Affective Memory

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Abstract

Only a fraction of the events that we experience will be remembered, and even when the occurrence of an event is remembered, only a portion of its details will be retrieved. This selectivity is a hallmark feature of episodic memory. Events that elicit an affective response tend to be prioritized in memory, although there is often an unevenness to those memories, with some details remembered well and others forgotten. In this chapter, we examine the many ways in which an affective response can modulate memory. We organize the chapter around those processes that act as an event is initially experienced and encoded, updated or prioritized by new learning, and retrieved. In each of these sections, we integrate knowledge learned from laboratory assessments of behavior with that acquired through investigations of neural mechanisms.

Keywords

consolidation, emotion, encoding, episodic memory, flashbulb memory, prioritization, retrieval, tagging, updating

Introduction

A hallmark feature of episodic memory is its selectivity. Memories for events that evoke an affective response – events that we perceive as good or bad, that get our heart to race or to skip a beat – are no exception to this rule of selectivity. Extensive research into how individuals retain memories of public disasters and personal triumphs has revealed that, while the occurrence of these events is likely to be remembered, the details of the events are not always remembered consistently, with event details omitted, distorted, or inserted (Holland & Kensinger, 2010; Neisser & Harsch, 1992). If anything, the unevenness with which an event is remembered may be exaggerated by an affective response, with particularly good memory for some event details and associations offset by particularly poor memory for others (Kensinger & Schacter, 2016).

This selectivity can be understood, in part, by conceiving of an episodic memory trace not as a static entity but as a dynamic set of connections (see also Chapter 2.1). There is selectivity in how those connections are formed (encoding); in how they are stabilized or prioritized over time (consolidation); and in which connections are re-activated by an internal or external cue (retrieval). Affective reactions can intervene at each of these stages, shaping the selective pressures at work (see Figure 1).

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Affective reactions also often have propagating effects, leading reactions that arise earlier in the formation of a memory to influence not only how the connections of the memory trace are established but also how they are maintained over time or re-activated at the moment of retrieval. Often, benefits accrue across memory stages; but there are interesting counter-examples, when the facilitation provided by an affective reaction at one memory stage means that more effort is required at a later stage.

In this chapter, we walk through the interactions between affect and memory that lead to selective effects as information is encoded, as it is stored and updated, and at the moment of retrieval. We often parse these stages further, and we delve into questions of when affective influences may be specific to these memory phases and when they may reflect more general influences that modulate memory as a by-product or downstream consequence. When relevant, we integrate the knowledge gained from behavioral examinations of affective memory with the insights gathered by viewing memory mechanisms through the lens of functional magnetic resonance imaging (fMRI) or event-related potentials (ERP).

Affective memory encoding

Affective reactions (see Box 1 for a brief discussion of how affect is defined) influence encoding at many levels. The *affective state* we are in as we encounter information can influence the way that information is attended, interpreted, and incorporated into existing schemas. If we are happy as we walk across campus, we may notice others smiling at us as we walk to our office, savor the gentle breeze, and be reminded of other beautiful spring mornings. The same context may be experienced and remembered quite differently if instead we are anxious about the meeting we are about to enter. The *transient affective reactions* we have to discrete stimuli can also affect how we remember the information. Perhaps we startle upon hearing a loud noise, or notice our heart pounding as we ascertain whether a statement was meant as an insult. The affective reactions we have *just after* the occurrence of an event can also affect the way the just-presented information is prioritized in memory (Figure 2). In this section, we review these different types of affective influences on memory encoding.

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Affective states and memory encoding

Studies typically examine the influence of an affective state on memory encoding by inducing participants into a particular state just prior to encoding and then comparing those individuals to a control group whose state was not manipulated or to a group induced into a contrasting affective state. Participants are commonly induced into a positive or negative mood by listening to music, watching film clips or photographs, or retrieving autobiographical memories with targeted affective content (Robinson, Grillon & Sahakian, 2012). Participants also can be induced into high-stress affective states, by performing a public speaking task (Kirschbaum et al., 1993) or experiencing physical stress by placing their hand into a bucket of ice water (McRae et al., 2006). These studies generally have revealed that when individuals are in a positive affective state, they are more likely to notice the good things going on around them, to sustain attention to positive information (Wadlinger & Isaacowitz, 2005; Isen, 2000), and to interpret a stimulus more positively (Clore, Schwarz, & Conway, 1993; Garcia-Marques, Mackie, Claypool & Garcia-Marques, 2004). The opposite pattern can hold when participants are in a negative mood, creating mood-congruency effects in attention and memory (see Blaney, 1986; Bower, 1981 for early studies), although there is some evidence to suggest that the congruency effects are stronger for induced positive mood than for induced negative mood (see

Challis & Krane, 1988 for early example; see Box 2 for brief discussion of accounts of mood congruency effects).

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Transient affective reactions and memory encoding

The more transient affective reactions elicited by stimuli also have large effects on the likelihood that information is encoded into memory, and much of what we have learned about the effects of affective reactions on memory stem from experiments that have honed in on the effects of these short-lived reactions (see also Box 3). In the typical experiment, participants are presented with brief stimuli that alternate between those that elicit affective reactions (either positive or negative) and those that elicit minimal affect (neutral stimuli). The stimuli are typically intermixed, such that affective reactions are short-lived and quickly altered by the presentation of the next stimulus. In some designs, the affective reactions are triggered by the stimuli for which memory will be tested: Participants may view an image of a snake followed by a hot air balloon followed by a bookshelf, and their memory for these items and others is later tested. In other designs, the affect may be elicited by a co-occurring stimulus: Participants may receive a mild shock or hear white noise while they view a subset of otherwise-neutral images.

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There has been extensive focus on the emotional enhancement of memory (EEM), or the tendency for the stimuli associated with these short-lived affective reactions to be remembered better than the stimuli not associated with them. While the heuristic of the EEM is useful, as with any heuristic, it is too simple a construct for the complex effects that these reactions have on memory. The EEM appears to be most likely to arise when items eliciting affective reactions are intermixed with other items rather than presented in a block (Schmidt & Saari, 2007), when memory is tested after longer delays (Sharot et al., 2007), and when memory tasks are designed to minimize the effects of response bias (see Bennion et al., 2013 for further discussion).

A number of these boundary conditions are consistent with the proposal that, when memory is tested after shorter delays, the EEM can be explained by cognitive factors alone (Talmi & McGarry, 2012). In particular, Talmi and colleagues (Talmi & McGarry, 2012; Talmi, 2013) propose that cognitive factors of organization, distinctiveness, and attention can explain the EEM in immediate memory. Thus, when paradigms minimize these influences (e.g., use blocked lists of emotional stimuli to minimize their distinctiveness), the EEM is less likely to occur. This proposal underscores that, in studies that vary affective reactions by varying the stimuli, care must be taken to distinguish a "true" EEM, that is, a memory enhancement caused by emotion *per se*, from enhancements due to confounding factors. For instance, it is easy to overlook differences in the semantic relatedness of the items selected to elicit affective reactions versus those selected for a control condition, e.g., selecting stimuli related to death and injury to elicit affective reactions while selecting stimuli from a broad set of categories for the control condition. Doing so can lead to an apparent EEM (Talmi et al., 2007), and the effect of semantic relatedness can be exaggerated when memory tasks are not designed to reduce the effects of response bias (Dougal & Rotello, 2007; White et al., 2014). It also is important to distinguish an EEM from a memory enhancement caused by more general factors that are not unique to emotional content, such as those shared by self-relevant information (see Box 4). It is equally important to distinguish affective influences on *memory* from effects on *attention* that can have downstream consequences for memory. For instance, emotional stimuli can capture attention (e.g., Carretie, 2014; Vromen et al., 2016) and participants can find it challenging to disengage from those stimuli to process other stimuli (e.g., Mishra et al., 2017). Although the facilitated processing of emotional stimuli does not always lead to a more durable memory trace (discussed in Bennion et al., 2013), these attentional effects can masquerade as memory effects.

