While no memory is immune to distortion, negative events can sometimes be maintained with greater consistency or less distortion than positive memories (reviewed in Kensinger & Schacter 2016). Moreover, the visual details of negative events sometimes can be retained with greater precision (reviewed in Bowen et al. 2018).

Although differences in how positive and negative events are experienced and stored in memory are no doubt important for these effects, recent research has revealed an additional role for differences at the moment of memory retrieval. It has long been proposed that memory retrieval succeeds when there is a match between the state at encoding and the state at retrieval; this need for a good match has been a core feature of many theories of memory, including the encoding specificity principle (Tulving & Thomson 1973), transfer-appropriate processing (Morris et al. 1977), and context- or state-dependent effects on memory (DuBrow et al. 2017, Eich 1980). An important neural signature of memory retrieval is recapitulation, or the ability for the brain to reconfigure itself to resemble its activation or connectivity profile at the time of encoding (reviewed in Danker & Anderson 2010, Rugg et al. 2008). When recapitulation occurs, there is memory success (Waldhauser et al. 2016, Wing et al. 2015) and often the accompanying phenomenology of a subjectively vivid memory (Wheeler et al. 2000).

A series of studies showed that when the content of a memory trace included negative affective valence—even if the memory cue did not contain that valence—there was a greater likelihood of recapitulation, especially in sensory regions of the brain, than when the content of the memory trace was positive or neutral (Bowen & Kensinger 2017b, Kark & Kensinger 2015). This pattern

has been revealed in two different paradigms: one using a visual (line drawing) cue to probe memories of colorful, emotional images, and another using a verbal (neutral word) cue that earlier had been paired with emotional faces or scenes. In both designs, when the memory trace contained negative content, the pattern of activation during successful retrieval looked more similar to the pattern of activation during encoding than it did when the memory trace contained positive or neutral content. Intriguingly, a data-driven approach revealed that, of the many factors that could influence retrieval activity (e.g., memory accuracy), the emotion contained within the memory trace is one of the strongest predictors of retrieval activation patterns (Bowen & Kensinger 2017a). In particular, partial least squares analysis was used to investigate the spatiotemporal whole-brain patterns of network connectivity that were inherent in the memory retrieval data. The results revealed that, even though there was no emotion inherent in the retrieval cues, one of the strongest predictors of the retrieval activity was the emotion that had been associated with the cue at the time of encoding.

This body of research, revealing reliable differences in the way in which positive and negative events are retrieved from memory, led to the proposal of a new model of emotional memory that differs from prior models in a few ways: It emphasizes the role of valence among arousing memories, it underscores the importance of the way sensory regions become incorporated into memory networks, and it puts emphasis on the importance of retrieval processes (Bowen et al. 2018) (see **Figure 2**). Since the time of that publication (Bowen et al. 2018), the valence

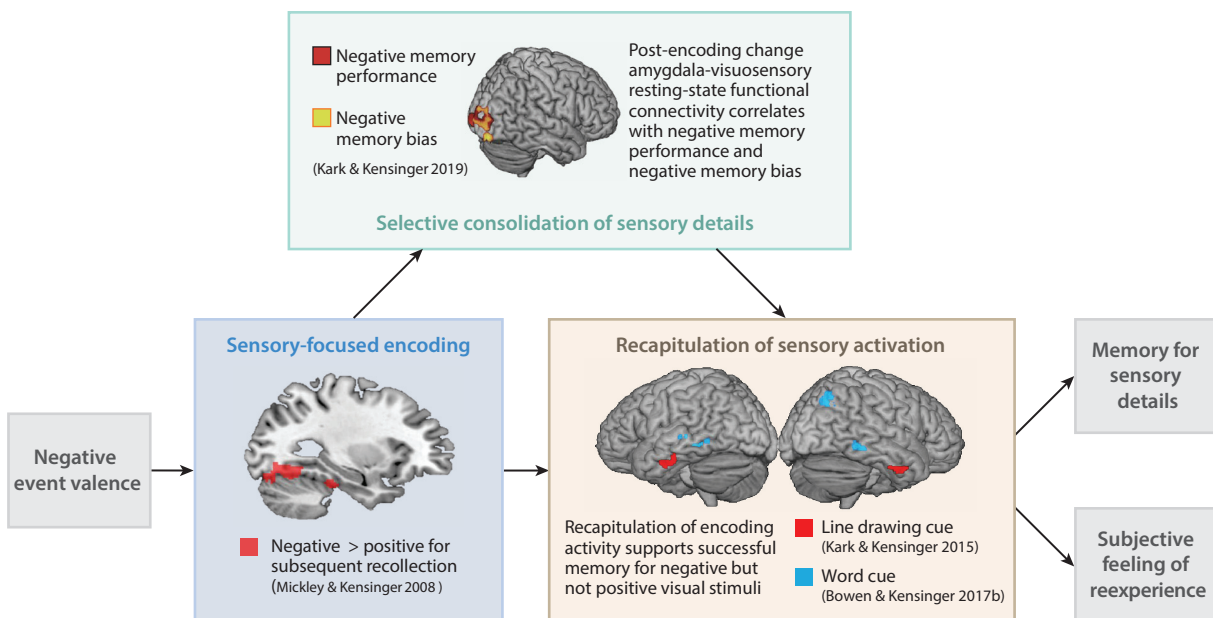


Figure 2

In a model given the mnemonic “NEVER Forget,” Bowen et al. (2018) propose that Negative Emotional Valence Enhances Recapitulation: When a memory contains negative content, there is greater overlap in the regions that are active during the initial processing of the event and those active again during the retrieval of the event. This match is proposed to be important for the enhanced vividness associated with a negative memory.

differences in recapitulation have been replicated when memory was tested after a longer delay (Kark & Kensinger 2019). Kark & Kensinger (2019) also showed that the enhanced sensory recruitment during the retrieval of negative memories is linked to the tendency for participants to retrieve more negative than positive memories. Moreover, valence differences in memory retrieval have been linked to individual differences in the post-encoding coupling between the amygdala and sensory regions, as measured by resting-state functional connectivity (RSFC): Individuals with the greater coupling show better memory for negative information and a greater tendency toward a negative memory bias (Kark & Kensinger 2019).

These results demonstrate that, although much can be similar about how positive and negative arousing events are encoded and stored in memory (LaBar & Cabeza 2006, Murty et al. 2010), retrieval outcomes can differ based on the valence of the content being retrieved (see also Buchanan et al. 2005, Claire et al. 2016). Memories with negative content have a stronger sensory signature at retrieval and are associated with a greater tendency for the brain to reconfigure itself at retrieval to resemble its state at encoding. The results also suggest that there can be individual differences in these sensory signatures for negative events that can relate to the likelihood of remembering negative content; this pattern emphasizes the interaction between the content of the memory being retrieved and the individual. Although some individual differences may reflect stable traits, below we hone in on a more dynamic contributor to this interaction: the goal state of the individual.

Influence of Goal States and Directive Functions on Emotional Memory Retrieval

Although the studies reviewed so far emphasize the influence of the valenced content of a memory trace on its retrieval, this content is not accessed in a vacuum. A person's goals at the time of retrieval, and the function the memory will serve, can influence which memories, and which aspects of a memory trace, are retrieved (Holland et al. 2010, Pillemer 2009). Thus, a person's goals can affect how prominently positive or negative aspects are incorporated into a memory. For example, if you are trying to persuade a friend to join you on a trip to Disney World, you may bring to mind memories of the fun rides and activities on your past trips to the park and share them with your friend. By contrast, if you are trying to decide whether it is worthwhile to purchase a pass to skip the lines at Disney World, you may bring to mind the wait times for the rides and the portions of the park that had the densest crowds. It is the same trip to Disney World being remembered in each case, but the features that come to mind differ depending on the reason for which the memory is being retrieved.

The functions of memory are typically categorized into three broad categories: to create self-continuity and self-image, to direct behavior in the present or in the future, and to enable social bonding (e.g., Bluck & Alea 2002, Pillemer 1992). To allow the memory system to serve these functions, memory traces are constantly being updated to fill in missing information, to make irrelevant details less accessible, or to emphasize important aspects. In other words, the reason a memory is being retrieved can affect how it is remembered.

Autobiographical memory paradigms are particularly useful in examining the functions of emotional memory (see the sidebar titled *Episodic and Autobiographical Memory Paradigms*). Research has revealed that emotional memories can serve important functions at the time of retrieval; remembering the emotion associated with an event serves as a shortcut, providing individuals with a single metric with which to evaluate a past event. This shortcut can serve directive functions—allowing individuals to decide quickly whether they would want to repeat an experience in the future (Levine et al. 2009)—and it features prominently in the life stories that serve self and social functions (Krans et al. 2009). The extent to which emotional memories serve

EPISODIC AND AUTOBIOGRAPHICAL MEMORY PARADIGMS

In episodic memory paradigms, participants learn often-large sets of information and retrieve the information shortly thereafter. In autobiographical memory paradigms, participants recall personal events, often months or years later. Autobiographical paradigms have ecological validity but lack ways to control memory content or evaluate memory accuracy. Episodic paradigms provide experimental control but cannot capture many real-world functions of memory retrieval. While emotional memory is assessed with both paradigms, reactions elicited in episodic paradigms typically lack the features of a full-blown emotional response and would be better labeled as affective memory, with affect signifying a fleeting and relatively automatic response to pleasantness or unpleasantness (Baumeister et al. 2007, Winkelman & Trujillo 2008).

Because of these differences, effects do not always generalize across paradigms. Most notably, negative valence is associated with increased episodic memory vividness (Ochsner 2000) but reduced autobiographical vividness (Destun & Kuiper 1999, Schaefer & Philippot 2005). This reversal may relate to the higher self-relevance of autobiographical memories: When events are highly self-relevant, positive experiences may be retrieved more vividly than negative ones (D'Argembeau & Van der Linden 2008). The reversal may also relate to the different memory delays: Negative event vividness may dissipate over time (fading affect bias; see Walker et al. 1997).

these functions may differ by valence, with positive memories more likely to be retrieved to serve self and social functions and negative memories more likely to be retrieved for directive functions (see Rasmussen & Berntsen 2009). Further, the function served by an emotional event can alter how the event is retrieved, contributing to the differences in how individuals process positive and negative events from their lives. Negative emotions tend to fade faster than positive emotions, a phenomenon known as the fading affect bias (Walker et al. 1997), and negative memories are judged as more remote than they actually are, while positive memories are judged as more recent (Ross & Wilson 2002). This fading of negative affect may have implications not only for how we remember our past, but also for how we envision our future. For instance, it may be harder to bind together the details of a simulated future negative event in a durable way, making it more difficult to remember those negative simulations over time compared to positive or neutral simulations (Szpunar et al. 2012). These biases may be driven by an underlying goal of maintaining a positive self-image (see Walker & Skowronski 2009); we may be motivated to distance ourselves from our negative memories and to hold close our positive memories.