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Affective tagging

Further insight into these boundary conditions of the EEM can be gained by thinking about the "affective tagging" processes that likely lead to the EEM (Richter-Levin & Akirav, 2003). That is, at the moment that an event triggers an affective response, a cascade of processes is thought to be set in motion, "tagging" the content tied to that affective response as important to encode into memory and to consolidate over subsequent delays. Although the mechanistic details of this tagging process remain a topic of discussion (Bergado et al., 2011), the amygdala is thought to play a critical role. Richter-Levin and Akirav (2003) proposed that when amygdala activation arose in response to an event, that activation aided in enhancing synaptic plasticity in other brain regions and in reducing the threshold of activation required for lasting changes in plasticity to arise. Recent work by Inman and colleagues (2018) has demonstrated that brief amygdala stimulation is sufficient to lead to better retention of otherwise-neutral stimuli. Moreover, at the time of retrieval, oscillatory pattern analyses suggested that increased interconnections between the amygdala, hippocampus, and perirhinal cortex correlated with the memory enhancement provided by the initial amygdala stimulation. These results are consistent with a large body of work in nonhuman animals (McGaugh, 2004), demonstrating that stimulation of the basolateral nucleus of the amygdala leads to improved retention of information over a delay and enhances markers of synaptic plasticity in the hippocampus and perirhinal cortex (Roozendaal et al., 2008; McReynolds et al., 2014). Together, this literature is consistent with the proposal that amygdala activation can facilitate tagging processes that enable long-term memory storage (Richter-Levin & Akirav, 2003).

Extensive fMRI research has corroborated the general role of the amygdala in the formation of episodic affective memories, with amygdala engagement at encoding correlating with memory for events that elicit affect, but not for neutral events. It continues to be discussed how this amygdala activation shapes the emotional memory network. Some theories propose that affective reactions shift from a “cold” hippocampal-driven network to a “hot” amygdala-driven network (Metcalfe & Jacobs, 1998), or more generally propose that amygdala and hippocampal networks work in opposition to one another (Bisby et al., 2016). Thus, encoding for emotional relative to neutral information may be enhanced because affective reactions shift encoding resources away from the hippocampal networks that support memory for neutral events and toward amygdala networks that support memory for affectively-laden events. Counter-evidence reveals beneficial interactions between the amygdala and other regions of the medial temporal-lobe, with a number of models explaining the time-dependence of the EEM (i.e., that the emotion advantage becomes more pronounced over time) by interactions between the amygdala and the hippocampus (reviewed by Phelps, 2006). In contrast to these alternatives, Yonelinas and Ritchey (2015) have proposed that the amygdala mediates item-emotion bindings while the hippocampus supports item-context bindings. Thus, it remains a point of discussion as to how the amygdala intersects with other medial temporal-lobe regions to modulate memory.

While most studies examining the effect of short-lived affective reactions on memory have either focused on negative stimuli or have collapsed analyses of negative and positive stimuli, there is suggestive evidence that the amygdala-related "tagging" processes may proceed differently depending on the valence of the affective reaction. In a recent study, Kark and Kensinger (2019b) measured arousal responses during encoding objectively, using the metric of heart-rate deceleration, and examined the relation between arousal, amygdala connectivity, and subsequent memory vividness. Kark and Kensinger found that for negative stimuli, amygdala connectivity to visuosensory regions during encoding was more strongly related to memory vividness in the presence of an arousal response. No such modulatory relation of arousal was present for neutral or positive stimuli. In other words, arousal increased the link between amygdala connectivity and subsequent memory vividness for negative, but not positive, stimuli. Moreover, that link between amygdala connectivity and negative memory vividness was only revealed when we considered the arousal response elicited by the negative stimuli. This latter pattern, while not predicted a priori, is consistent with "tagging" theories: As the arousal elicited by negative events increases, tags are set, prioritizing those memory traces for consolidation, and leading to the enhanced link between amygdala connectivity and subsequent memory vividness in the presence of increased arousal.

Importantly, while "tagging" may increase the likelihood that an event is remembered, it does not necessitate that details associated with that event will be remembered equally. Another mechanism, conceptualized in the Glutamate Amplifies Noradrenergic Effects (GANE) model, may enable arousal to prioritize the perception and retention of high-priority representations –

those linked to affective reactions or goal states – at the expense of lower-priority representations, creating the unevenness that is often a hallmark of emotional memory (Mather et al., 2016). In brief, this model suggests that, with arousal, neurons within the locus coeruleus release relatively low levels of noradrenaline in a distributed fashion, sufficient to activate only a subset of noradrenergic receptors, those that tend to lead to inhibitory effects. But in the presence of already-high neural activity, a different type of receptor (beta-adrenergic) is activated, triggering glutamate release and leading to an excitatory effect and thus to an amplification of the already-existing neural activity. Thus, the authors propose that arousal can create "hot spots" of elevated activity in the context of otherwise diffuse inhibition, thereby leading to a focus – and increased likelihood of encoding – information that had high-priority for processing at the time of the arousal response.

This model helps to explain extensive laboratory and real-world evidence that has revealed so-called memory trade-offs (Kensinger et al., 2007) or weapon focus effects (Loftus et al., 1987), whereby some features of emotional events are remembered well, but at the expense of other elements (see also Chapter 12.4 for discussion of Eyewitness Memory). Similar memory-narrowing effects can be seen with stress, which also results in changes in norepinephrine levels: When individuals are stressed, they are more likely to remember information relevant to the stressor but are less likely to remember other information that is encountered (see meta-analysis by Shields et al., 2017 and Chapter 9.9). The GANE model also may provide a neurochemical explanation for extensive neuroimaging and patient research that has suggested that amygdala engagement—strongly tied to the arousal response—is linked to the ability to remember select details or the "gist" of the event, but not to remember all of the event details (e.g., Adolphs et al., 2005; Kensinger & Schacter, 2006; see also Sakaki et al., 2014).

Although much less research has used electroencephalography (EEG) than fMRI to study emotional memory (see Box 5), event-related potentials (ERP) may provide a powerful method to detect the temporal patterns of emotion modulation of memory and to test key predictions of the GANE model (Talmi & Barnacle, 2016). A parietally-distributed late positive potential (LPP) is the most consistent ERP marker of the increased processing allocated to emotional stimuli during initial encoding, with a larger positive potential to emotional stimuli starting around 400 ms after stimulus onset (Citron, 2012; Hajcak, Weinberg, MacNamara, & Foti, 2012). One possibility is that this component reflects the widespread cortical effects of the locus coeruleus-norepinephrine system that is central to the GANE model (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Nieuwenhuis, 2011). It remains debated whether the timing of the modulatory effects revealed with ERP are consistent or inconsistent with the GANE model (see Talmi & Barnacle, 2016), but the extant data emphasize the modulatory effects of emotion on encoding processes.

Whatever the precise mechanism represented by the LPP, a posterior positivity very similar to the LPP is one of several components that is commonly reported to differ between subsequently remembered and forgotten stimuli (reviewed in Wagner, Koutstaal, & Schacter, 1999; Wilding & Ranganath, 2012), and the LPP itself has often been linked to memory-related processes (Fields & Kuperberg, 2016; Hajcak et al., 2012; Olofsson, Nordin, Sequeira, & Polich, 2008). Thus, the LPP may be an ERP marker of the tagging of emotional stimuli leading to better memory; this proposal seems generally consistent with evidence that larger LPP amplitudes are linked to a larger behavioral EEM (Palomba, Angrilli, & Mini, 1997), that posterior LPP-like subsequent memory effects are larger for emotional stimuli (Dolcos & Cabeza, 2002; Righi et al., 2012), and that the scalp distribution of the subsequent memory effect can depend on the types of factors that influence the EEM, including the task demands and whether the lists are mixed or pure valence (Fields, 2017; Watts, Buratto, Brotherhood, Barnacle, & Schaefer, 2014). Nevertheless, there remains more to be understood about the ERP and EEG correlates of emotional memory processes.

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Affective memory encoding: Summary

Affective reactions—both those triggered by an event and those affective states present at the time of the event – can influence the way that information is attended and encoded into memory. The modulatory influences of those affective reactions often "tag" an event as important to remember, while also leading to an unevenness in the details that are encoded into memory. The processes that act during encoding can increase the likelihood that events with affective relevance are prioritized in memory.

Post-encoding prioritization and modification of affective memories

The set of processes described in the prior section assumes that affective reactions occur in close proximity to an experienced event. Importantly, the processes that affect memory do not have to be in place at the moment of the event but can occur *just after* the event, modulating memory retroactively. Manns and Bass (2016) review many of these studies, conducted in rats, which together reveal that when amygdala stimulation occurs shortly after the occurrence of neutral stimuli, the memory for those neutral stimuli is enhanced. In particular, brief electrical stimulation to the basolateral amygdala (BLA) after the presentation of novel objects enhanced the retention of those objects in memory over a one-day delay. Interestingly, these results also suggested that these retroactive effects were associated with changes in hippocampal spiking patterns. As Manns and Bass (2016) summarize, “The results extend the previous findings by highlighting the capacity of the BLA to prioritize memories on a moment-to-moment basis even after the moment has passed and suggest that one route is by regulating spike-timing dependent plasticity in the hippocampus across the most recently active synapses.”

These studies have examined amygdala stimulation in close temporal proximity to the events. But sometimes, the importance of a moment is not recognized until later. Perhaps your computer makes a novel sound while you are in your office typing a paper. The moment passes without you giving the sound a second thought. An hour later, your computer crashes and you are unable to reboot. Suddenly, the sound takes on increased importance. Fortunately, tagging mechanisms can act across this longer timeframe, to ensure that the sound can become part of a durable memory trace, allowing you to describe it to a technician later that day. Although there remain open questions about the time frame over which re-prioritization can occur, recent work has converged on the conclusion that – at least for a window of time – memories remain malleable and able to be re-prioritized when the affective salience of information is realized (Dunsmoor et al., 2015).

Affective learning and memory prioritization

Dunsmoor and colleagues (2015) provided important evidence that new information can affect the likelihood that prior episodic events are retained in memory. In their study, participants viewed images from different semantic categories (i.e., tools and animals). A few minutes later, participants viewed different images from those categories, this time receiving mild electric shocks when images from one of the categories was presented. Participants later remembered the items from the shocked category better than the items from the control category; critically, that pattern held even for those items that had been presented in the first block. Even though at the time of their presentation, there was nothing different in the affective salience of those tools and animals, the later knowledge that one of those categories was associated with an aversive shock was sufficient to be able to retroactively alter the strength of the memory representations, boosting the retention for that now-affectively-salient category. While Dunsmoor and colleagues used aversive learning to demonstrate the retroactive re-prioritization of memory, Patil et al. (2016) revealed a similar retroactive memory enhancement by reward. These results suggest that when good or bad things happen, that new knowledge can be used to retroactively enhance related memory traces.

The pattern of results reported in these studies (Dunsmoor et al., 2015; Patil et al., 2016) seems consistent with "tagging" theories (Redondo & Morris, 2011; Frey & Morris, 1998), both in their occurrence and also in their more specific features, including their delay-dependence: The retroactive effects were not noticeable when memory was tested just a few minutes after the association had been formed between a category and a shock, but they were noticeable hours later. Thus, it may take time for information to be re-prioritized in memory. This makes sense biologically, with prior events having the ability to affect downstream memory allocation (see Rogerson et al., 2014). The time-dependence also may serve an adaptive function, helping to ensure that memory traces are re-prioritized when new information is stable or accurate, and not when there is high variability in the new learning signal. For instance, if you return home and are distraught to realize that you cannot find your phone, it would be adaptive to prioritize the information about the path you took from your office from your home. But this would be wasted neurobiological effort if you found your phone moments later. The time-dependence may help to ensure that memories are not reprioritized when we momentarily believe something to be true (e.g., our phone is lost) but soon have that belief disconfirmed.

Affective learning and memory updating

While the studies described so far have focused on the effect of new affective reactions on the prioritization of existing memory traces, others have focused on how affective reactions influence the ability to integrate across events or to update memory traces. The research on affective influences in these domains is relatively scarce, but the extant data suggest a possible distinction from the pattern discussed so far: Emotion may not benefit, and in fact may curtail, at least some aspects of memory integration or memory updating. In a number of studies, Mather and colleagues have provided evidence that it may be harder to update emotional memories than neutral ones (Mather & Knight, 2008; Novak & Mather, 2009; Nashiro, Sakaki, Huffman & Mather, 2013; Sakaki, Niki, & Mather, 2011). For example, Mather and Knight (2008) asked participants to learn associations between neutral faces and either emotional pictures or neutral pictures. They then learned face-location pairings for all of those faces. The key result was that participants performed more poorly at remembering the location of the neutral faces that had previously been associated with negative pictures. Control conditions suggested that this pattern was not related to a general impairment of emotion on memory but rather to a more specific difficulty learning new associations for affectively-relevant stimuli.

Further research is needed, but it is an intriguing possibility that affect may enhance the ability for new information to *prioritize* existing episodic memory traces and at the same time reduce the ability for new information to *modify* existing episodic memory traces. If this pattern held, it could explain some of the reasons why affective associations are hard to unlearn and may require additional involvement of prefrontal circuitry (Sakaki et al., 2011). It could also reveal some benefits to memory accuracy conveyed by affect: although emotional information is no doubt prone to misinformation (e.g., Van Damme & Smets, 2014; Segovia, Strange, & Takarangi, 2017), there also are circumstances under which emotion may reduce the susceptibility to misinformation via social contagion or collaborative retrieval (Kensinger, Choi, Murray & Rajaram, 2016), perhaps because the emotional memories are less likely to be updated with the misinformation.