In addition to the three functions described above, it has been suggested that emotional memories can be used to serve an additional emotion regulation function (Gross 1998) at the time of retrieval (see Pasupathi 2003, Pillemer 2009). Because retrieving emotional autobiographical memories from the past can bring back some of the emotions tied to the original experience (Bower 1981), it is possible to selectively recall particular positive memories to bring back those positive emotions and enhance mood. This alteration typically goes in a hedonic direction, shifting a negative emotional experience to be less negative and perhaps more positive (reviewed in Holland & Kensinger 2010), although utilitarian regulation in nonhedonic directions can also occur (Tamir et al. 2007). For instance, if people believe that feeling anger will be useful—for example, by making them more effective at negotiating or better performing in a game such as football—they are willing to take steps to increase the experience of that negative emotion (Tamir et al. 2013).

Using emotional memory retrieval as a strategy to alter mood can lead to many adaptive outcomes. For instance, cuing positive memory retrieval in the lab has been proposed to increase motivation (Stephan et al. 2014), optimism (Cheung et al. 2013), creativity (van Tilburg et al.

2015), inspiration (Stephan et al. 2015), and patience (as measured using a temporal discounting task; Lempert et al. 2017). Retrieval of these positive events recruits the neural circuitry typically associated with reward processing (Speer et al. 2014), suggesting an immediate reward from retrieval. Retrieval of positive memories may also buffer individuals from effects of acute stress: Speer & Delgado (2017) exposed participants to an acute stressor and then asked them to retrieve either positive or neutral autobiographical memories. Those who recalled positive memories had a dampened cortisol response and lower ratings of negative affect compared to those who recalled neutral events. In other words, retrieving positive autobiographical events may have made the individuals more resistant to the physiological and emotional consequences of acute stress.

Laboratory studies commonly manipulate the memories that participants are asked to retrieve or the situations in which individuals find themselves so as to change the reasons for retrieving a memory. However, it is not just the external situation that can affect which memories come to mind. There are also both stable and dynamic individual differences—in personality traits and retrieval goals—that can influence why an emotional memory is retrieved, thereby influencing how it is retrieved. For instance, individual differences in how a person thinks about time are related to the extent to which they exhibit the fading affect bias: The tendency of negative events to fade faster than positive ones was revealed to be stronger in individuals who were classified as either present or future oriented compared to those classified as past oriented (Wheeler et al. 2009). There may also be individual differences in the extent to which positive memories can be used to regulate negative emotions. Individuals who score high in general positive affectivity are more likely to demonstrate mood incongruent recall following a negative mood induction than those who have low positive affectivity (Rusting 1999). In other words, people who tend toward more positive affect are more likely to retrieve a positive, relative to a negative, memory following negative mood induction. In addition, individuals who report being more resilient benefit more from positive memory recall, reporting enhanced mood following memory retrieval despite recent exposure to an acute stressor (Speer & Delgado 2017).

Not all individual differences are stable; some aspects of emotional memory retrieval may shift across the adult life span. It has been suggested that an individual's age is a predictor of retrieval goals, with older adults more motivated than young to maintain positive affect, leading to systematic age differences in how emotional memories are retrieved (Reed & Carstensen 2012) (see sidebar titled *Effects of Age*). An individual's goals can also change from one moment to the next, affecting how details of past events are brought to mind and whether events are used for

EFFECTS OF AGE

Compared to young adults, older adults demonstrate positivity effects in memory, that is, increased retrieval of positive relative to negative information (Mather & Carstensen 2005, Reed & Carstensen 2012). During event experience, older adults attend more to (Isaacowitz et al. 2006, Mather & Carstensen 2005) and elaborate more on (Kensinger & Leclerc 2009) positive information relative to negative information. In some of the first research to examine how age affects the way that emotional memories are reconstructed at the time of retrieval, we revealed that older adults engage in retrieval-specific manipulation of emotional memories (Ford & Kensinger 2017, 2018; Ford et al. 2014): When older adults recruit the dorsomedial prefrontal cortex during negative event retrieval, this decreases hippocampal recruitment and reduces the subjective detail of a negative memory. This pattern is specific to older adults' retrieval of negative memories and does not extend to young adults nor to older adults' retrieval of positive memories. Thus, older adults' positivity effect may be supported by a prefrontal-mediated retrieval mechanism that reduces the experience of negative affect as soon as a negative event comes to mind.

regulatory purposes (e.g., Holland et al. 2010). For instance, the sensory engagement that typically is greater during the retrieval of negative compared to positive events can be reduced if participants have the goal of diminishing their negative affect during retrieval (Holland & Kensinger 2013).

Retrieval as an End Point: Summary

Negative and positive events are often remembered differently, with negative memories coming to mind with greater sensory recapitulation than neutral or positive memories. Yet the goals of the individual, and the functions that the memory will serve, can also influence how a memory is retrieved. When individuals retrieve an event with the goal of regulating negative emotion, they can retrieve different details and show less sensory activation during the elaboration of a negative memory. This research highlights that although there may be default differences in the way that positive and negative memories are retrieved, dynamic processes acting at the time of retrieval influence how an emotional memory is constructed. The way these processes are engaged is influenced by situational and individual differences and guides the content that comes to mind, the richness of the retrieved representation, and the ability for the retrieved memory to serve a directive function.