It is also possible that, although aversive learning and reward learning can both adjust the *priority* of existing memory traces, the nature of the affective reactions may influence how ably they can *modify or update* memory traces. Positive affect is associated with a broader scope of attention (Fredrikson, 2004), and with enhanced associative binding (Madan, Scott, & Kensinger, 2019). By contrast, negative affect is more likely to impair associative binding, even when the subjective vividness of a memory is high (e.g., Rimmele et al., 2011). These results raise the possibility that positive affect may be more likely than negative affect to benefit memory integration. Somewhat consistent with this possibility, Clewett & Murty (2019) review evidence that has led them to propose that when the dopaminergic system is recruited, it will facilitate the ability to integrate disparate features of an event together into memory and will increase the likelihood that associative connections form across different events. However, they further propose that the dopaminergic system will be more engaged not when individuals are in a positive state but rather when they are in a state of high "behavioral activation," experiencing vigor and novelty-seeking. While that state of high behavioral activation may often occur when in a positive mood, they note that it is not uniquely associated with positive affect or reward and can also occur with distal threats.

Affective states and memory prioritization

Clewett & Murty's (2019) proposal puts front-and-center the *state* that someone is in as a key modulator to what becomes prioritized in memory. The importance of these state effects has been revealed in a number of behavioral and fMRI studies. For example, Tambini and colleagues (2017) revealed that there can be what they termed "carry-over" effects of emotional brain states that influence how subsequent neutral experiences are remembered. In particular, they found that neutral stimuli encountered up to approximately 30 minutes after exposure to emotionally arousing stimuli were more likely to be recollected after a delay than neutral stimuli studied absent that emotional brain-state. Somewhat similarly, Kark and Kensinger (2019a) revealed that individual differences in the changes in the brain's resting-state functional connectivity from pre-encoding to post-encoding predicted the likelihood that individuals would show a negativity bias in memory. Longer-term states experienced after the occurrence of neutral stimuli can also affect the consolidation of information. For instance, watching a pleasant or unpleasant video shortly after reading a list of neutral words can improve memory for those words one week later (Nielson & Powless, 2007). Similarly, a meta-analysis by Shields and colleagues (2017) revealed that the experience of stress shortly after the occurrence of an event typically enhances memory.

Affect and memory de-prioritization

We have so far discussed the processes that enable affective reactions to give additional prominence to memories. But sometimes, the opposite is warranted: We may be well served by *de-prioritizing* an affective memory trace or by de-coupling a stimulus from its affective association. The de-prioritization of affective memories has been best studied within the framework of reconsolidation, which refers to the set of processes that enable a re-activated memory to be re-stored in memory. Although the exact features of reconsolidation, and their ability to extend to episodic memory, remain controversial, the general framework suggests that, at the moment of retrieval, when a memory is brought back online, the memory trace enters a labile state, providing an opportunity for it to be re-prioritized, modified, or incorporated into a new context (e.g., McKenzie & Eichenbaum, 2011; see Chapter 6.7). Studies in rodents revealed that if a protein synthesis inhibitor was administered while the memory of an aversive association was in that labile state, the memory of that association would not be re-stored and the animals behavior suggested they had forgotten the association (see reviews by Haubrich & Nader, 2018; Dudai, 2006). Additional research suggested that it was possible, through the administration of beta-blockers, to wipe out the affective tone of previously-fearful stimuli (Kindt et al., 2009).

In the episodic memory domain, reconsolidation processes likely blend memory re-prioritization with memory updating functions: It is likely that, rather than scaling the priority of an entire memory trace, reconsolidation processes will act to bring some features into prominence and others into the background. For instance, misinformation effects, or the tendency for individuals to incorporate false information into memory traces (Loftus et al., 1989), may arise when erroneous information becomes incorporated into a memory when it is in its labile state prior to reconsolidation. How exactly this memory reconfiguration would arise remains a topic of active research, but the clinical relevance of being able to de-prioritize affective memories or affective associations is likely to be high, making this a warranted direction for future research.

While reconsolidation describes a bottom-up mechanism that can enable the de-prioritization of affective processes, directed forgetting describes a top-down, strategic set of processes, that can be engaged in order to de-prioritize the likelihood of retaining information over the long term (see also Chapter 6.3). In the typical directed forgetting paradigm, participants are told that just-presented information is not important to remember. Individuals are thought to engage frontal control processes to support the selective forgetting of the irrelevant information (e.g., Wyllie et al., 2008), which may encompass both inhibition of the to-be-forgotten items and selective rehearsal of the to-be-remembered items (e.g., Anderson, 2003; Fawcett & Taylor, 2008; Nowicka, Marchewka, Jednoróg, Tacikowski, & Brechmann, 2011). It remains debated how affect modulates directed forgetting. Some research suggests that the deeper processing of negative affective stimuli makes them resistant to directed forgetting (e.g., Bäuml & Kuhbandner, 2007; Hauswald et al., 2011) and harder to forget than other stimuli (e.g., Bailey & Chapman, 2012; Korfine & Hooley, 2000; Nowicka et al., 2011; Yang et al., 2013), yet other research has suggested that it may be easier to forget negative stimuli (Brandt et al., 2013; Depue, Curran, & Banich, 2007), particularly if they are low arousal (Depue, Banich, & Curran, 2006; Depue, Curran, & Banich, 2007; McNally et al., 1998). Results have also been somewhat mixed in studies using ERP to examine directed forgetting, although the general pattern that emerges is that, when emotional items receive greater processing at encoding – as indexed by an enhanced LPP – they are harder to forget (Hauswald et al., 2011). By contrast, emotional items may be no harder to forget than neutral if there is no such enhancement in the LPP (Brandt et al., 2013). There is also some ERP evidence to suggest that, even when behavioral differences do not arise, directed forgetting may be more effortful for negative stimuli: Yang and colleagues (2012) reported no behavioral differences in the directed forgetting of neutral and negative stimuli, but there was a larger frontal positivity to the negative stimuli, suggesting that the forgetting of the aversive information may have required more cognitive effort (see also Nowika et al., 2011; Yang et al., 2013).

An additional question relates to the longevity of directed forgetting effects. Unlike reconsolidation, which is thought to lead to permanent changes in the memory trace, it is less clear how long-lasting the effects of directed forgetting may be. Blaskovich et al. (2017) revealed that the effects persisted after two hours spent either awake or asleep, and Hupbach (2018) provided evidence that there can be relatively long-lasting consequences, with effects of directed forgetting persisting after either a 12-hour or 24-hour delay. These experiments also suggested an effect of sleep, with sleep vs. wake preferentially consolidating the information that had been associated with a 'remember' cue during encoding (Hupbach, 2018) and with the directed forgetting benefit linked to REM sleep during a nap (Blaskovich et al., 2017).

More generally, offline processes may enhance the likelihood that updates to memories—whether they be re-prioritizations or modifications—become long-lasting. There is intriguing overlap between the brain networks implicated in memory updating and those implicated in spontaneous thought (Christoff et al., 2018). Given the large fraction of time that individuals spend reflecting on their affective states or others' states, it will be fruitful for research to delve into questions of how these offline processes may adjust the prominence of affective memories. Offline processes during sleep have specifically been shown to prioritize the consolidation of future-relevant information, including emotional information, and it is therefore unsurprising that extensive research has suggested that sleep can help to preserve memory for emotional information, sometimes even at the expense of nonemotional information (reviewed by Payne & Kensinger, 2018). But interestingly, while sleep sometimes acts to further prioritize already high-priority memories from the waking day, other times the offline processes during sleep enable weakly-learned information to take on increased prominence in memory (Schapiro et al., 2018). Research is just beginning to underscore that affective states and stress levels before (Bennion et al., 2013) and during sleep (van Marle et al., 2013) can relate to the ability for information to be prioritized or integrated in memory (see also Chapter 6.9).

Affect and memory prioritization: Summary

Affect can retroactively and proactively influence the strength and content of a memory. New learning about the affective relevance of information can retroactively influence the likelihood that memory traces are prioritized for consolidation. Affective brain-states can retroactively prioritize memory for previously-experienced events, and they also can carry-forward to influence the likelihood that ostensibly neutral information is retained in memory. Changes in affective state also can influence whether individuals are biased to retain negative or positive information over longer-term delays. Current research is focused on clarifying how affect modulates the ability for new knowledge to be used to update previously-learned information and is continuing to delve into the processes that can weaken the priority of affective memories, directions of research that are likely to have important clinical relevance.

Retrieval of affective memories

When we think about memory retrieval, we often think about the volitional attempt to remember a prior moment in time. Many of the experiments examining the retrieval of affective episodic memories have focused on this strategic aspect of retrieval, by making it known to participants that their task goal is to remember previously-presented content. But in daily life, retrieval often arises spontaneously, with information recovered in the absence of any goal to remember a prior event (Hintzman, 2011). In fact, it has been proposed that spontaneous retrievals occur as frequently as intentional retrievals (Berntsen, 2010), with affective memories often among those events that are spontaneously retrieved (Bernsten, 2009). In this section, we first discuss the effects of affect on spontaneous retrieval and then turn to the effects of affect on intentional retrieval.

Affect and Spontaneous Episodic Memory Retrieval

A downstream consequence of the fact that affective memories are more likely to be deeply encoded and prioritized for memory storage and re-activation may be that these emotional events are more likely than neutral events to be spontaneously or involuntarily retrieved. In everyday life, involuntary memories often are of events that elicited positive affect (see Bernsten, 2009). However, intrusive and involuntary retrievals of a negative event are common in trauma survivors and arise across a range of affective disorders (see Brewin, Gregory, Lipton, & Burgess, 2010). In fact, involuntary retrievals are among the most distressing symptoms reported by individuals with Post Traumatic Stress Disorder and they correlate with PTSD symptomology (Michael et al., 2005; see Chapter 9.10 for further discussion of PTSD). In laboratory settings, affect can enhance the likelihood of spontaneous retrieval. For instance, after being shown either an emotionally negative or a neutral film, people remembered having more spontaneous recollections about the emotional film in the days following its presentation (Ferree and Cahill, 2009).

Additional evidence that spontaneous retrieval is enhanced for affective memories has come from event-related potential (ERP) studies that compare memory signatures on an explicit memory retrieval task versus a task that does not include an explicit goal of memory retrieval. ERP studies are well suited for this comparison, because there are two ERP signatures that have reliably been tied to memory retrieval (reviewed in Rugg & Curran, 2007; Wilding & Ranganath, 2012). When ERPs are recorded such that they are time-locked to a stimulus that is to be judged as old or new, the first signature is a frontally distributed negativity that arises between approximately 300 and 500 ms after stimulus onset. We will refer to this effect as the FN400 (for a discussion of the relationship of this component to the N400 component widely studied in psycholinguistics, see Voss & Federmeier, 2011). This signature is reduced (i.e., less negative) for more familiar stimuli, such that the FN400 has been taken as an indicator of memory familiarity. The second signature is a left parietal positivity from around 400 to 800 ms; this effect is larger for recollected items, or those items for which specific episodic details can be retrieved (see Chapter 5.6 for more discussion of Dual-Process models of memory, that distinguish familiarity from recollection).

Notably, while these memory signatures tend to be measured on tasks that require intentional episodic retrieval (i.e., participants are asked to make an old/new decision), the signatures remain present for affective stimuli even when the task does not require intentional memory retrieval to occur. For instance, Weymar, Bradley, El-Hinnawi, and Lang (2013) found left parietal old/new effects for both emotional and neutral stimuli when a typical intentional retrieval test was used. However, when participants' task was a semantic assessment of stimuli, a task that did not require intentional retrieval, previously presented photographs elicited an old/new effect only for emotional stimuli (see also Ferrari et al., 2012). These results suggest that memory retrieval is occurring for affective stimuli, even when the task does not demand it, consistent with a profile of enhanced spontaneous or involuntary retrieval for affective information. Also consistent with this general proposal is a study by Maratos and Rugg (2001), who found that emotional context modulated old/new effects when the task did not require explicit retrieval of this context, but those differences were absent when explicit source retrieval was required. In other words, emotion did not influence the signatures of intentional retrieval of a study context, but it did enhance the likelihood that participants were spontaneously retrieving that emotional context even when it was not a required part of the task.

An influential model of involuntary memory by Bernsten and colleagues (Berntsen, 2009; Berntsen, Staugaard, and Sørensen, 2013; Staugaard & Bernsten, 2014; Staugaard & Bernsten, 2014) places emphasis on two primary factors: the emotional arousal of the event and the retrieval cue discriminability (Staugaard & Bernsten, 2014). Cue discriminability refers to the ability for a cue to probe a specific memory. If there are many different associations between cues and memories, then cue discriminability would be low (i.e., the cue would be "overloaded") because a cue could elicit any number of memories, but if the cue is strongly associated with a single memory, then cue discriminability would be high. According to their model, when cue discriminability is high, so is spontaneous retrieval of a memory from that cue. Although the role of cue discriminability holds for all memories, regardless of their affective salience, Staugaard & Bernsten (2014) have proposed that over time, emotional arousal becomes an increasingly important additional factor in predicting spontaneous or involuntary remembering. They reported evidence that, over short delays, emotional and neutral stimuli were equally likely to be involuntarily retrieved, and stimuli with unique cues (i.e., high cue discriminability) were more likely to be involuntarily retrieved. But when retrieval delays were increased to a day or a week, cue discriminability no longer predicted more involuntary memories, and instead emotional stimuli came to mind more often than neutral ones.

These delay-dependent patterns suggest that the involuntary retrieval of emotional memories relates to the way that they are being consolidated over time. A bidirectional relation between involuntary retrieval and consolidation seems plausible. Enhanced consolidation may enhance involuntary retrieval: if emotional memories are prioritized for consolidation, then they may have stronger associations with the cues over time, making it more likely that they will be involuntarily activated by that cue. Reciprocally, the involuntary retrievals may serve to enhance consolidation: Spontaneous retrieval creates an opportunity for an event to be re-encoded and for the memory trace to become strengthened via consolidation.