RETRIEVAL AS A STARTING POINT: RETRIEVAL PROCESSES INFLUENCE THE DOWNSTREAM ACCESSIBILITY AND RICHNESS OF EMOTIONAL MEMORIES

The memory functions described above explain why a particular event might be recalled at a given point, as well as how it can affect the individual at the time of retrieval. Critically, many of these functions require that the memory influence ongoing thought or future behavior, rather than only altering experience in the moment. This ability for retrieval processes to elicit effects that continue into the future supports the view of retrieval as a starting point.

A number of different lines of research have shown that the act of retrieval can alter the underlying memory representation, thereby influencing subsequent storage and retrieval. This research has focused on three general phenomena: (a) the enhancing effects of retrieval on the memory representation, increasing the likelihood and richness of future retrievals; (b) the detrimental effects of not retrieving information, decreasing the likelihood and richness of future retrievals; and (c) the effects of retrieval on memory malleability, making the memory more susceptible to manipulation and to the incorporation of erroneous details. We review these three general phenomena in turn and discuss how emotion may modulate them.

Beneficial Effects of Retrieval

Retrieving a memory at one time point often makes it easier to retrieve that memory later. It is intuitive that autobiographical events we have thought about previously will spring to mind more easily than those not previously retrieved. Laboratory tasks have confirmed this beneficial effect of retrieval. For instance, the testing effect, also termed the retrieval practice effect, reveals that taking a quiz is more advantageous to performance on a subsequent memory test than restudying the information (see Roediger & Butler 2011, Rowland 2014 for reviews). A potential explanation for this enhancement is that the effort of retrieving information strengthens the memory representation, consistent with evidence that more difficult retrieval tasks (e.g., recall vs. recognition) bestow a greater benefit on subsequent memory accessibility (see Rowland 2014 for a meta-analysis). It has also been proposed that, during retrieval, participants activate representations of the prior study

context, enriching the context representations associated with the memory trace and leading to a broader set of cues that can elicit retrieval on subsequent attempts (Karpicke 2017, Liu et al. 2017).

Relatively little research has examined whether emotion modulates these beneficial effects of retrieval. In one study using cued recall, the authors reported an equal testing effect for negative and neutral information (Emmerdinger et al. 2018). Another recent study revealed that the inclusion of a source retrieval task following encoding enhanced subsequent memory relative to restudy, and this benefit was equal for negative and neutral items (Jia et al. 2018). These results suggest that emotional memory traces can become strengthened by processes that unfold during retrieval, enabling the retrieval of an emotional event to increase its accessibility.

Detrimental Effects of Not Retrieving Information

Although retrieving a memory is often beneficial for subsequent attempts, retrieval-based detriments can also be found. For instance, the retrieval-induced forgetting (RIF) paradigm highlights subsequent memory impairments as well as enhancements that arise from retrieval (see Anderson 2003, Bäuml et al. 2010 for reviews). In the standard RIF paradigm, participants learn lists of categorized words. In a retrieval practice session, they perform cued recall for half of the categories. On a final memory test, memory is enhanced for those items that were retrieved on the cued-recall practice (Rp+) compared to items from categories that were not cued (NPr), revealing a beneficial role of the retrieval practice. Yet nonrecalled items from cued categories (Rp−) are remembered more poorly than those from unpracticed lists (NPr). Thus, there is a detrimental effect of retrieval when related content is activated.

The RIF phenomenon can be seen outside of the laboratory, when individuals do an end-of-day review for events they experienced (Cinel et al. 2018) and in everyday conversations (Cuc et al. 2007). When we discuss past events with another person, it is common to discuss certain details of the event and not others. The discussed details (Rp+) show memory benefits on a later memory test, while the unmentioned details (Rp−) suffer memory detriments. This effect has been termed socially shared retrieval-induced forgetting (SS-RIF).

The existing evidence suggests that RIF occurs for emotional information as well as for neutral information (Kuhbandner et al. 2009) and that SS-RIF similarly occurs for emotional as well as nonemotional memories (e.g., Barber & Mather 2012, Stone et al. 2013). RIF has even been proposed as the mechanism underlying the positivity bias in autobiographical memory (Storm & Jobe 2012; see also Nørby 2015). As noted previously in this review (see also sidebar titled Episodic and Autobiographical Memory Paradigms), individuals have a tendency to reflect on positive past events more than negative past events, likely in order to retain a positive self-concept. Over time, participants' retrieval of positive moments from their past may inhibit their ability to recall negative moments from their past (Marsh et al. 2018). Consistent with this proposal, Storm & Jobe (2012) found that participants who showed less RIF on a laboratory assessment of memory inhibition also showed a weaker positivity bias on an autobiographical retrieval task.

Although it is apparent that retrieval of emotional events can be inhibited, the results are inconsistent with regard to whether emotion modulates RIF strength. Some studies show equivalent RIF for neutral and emotional information (Barber & Mather 2012, Barnier et al. 2004), while others suggest that RIF may be reduced for emotional information (Dehli & Brennen 2009, Moulds & Kandris 2006). The valence of the information as well may affect the magnitude of the results, but it is not clear whether RIF is greater for positive or for negative information (Harris et al. 2010, Wessel & Hauer 2006). Part of the reason for these contradictory results may be that the impairing effects of retrieval can arise for a combination of reasons (see Jonker et al. 2013, Kim et al. 2017), two of which we elaborate on below.