Involuntary retrievals can also enhance the likelihood that information is able to come to mind voluntarily. If information has been refreshed and strengthened via involuntary retrieval, it may be more likely to come to mind when desired. Involuntary retrievals may have a downside, however: despite enhancing the likelihood that the memories will come to mind when desired, they also may lead individuals to have less control over the way in which they retrieve those events, leading to stereotyped retrievals with challenges retrieving details that were not part of the involuntarily retrieved memory, or to difficulties modulating the affective intensity of the memory. In the next sections, we turn to the voluntary retrieval of affective memory and to the control of affective memory retrieval.

Affect and Intentional Episodic Memory Retrieval

A number of ERP studies have reported a larger left parietal old/new effect to emotional stimuli on tasks assessing voluntary or intentional memory retrieval (see Figure 3; Inaba, Nomura, & Ohira, 2005; Johansson et al., 2004; Langeslag & Van Strien, 2008; Newsome, Dulas, & Duarte, 2012; Schaefer, Pottage, & Rickart, 2011; Schefter, Knorr, Kathmann, &

Werheid, 2012; Weymar, Low, & Hamm, 2011; Weymar, Low, Melzig, & Hamm, 2009; Weymar, Low, Modess, et al., 2010; Weymar, Low, Schwabe, & Hamm, 2010). These results are consistent with enhanced recollection for emotional items, and the few studies that have directly used a remember/know paradigm (Rajaram, 1993; Tulving, 1985) to distinguish recollection from familiarity have provided evidence that the left parietal old/new effect is larger for emotional stimuli given a remember judgment compared to those given a know judgment (Schaefer et al., 2011; Weymar, Low, Schwabe, et al., 2010; see also, Johansson et al., 2004).

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insert Figure 3 about here

While these studies suggest affective modulation of episodic memory retrieval, this pattern is far from universal, with some studies showing no effect of emotion (McNeely, Dywan, & Segalowitz, 2004; Meng et al., 2017; Versace, Bradley, & Lang, 2010; Windmann & Kutas, 2001) and even a few showing smaller old/new effects for negative stimuli (Koenig & Mecklinger, 2008; Lavoie & O’Connor, 2013; Maratos et al., 2000). Rather than reflecting random variability, the ERP effects seem to pattern with the behavioral results: studies that have found a smaller left parietal old/new effect of negative stimuli have generally shown worse old/new discrimination for negative stimuli (but see Lavoie & O’Connor, 2013). Meanwhile, studies showing larger left parietal old/new effects for negative stimuli have generally found better behavioral discrimination as well. No study we are aware of has found a larger or equal left parietal effect coupled with worse memory performance. These results underscore the variability in the EEM (Bennion et al., 2013) and the challenges in predicting *a priori* when an

EEM will occur. At the same time, they suggest that when an EEM does occur, it is likely to be linked to an increased recollection for emotional items.

While there are mixed results at short delays, all of the ERP studies examining old/new effects after a day or more have found advantages for emotional stimuli in the left parietal effect (Schaefer et al., 2011; Weymar et al., 2009; Weymar, Low, Modess, et al., 2010; Weymar, Low, Schwabe, et al., 2010). These results are generally consistent with behavioral evidence that the EEM is more likely to arise after longer delays (Yonelinas & Ritchey, 2015) and that delays long enough to include sleep are likely to lead to refinements in emotional memory retrieval networks (Payne & Kensinger, 2011). They also are consistent with fMRI evidence that retrieval of affective content can intensify connections among medial temporal-lobe regions (Takashima et al., 2016).

Although many of these effects may extend to all stimuli that elicit an affective reaction, there is intriguing evidence that some effects may depend on whether that reaction is of positive or negative valence. A couple of studies have reported equally sized left parietal old/new effects for negative and positive stimuli (Langeslag & Van Strien, 2008; Weymar et al., 2009), but positive stimuli have more often elicited a smaller effect (Inaba et al., 2005; Johansson et al., 2004; Newsome et al., 2012; Weymar et al., 2011). These results are consistent with behavioral evidence that negative stimuli may be particularly likely to promote recollection (Ochsner, 2000). This is consistent with theoretical models that posit that negative stimuli and events are particularly likely to produce vivid memories, greater recollection of sensory details, and a greater degree of neural recapitulation (Bowen, Kark, & Kensinger, 2018). Weymar and colleagues (2011) additionally presented evidence that the effects of valence may become exaggerated over time: They found that both negative and positive stimuli elicited larger parietal old/new effects one week after retrieval, but only negative items continued to show this effect at a one year delay.

The tendency for negative stimuli to be associated with stronger retrieval signatures of recollection is consistent with a recent proposal (Bowen, Kark, & Kensinger, 2018) that negative valence enhances the likelihood that the neural networks engaged at encoding are recapitulated at the time of retrieval. This model—Negative Emotional Valence Enhances Recapitulation (with the acronym NEVER and mnemonic "never forget")—grew out of the results of Bowen et al. (2017a, 2017b) and Kark & Kensinger (2015): In those studies, there was greater overlap between encoding and retrieval activation when retrieved stimuli were negative than when they were positive. Importantly, both paradigms used in those studies incorporated relatively neutral cues to prompt memory for the stimuli (see Box 4).

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insert Box 4 about here

To test the tenets of the NEVER model, Kark & Kensinger conducted a series of analyses on a new dataset (Kark & Kensinger, 2019a, 2019b). They replicated the prior results from Kark & Kensinger (2015), showing that negative events were retrieved with greater encoding-to-retrieval overlap than were neutral or positive memories, especially within regions of the ventral visual stream. They also discovered that the individuals who showed a stronger pattern of activation within ventral visual stream regions were those who showed a stronger negative memory bias on the recognition memory task (i.e., a greater tendency to remember negative compared to positive stimuli). Negative memory biases are common in depression and anxiety disorders (see Chapter 9.8 for further discussion of depression, anxiety, and memory), though in this sample there was no evidence that they were maladaptive. Interestingly, the results provided suggestive evidence that individual differences may be related to the way that ventral visual stream regions became connected to the amygdala post-encoding: Individuals with stronger pre-to-post encoding strengthening of amygdala-visual connectivity were more likely to show strong engagement of ventral visual regions during the retrieval of negative events and a negative memory bias. Although the sample size in this fMRI study was relatively low to examine individual differences (N=29) and thus replication of the result will be particularly important, these results suggest the intriguing possibility that, when sensory regions stay incorporated into emotional memory networks post-encoding, this may set up a sensory-driven retrieval of negative events, resulting in a negative memory bias.

Another model of emotional memory that has placed emphasis on the role of retrieval processes is the emotional Context Maintenance and Retrieved model (eCMR; Talmi, Lohnas, & Daw, 2018). Like the NEVER model, this model emphasizes the importance of a match between encoding and retrieval states for memory success (e.g., Tulving & Thompson, 1973; Danker & Anderson, 2010). But the eCMR, like other context models of retrieval (Howard & Kahana, 2002; Polyn et al., 2009), focuses on the transient changes in brain state that can affect which memories are accessible at any moment during retrieval. The eCMR therefore conceives of the effects of emotional memory as a result of the malleable temporal and emotional contexts across which retrieval occurs, emphasizing the importance of how memories will be prioritized for retrieval, given the goals of the rememberer (see DuBrow, Rouhani, Niv, & Norman, 2017 for additional discussion of the role of context in memory prioritization). eCMR further proposes that emotion adds two additional variables that are of relevance to that prioritization: emotional stimuli belong to an *emotional category*, and thus share some semantic relation, and emotional items can modulate *attention.* This latter category was found to be particularly important for understanding how emotion modulates retrieval, consistent with evidence that the prior emotional study history of items can affect visual attention to stimuli at retrieval (e.g., Ventura-Bort et al., 2016; Bennion et al., 2017).

These retrieval models dovetail with the mood-congruency literature to emphasize the power of the retrieval context for understanding emotional memory enhancements. Together, these literatures suggest that emotional memories can gain prominence at retrieval both when there is synergy between memory content and an individuals' sustained affective state (i.e., mood-congruency) and also when transient affective reactions propagate changes to upcoming retrieval attempts to make emotional memory retrieval more likely. Although the transient and sustained effects may be mechanistically distinct, in unconstrained settings, these influences are likely to co-occur. For instance, the repeated retrieval of emotional memories triggered by transient affective reactions is likely to increase the tendency for the memories to induce a mood state.

Affect and Retrieval Accuracy

As we noted at the outset of this review, while affective experiences are often more likely to be retrieved after a delay than neutral experiences, the details of those events are not always remembered consistently (Holland & Kensinger, 2010; Neisser & Harsch, 1992). In one influential study, Talarico and Rubin (2003) found that memories for the September 11th terrorist attacks declined in accuracy at a similar rate to memory for every day events, even while the subjective confidence and vividness of the September 11th memories remained much higher. In controlled laboratory studies, recall and recognition rates are generally higher for emotional stimuli, but so are false recall and false recognition. In recognition tasks particularly, this has resulted in similar, or sometimes worse, memory discrimination for emotional compared to neutral items (Budson et al., 2006; Ehlers, Margraf, Davies, & Roth, 1988; Johansson, Mecklinger, & Treese, 2004; Maratos, Allan, & Rugg, 2000; Windmann & Kruger, 1998; Windmann & Kutas, 2001).

There are likely many factors that reduce the accuracy of affective memory retrieval (see Chapter 6.4 for further discussion of memory errors and distortions). One is that emotional items—and negative items, in particular—may seem more familiar, even when they have not been previously studied, perhaps because emotional arousal leads to feelings of fluency (Sharot, Delgado, & Phelps, 2004) or because they tend to be more semantically related to each other (Maratos et al., 2000). Consistent with this proposal, across several studies, the familiarity-related FN400 has shown reduced amplitude (reflecting greater familiarity) to negative new items (Johansson et al., 2004; McNeely et al., 2004; Windmann & Hill, 2014; Windmann & Kutas, 2001). This enhanced familiarity could explain higher false alarm rates and worse behavioral discrimination.

The unevenness of affective memories may also contribute to their tendency to be remembered with erroneous or inconsistent details. Phelps & Sharot (2008) argued that for affective memories, the subjective feeling of remembering may be tied to memory for just a few key details; by contrast, for neutral experiences, the subjective feeling of remembering may be linked to the ability to retrieve a broader array of contextual details. Indeed, the amygdala is thought to enable encoding of only a select subset of episodic details (reviewed by Holland & Kensinger, 2010). Yet individuals may assume that because they can remember one aspect of an event vividly and accurately, the other details they have retrieved are also accurate. For affective memories, this assumption may lead individuals to be particularly prone to false endorsements (see Kensinger, 2009 for further discussion).

Affective memories can be contorted not only in their details, but also in the way the previously-experienced affect is remembered. Individuals are often inaccurate when recalling the intensity of emotions experienced during a past event, with their memory for previous emotions influenced by the affect experienced at the end-point of the event (reviewed by Fredrickson, 2000) and by knowledge acquired after the time of the event or by semantic knowledge of which emotions should be felt (Robinson & Clore, 2002). Some of these errors may serve adaptive functions. Memory retrieval can be used to serve a number of important functions in daily life, ranging from social, self, and directive goals (Bluck et al., 2005) to an ability to envision and plan for the future (Schacter & Addis, 2009). The reconstruction of past emotions based on current goals and knowledge can enable memory retrieval to serve these goals. For instance, Ross (1989) suggests that memory retrieval may either exaggerate or minimize the difference between past and present feelings, depending on how an individual relates the memory to their sense of self. Levine and Safer (2002) similarly focus on the benefits of reconstruction of past emotions, likening memory for emotion to updating a map based on new information.

Investigations of the effect of emotion regulation goals on affective memory retrieval serve as a relevant example of the beneficial effects of memory reconstruction. Emotion regulation refers to the processes used to alter which emotions, or how intensely emotions, are experienced or expressed (Gross, 1998). For instance, individuals in a sad mood tend to first show mood congruent memory retrieval effects but then show mood *in*congruent effects (Sedikides, 1994; Josephson, Singer & Salovey, 1996). Mood incongruent recall has been proposed to result from individuals' attempts at mood repair, retrieving positive memories so as to curtail a negative mood (Isen et al., 1978; Isen, 1984). Holland, Tamir, and Kensinger (2011) found that even when individuals are instructed to retrieve a particular event, their emotion regulation goals may lead them to retrieve different details of that past emotional event. In that study, individuals preparing to meet with a sad individual increased the amount of negative emotional language they used in reporting past events in comparison to a baseline recall of the same events; those who thought they would be meeting with a happy individual demonstrated the opposite pattern. Interestingly, this pattern was strongest for the second memory retrieved, consistent with proposals that emotion regulation goals may take time to implement and thus may be more evident after the first attempt at memory retrieval (e.g., Josephson et al., 1996).

Retrieval of Affective Memories: Summary

Affective memories come to mind involuntarily and voluntarily. Affective events are overrepresented among spontaneously retrieved memories (Bernsten, 2009; Ferree and Cahill, 2009). This spontaneous retrieval is likely to be both a consequence and a cause of the enhanced consolidation of affective events, leading these events to be more accessible when voluntarily sought for retrieval. When affective memories are voluntarily retrieved, they often are associated with signatures of recollection. This pattern is particularly strong for negative memories, and negative affective memories—and memory biases—may also have a stronger sensory signature. But despite these signatures of recollection, affective memories are not perfect representations of the past; they contain distortions and inconsistencies (see reviews by van Giezen et al., 2005; Neisser & Harsch, 1992). These distortions can serve adaptive functions: The emotion that we feel at retrieval, or that we want to feel, can influence not only which events from our past are most accessible but how we reconstruct those past experiences and emotions.

Affective Modulation of Other Forms of Memory

While we have primarily focused on how affective reactions modulate long-term memory, and particularly episodic memory, this is not to indicate that affective reactions do not also influence other forms of memory. Here we briefly mention two relevant literatures: conditioning, a form of implicit memory, and working memory.