Inhibitory suppression effects. It has been argued that Rp– items undergo active inhibition during rehearsal of Rp+ items, making them less likely to be remembered later (e.g., Anderson & Spellman 1995). Researchers have designed the think/no-think paradigm to examine more directly the role of active inhibition on memory (Anderson & Green 2001; see Anderson & Levy 2009 for review), explicitly instructing participants to suppress memory retrieval. Participants first study a list of cue-target pairs and learn to retrieve the target when the cue is provided. Then, they are presented with some of the cues and asked to either remember the target (think trials) or to avoid retrieving the target (no-think trials); remaining cues are not presented in this phase to provide control trials. In a subsequent memory test, targets from think trials are remembered better than targets from control trials, and targets from no-think trials are remembered worse than those from control trials. Similar to the RIF paradigm, the think/no-think paradigm depicts both the enhancing effects of retrieval (i.e., improved memory for the think trials) and the detrimental effects of intentionally not retrieving information (i.e., impaired memory for the no-think trials).

Especially for emotional memories, the ability to strategically push them out of mind could hold adaptive power. When meeting a close friend's new puppy, it would be best if the memory of the stray dog that attacked one as a child was not at the forefront of one's mind. There is strong evidence from think/no-think studies that emotional information can be intentionally forgotten (van Schie et al. 2013), often showing suppression effects that are as great or greater than those produced by neutral information (Depue et al. 2006, Murray et al. 2011). However, the effects of valence have been mixed, with some studies showing greater suppression effects for positive stimuli (Marx et al. 2008), others showing greater suppression effects for negative stimuli (Lambert et al. 2010), and still others showing no differences as a function of valence (Murray et al. 2011). Recent proposed links between memory inhibition and emotion inhibition (Engen & Anderson 2018, Gagnepain et al. 2017) may begin to clarify some of these discrepancies. For instance, inhibition of hippocampal targets may have broad influences on the accessibility of bound elements of memory traces, while inhibition of amygdalar targets may have stronger influences on the accessibility of emotional contexts or affective reactions to memories. Thus, it is plausible that there are across-paradigm or across-participant differences in how inhibitory processes are deployed to act upon hippocampal or amygdalar targets that may affect whether emotion modulates the magnitude of memory suppression.

Offline effects. The enhancing and impairing effects of retrieval can be revealed over short delays as well as long delays, if they include sleep (Abel & Bäuml 2012, Racsmány et al. 2010), suggesting that sleep may help to preserve both the beneficial and the detrimental effects of retrieval. Indeed, while there is still much that is unknown about the mechanisms underlying the effects of sleep on episodic memory, many working theories emphasize the ability of sleep to downregulate some synaptic connections more than others (see Tononi & Cirelli 2014) and to enable forgetting as well as remembering (Feld & Born 2017, Poe 2017, Stickgold & Walker 2013).

The effects of sleep may be particularly robust for emotional memories and may explain some of the time-dependent effects of emotion on memory (LaBar & Cabeza 2006, Payne & Kensinger 2018). Of most relevance to the current discussion of enhancing and impairing effects, sleep may perpetuate the unevenness of emotional memories, or the tendency for some event details to be remembered better than others (Kensinger & Schacter 2016, Mather & Sutherland 2011). The weapon focus effect (Loftus et al. 1987) refers to a real-world instantiation of this unevenness: Witnesses to a crime often remember the salient weapon but not other details such as the perpetrator's face or outfit. This unevenness is apparent even over short delays, but processes that act during sleep may serve to maintain or even exaggerate the differential weighting of emotional over neutral details (reviewed in Payne & Kensinger 2018). These results are generally consistent with

the proposal that sleep does not indiscriminately strengthen memories, but it rather strengthens content with the most future relevance: Emotion and recent retrieval may both be strong signals of information's future relevance, enabling that content to be maintained at the expense of other competing content.

Retrieval Enhances Memory Malleability

As demonstrated in the animal literature and extended to human memory, the act of retrieval can put a memory into a fragile state, making it prone to distortion or disruption (for recent reviews, see Elsey et al. 2018, Lee et al. 2017). In other words, sometimes bringing an event to mind can lead to a lessened likelihood of its accurate retrieval in subsequent attempts, if something happens shortly after retrieval to disrupt or distort the memory. Often, in daily life, that something includes exposure to erroneous information.

In the traditional misinformation paradigm (Loftus 1979), participants witness an event, are exposed to erroneous or misleading content about that event, and then are tested on the details of the event. Participants frequently intrude the misinformation. Chan and colleagues (2009) extended this paradigm by adding a memory test between the event and the misinformation. In their study, after viewing a video of a terrorist event, half of the participants completed a cued-recall test on 24 video details. All participants then listened to an 8-minute narrative that described the event in detail, including 8 false pieces of information. This was followed by a final cued-recall test. Individuals who had taken the cued-recall test just before exposure to the misinformation were more likely to incorporate the misinformation into their later recalls than were those who had not retrieved the information just prior to exposure to misinformation. This tendency for information that has recently been retrieved to be more susceptible to the misinformation effect—at least in those unaware of discrepancies between the original event and the misinformation presented (Butler & Loftus 2018)—is termed retrieval-enhanced suggestibility (Chan et al. 2009, Gordon et al. 2015; cf. Rindal et al. 2016).

Although emotional information is prone to misinformation (e.g., Segovia et al. 2017, Van Damme & Smets 2014), there is a paucity of research examining whether emotion modulates retrieval-enhanced suggestibility. The existing data suggest that there are circumstances under which emotion may reduce the susceptibility to misinformation via social contagion or collaborative retrieval (Kensinger et al. 2016). This result could be broadly consistent with the suggestion that emotional memories are more difficult to update than neutral memories (Nashiro et al. 2013), although more research is needed.

While the incorporation of new information can be disruptive to the fidelity of a memory, the ability to flexibly update a memory based on new information or current goals can be essential for inferential learning (Bridge & Voss 2014, Zeithamova et al. 2012) and for affective well-being. After multiple experiences with friendly dogs, it would be adaptive to weaken the association between a dog and a painful bite. If that updating has not yet happened at the time of retrieval, then when meeting a friend's dog, it might be adaptive to reduce the affective reexperience of the original encounter with the dog, focusing instead on other aspects of the memory. Fortunately, although emotional associative memories might be harder to update than neutral ones (Mather & Knight 2008, Novak & Mather 2009)—i.e., it may be challenging to update the dog-bite association despite encounters with friendly dogs—extensive research has revealed that when individuals retrieve a memory with the goal of regulating their emotional response, they can dampen the emotional intensity not only at the moment of retrieval but also in future retrievals (Ahn et al. 2015, Holland & Kensinger 2013). Thus, the reframing of the dog-bite event at the time of retrieval—for example, by focusing on the fact that the bite healed quickly, or that it was triggered by a child's

unpredictable gesture and is unlikely to be triggered by adult behavior—can lead to longer-term changes in the emotional response to that memory.

Offline processes may enhance the likelihood that the updates to memories made at the time of retrieval become long-lasting. Although what is remembered and what is forgotten can parallel the strength of the encoded content, offline processes during sleep can also aid in the reprioritization of memory traces, enabling weakly learned information to take on increased prominence in memory (Schapiro et al. 2018) and facilitating the ability for newly learned information to become integrated in memory (Tamminen et al. 2017). Sleep may also be required to prioritize memory for initially irrelevant content based on new information about its affective relevance (e.g., Dunsmoor et al. 2015, Patil et al. 2016).

Emotional Memory Retrieval as a Starting Point: Summary and Future Directions

The literature reviewed above emphasizes that emotional memories, like all memories, are malleable. At the time of retrieval, they can be put out of mind entirely, or some details can be elaborated at the expense of others. Their details can be updated and new associative connections formed. Their emotional intensity can be regulated. All of these retrieval outcomes can affect how information is processed over offline periods and can propagate effects into subsequent retrieval attempts. In this final section, we briefly walk through a diagrammatic outline of these effects (see **Figure 3**) and outline some of the future directions that we think will be fruitful both for basic science and for potential translation to the clinic.

Figure 3 begins with a successful retrieval outcome (step ❶), showing the types of processes that can modulate the recollective experience, enabling better memory (moving upward on the diagram) or worse memory (moving downward on the diagram). These processes have immediate consequences for the richness of the retrieved memory and for the types of content that will dominate the recollective experience. These processes will also propagate effects forward to subsequent retrieval attempts (steps ❷ and ❸). We are still far from understanding the complete picture of how emotion may influence this trajectory, but here we highlight some aspects that are particularly likely to be modulated by emotion.

Elaboration and the (sometimes false) prominence of emotional details in memory. At the time of retrieval, individuals often elaborate and rehearse emotional content rather than other details. Sometimes, this focus can be beneficial; as noted earlier, retrieval of emotional content can be used as a mnemonic shortcut, reducing the need for elaboration of other content (Levine et al. 2009). However, it can also lead to a sometimes misleading prominence of emotional content in memory. For instance, individuals overestimate the frequency of salient but rare emotional events (Tversky & Kahneman 1974) and overweight extreme outcomes in decision making (Madan et al. 2014), leading to potentially maladaptive behavior. Although many theories discuss the accessibility of content as a key contributor to these biases (e.g., availability heuristic; see Tversky & Kahneman 1974), less is known about how enhanced accessibility of emotional content at one moment in time may propagate over offline periods or affect biases at later time points of retrieval.

Prominence of sensory details in memory. A similar point relates to the prominence of sensory content for negative memories. As discussed earlier, negative memories are associated with more sensory recapitulation than positive events (Kark & Kensinger 2015), and individuals with stronger post-encoding amygdala-sensory connectivity and with greater sensory retrieval signatures show larger negative memory biases (Kark & Kensinger 2019). Yet the specific types of sensory details

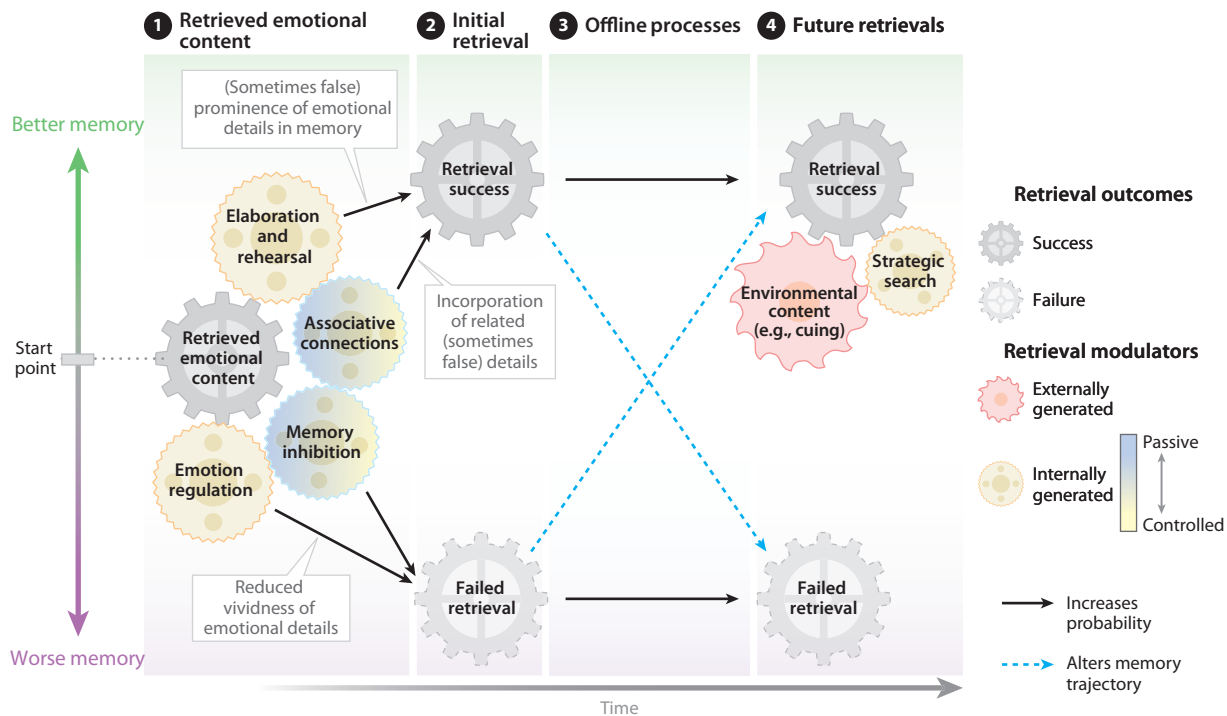


Figure 3

The trajectory of an emotional memory. Retrieved emotional content (1) can trigger a set of processes, some that improve the richness of the emotional memory and others that reduce it. The processes that enhance richness do not always enhance the fidelity of a memory; erroneous details can become associated and emotional details can take on a false prominence in memory. Importantly, those processes affect not only the quality of the initial retrieval but also the quality and likelihood of future retrievals, influencing whether retrieval of that content subsequently succeeds or fails. (2) Over time, and perhaps particularly over sleep, offline processes (3) can affect the likelihood of future retrievals. Often these processes will reinforce strong memories and prune weak memories; sometimes, however, offline processes can shift the balance, making weak memories more likely to be subsequently retrieved or deprioritizing previously strong memories. Environmental content (e.g., cuing) and internally generated processes (e.g., strategic search) as well can influence the likelihood of future retrievals (4) and propagate effects of retrieval downstream.

held in memory are still underspecified: Are they low-level details of stimuli or higher-level representations? Are there particular sensory domains that are prioritized, or is the integration across multiple modalities that is enhanced? Moreover, the way that these effects propagate downstream are unknown; future research will do well to examine how the prominence of sensory details retrieved at one time point relates to the subsequent affective reactivity to those memories, to the durability and richness of those memories over time, and to the ability to update and regulate those memories.

Associative binding and the incorporation of related (sometimes false) details. There is typically poorer associative binding of negative emotional memories compared to neutral memories (Bisby & Burgess 2013). An upside to this poorer associative binding is that it may make it harder for erroneous details to become incorporated into negative emotional memory traces, consistent with evidence that while negative memories are not immune to distortion, they may be less prone to such inaccuracies (Kensinger & Schacter 2016) and may be harder to update (Mather & Knight 2008, Novak & Mather 2009). Recent evidence suggests that positive emotion can sometimes

enhance associative binding (Madan et al. 2018), perhaps explaining why positive emotion can sometimes lead to increased memory distortion or overconfidence (Kensinger & Schacter 2016).

While the poorer associative binding for negative memories may provide some benefits to memory fidelity, it may also mean that emotional memories are less likely to be bound to encoded contexts, perhaps making them more susceptible to reactivation in irrelevant contexts. In affective disorders, negative content often comes to mind too readily or in irrelevant contexts. Although context-dependent retrieval effects are well known, and the role of context shifts in memory is an increasingly large focus of cognitive neuroscience research (DuBrow et al. 2017, Kim et al. 2017), there is still a dearth of research clarifying how emotion may modulate those effects.

Reduced vividness of emotional details: role of retrieval-induced forgetting. To our knowledge, no research has examined RIF for emotionally complex or bittersweet memories that include a mix of positive and negative content. It seems plausible that retrieval of positive details at one time point could lead to inhibition of the related negative content, such that over time those negative details become less accessible. We have shown that older adults are better able than young adults to focus on the positive aspects of a complex event (Ford et al. 2018a), and they provide more positive context for even their most negative memory narratives (Ford et al. 2016). Over time, older adults not only maintain their enhanced focus on these silver linings, but they also diminish their focus on negative details (Ford et al. 2018b). These results raise the intriguing possibility of a relation between an initial focus on the positive aspects and a diminution in the accessibility of negative details over time. RIF may be one mechanism by which individuals can, over time, dampen the vividness of the negative details by focusing on the positive ones. If this mechanism does explain some of the individual differences in how bittersweet events are remembered, it could also provide another avenue to understand how memory processes may contribute to the onset or duration of affective disorders; it is plausible that relatively small individual differences in memory inhibition processes could compound over time, making it harder for some individuals to inhibit negative details of events from springing to mind.

Relation between memory suppression and emotion regulation. Although emotional content will often feature prominently in memory, sometimes a person seeks to reduce the vividness of those details. Historically, two independent mechanisms have been used to account for how individuals accomplish this goal: They might suppress the details from coming to mind (a memory-suppression mechanism), or they might regulate their emotional reactions to the details as they retrieve them (an emotion-regulation mechanism). Engen & Anderson (2018) have recently proposed merging these mechanisms, noting that changing a memory may be one of the most effective ways to change emotion experience over the long term, and that there is overlap in the prefrontal processes used to dampen hippocampal and amygdalar activation patterns. Their proposal is based on recent evidence that hippocampal and amygdalar targets may be suppressed in parallel by the right dorsolateral prefrontal cortex (PFC) (Gagnepain et al. 2017), suggesting a common mechanism for memory suppression and emotion regulation.

Our research has separately highlighted a role for the dorsomedial PFC in reducing the vividness of older adults' negative emotional memories by reducing hippocampal activity (Ford & Kensinger 2017, 2018), suggesting another possible prefrontal site for the conjunction between memory retrieval suppression and emotion regulation (Ford & Kensinger 2017, 2018). Given evidence that, with attentional depletion, individuals sometimes switch from relying on lateral PFC regions for emotion regulation to relying on medial PFC regions (Morris et al. 2014), one possibility is that older adults engage the dorsomedial PFC for the implementation of memory

suppression and emotion regulation due to their reduced attentional capacity (e.g., McAvinue et al. 2012), while younger adults are more likely to engage lateral prefrontal regions for this purpose.

Retrieval tags and the offline processing of emotional memories. While steps ❶, ❷, and ❸ in **Figure 3** depict conscious retrieval epochs, we also schematize the offline processes (step ❹) that can serve to maintain or update the strength of memory representations. There is still much to be learned about how offline processes change the trajectory of emotional memories, and especially about how earlier retrieval signatures may predict whether offline processes serve to strengthen or weaken components of emotional memory traces. In fact, while much research has been focused on understanding which encoding markers serve as prioritization signals or tags to enable sleep to selectively act on some memories or some aspects of a memory over others (reviewed in Payne & Kensinger 2018), an open question is how retrieval processes modify those tags. If we bring to mind an event that once was highly arousing, but now we have a dampened affective response, what happens to that memory trace in the subsequent offline state? Conversely, what happens if we become agitated about an event that we had nearly forgotten before falling asleep? Future research is required to understand how the processes that act during retrieval can influence how emotional information is processed and prioritized and how affective reactivity and mnemonic content are integrated in offline states.

CONCLUSIONS

Emotion and emotional valence can have substantial and long-lasting effects on how we remember and reexperience past events. Processes at the time of retrieval can influence both the experience (retrieval as an end point) and the effects (retrieval as a starting point) of remembering these emotional events. These influences can be modulated by individual and situational differences.

At the time of retrieval, negative memories have a stronger sensory neural signature and a greater resemblance to the neural state at encoding, which might be tied to a tendency to retrieve negative events vividly. Despite these default differences in the way that positive and negative memories are retrieved, the retrieval of emotional events is guided by the goals of the individual at the time of retrieval. The dynamic processes that act at the time of retrieval can affect how vividly a negative or positive event is brought to mind and which details are recalled. Because of these dynamic processes, an emotional event will not be remembered in the same way by two different people, nor will it be remembered in exactly the same way by the same person in different contexts.

The act of retrieving a past event also leads to the reshaping of underlying memory traces, which can have long-term effects on thought and behavior. Thus, the way an emotional event is remembered affects not only the reexperience of the event at that moment in time but also how the event will be remembered in the future. While we are still far from a full understanding of how retrieval changes an emotional memory representation over time, the existing data underscore the importance of processes that act during retrieval and in the offline moments following retrieval. These processes can lead to unevenness in the way that emotional event features are remembered, with some details remembered better than others.

It is important to know how emotion affects processes at the time of retrieval because the way we feel at the time of retrieval affects our future thoughts, actions, and well-being. Understanding how emotion influences the experience of memory and the way memories change over time may also be of critical importance to clinical research. Many affective disorders are characterized by intrusive and persistent memories of negative events, often brought to mind by neutral or irrelevant cues. If processes at the time of retrieval could be engaged to reevaluate and reprioritize aspects of these memories, it could be possible to reduce their impact at future retrievals.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors' research on emotional memory has been supported by funding from the National Institutes of Health (MH080833 and MH116872) and the National Science Foundation (grant BCS-1744744). The authors thank Maureen Ritchey, Rose Cooper, Angela Gutchess, and members of the Cognitive and Affective Neuroscience Laboratory at Boston College for discussions that helped shape the ideas expressed.

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