Conditioning

Classical conditioning paradigms involve learning the affective significance of a previously neutral stimulus by pairing it with an affectively laden stimulus. Operant conditioning paradigms involve learning the relationship between behaviors and an affective outcome. These paradigms have been used extensively in animal models of learning and memory. In fact, while research in human cognition has often examined questions about basic memory mechanisms separate from affective processes, affect and motivation have always been at the center of the study of learning in animals: learning in laboratory settings is usually achieved because animals are motivated by some affective reaction or outcome. Thus, the large literature on these phenomena highlight the fundamental role of affective processes in learning. There is also a literature on these processes in humans, which is reviewed in Chapter 2.6

There has recently been renewed interest in the relationship of these basic learning mechanisms to episodic memories (e.g., Duncan, Semmler, & Shohamy, 2019). Some of this work was discussed in relation to post-encoding modification of memories in a previous section of this chapter (e.g., Dunsmoor et al., 2015). Recent investigations have highlighted the fact that emotional experiences will generally engage both basic learning mechanisms and episodic memory systems, and that there are bi-directional influences between these systems (see discussion in Dunsmoor & Kroes, 2019).

Working Memory

Although it has received less attention than long-term memory, there is also a literature on affective modulation of working memory (see Chapter 2.9 for discussion of working memory). This has typically been studied in two ways: by looking at how individuals maintain affective states in memory or by looking at how the affective content of information to be held in working memory affects the efficacy of the working memory system.

There is evidence that working memory for emotion may differ from working memory for other types of information (reviewed in Mikels & Reuter-Lorenz, 2019). For example, Mikels, Reuter-Lorenz, Beyer, and Fredrickson (2008) had participants maintain either visual information or the affective state induced by a stimulus in working memory. They showed that a secondary emotion regulation task selectively interfered with maintenance of affective states whereas secondary cognitive tasks selectively interfered with the maintenance of visual information. Such results may be expected from modern theories of working memory that suggest significant overlap in the neural regions engaged for perception, representation, short-term memory, and long-term memory (e.g., Jonides et al., 2008; Postle, 2016). Insofar as the perception and representation of affective states is neurally separable from visual information, we would expect that working memory for these types of information would be separable. Distinctions between affective working memory and working memory for other information may also show interesting patterns of individual difference. Consistent with results in long-term memory in which aging relatively preserves emotional memory while having a greater impact on memory for neutral material (Mather, 2012; Kensinger, 2009), Mikels, Larkin, Reuter-Lorenz, and Carstensen (2005) showed that older adults were impaired on working memory tasks for visual information, but showed no impairment vs. younger adults when required to keep affective states in working memory.

Other work has explored how the emotional properties of stimuli such as words and pictures influence their maintenance in working memory. Conflicting results have been reported in this literature (e.g., Kensinger & Corkin, 2003; Lindstrom & Bohlin, 2011). A recent meta-analysis found inconsistent effects of affective information on working memory performance that were overall small or non-significant (Schweizer et al., 2019), but the effects of emotion may depend on the task (and the relevance of affect to the task), and the specific aspect of working memory investigated (e.g., capacity and maintenance vs. interference resolution: Levens & Phelps, 2008).

Summary and Future Directions

We remember only a fraction of our experiences and emotion is one of the key factors that determines the selectivity of memory. It is anecdotally clear that emotional events and information are remembered better, and research shows that this is generally true. However, the story is more complex than this heuristic of an EEM. Emotion leads not just to better memory, but also to more uneven memories, with neutral details of an emotional event, or neutral stimuli in the context of emotional stimuli, often remembered less well than they otherwise would be. And while much research has focused on the emotionality of to-be-remembered stimuli themselves, the effects of emotion on memory are much more flexible. The affective state of the participant has effects on memory, with mood-consistent stimuli more likely to be remembered (e.g., Bower, 1981). Related effects can arise when the affective context reinstated by the retrieval of one event modulates the likelihood that an affectively-related event is retrieved. Thus, having retrieved one emotional memory, the probability of retrieving a second emotional memory increases (e.g., Long, Danoff, & Kahana, 2015; Talmi, Lohnas, & Daw, 2018). In addition, the affective "tagging" of a stimulus for better memory can occur some time after the stimulus is presented, as when later information leads to a re-evaluation of the stimulus value. This is likely adaptive, since we do not always know the emotional relevance of an event at the time it is experienced, but it also means that otherwise neutral and unconnected events can be remembered well when experienced in proximity to an emotional event.

Although much research has focused on the effects of emotion on memory encoding, emotion also has important effects on memory retrieval. Emotional memories are more likely to be spontaneously retrieved, and this likely contributes to the tendency for the emotional enhancement of memory to be strengthened over longer consolidation periods. And while much research has focused generally on the effects of affect, or honed in on the effects of arousal, there are important valence differences. Negative memories tend to be more vivid and contain more sensory details, and this subjective experience is supported by fMRI work showing greater overlap in the sensory activation engaged during encoding and retrieval of negative items. Once again, however, the relationship between emotion and improved memory is not always straightforward: in some cases highly negative memories may be experienced as subjectively quite vivid while not showing greater accuracy than neutral memories, and false memory for emotional items is often higher, perhaps because they seem more familiar.

Many effects of emotion on memory may have adaptive consequences. We often remember emotional events better because emotion serves as an indicator of the personal relevance of the information. Indeed, events and information experienced as emotional are often the most important things to be remembered in our lives, and in this sense emotion has a fundamental connection to what memory is for in the first place. Emotional biases can also be adaptive (e.g., Johnson & Fowler, 2011), and the beneficial effects of emotion on memory are likely to extend to the ways in which emotion distorts memory in addition to the emotional enhancement of memory.

On the other hand, like many of the features of memory (Schacter, 2001) and cognition more broadly (e.g., Gigerenzer, 2008), the same effects of emotion that are often beneficial can become maladaptive. For example, according to The Innocence Project (https://www.innocenceproject.org/eyewitness-identification-reform/), mistaken eyewitness identifications contributed to 71% of wrongful convictions (overturned by DNA evidence) in the United States. Thus, the failure of the confidence of highly emotional memories to match their accuracy can have very serious consequences (Wixted & Wells, 2017; see also Chapter 12.4). In the mental health domain, issues related to emotional memory, such as the spontaneous retrieval of negative memories, play a key role in disorders such as anxiety, depression, and post-traumatic stress disorder. For all these reasons, it is crucial that researchers continue to investigate the how and why of affective memory.

The study of affective memory is still a relatively young field within the broader field of research on human memory, and there are still many unanswered questions. We have highlighted what we think will be fruitful future directions throughout the chapter, and we conclude by noting two broad intersections that we think will be particularly valuable to investigate. First, future research needs to provide additional clarity on how the different time-courses of an affective response interact to influence memory. There is much more to be learned about how stress and mood states modulate the effect of a transient affective response on memory or the ability for new learning to retroactively enhance memory. For instance, if someone is in a bad mood while encountering new affectively-laden information, how does that mood state alter the ability for the new information to modulate the strength of already-encoded memories? Second, future research must continue to parse effects unique to affective modulation of memory from those modulatory influences that extend to other domains as well. The study of affective memory has proceeded with relatively little contact to related literatures of reward-modulated memory, self-referential memory, and action-imagery modulations of memory. Yet there are clear connections across these literatures that must be better understood (see Madan, 2010; Gutchess & Kensinger, 2018 for some discussion). By doing so, the next decades of research can lead us to a more complete picture of the complex ways in which affect modulates memory.

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Box 1. Defining Affect. Affect is defined by the American Psychological Association (APA) as "any experience of feeling or emotion, ranging from suffering to elation, from the simplest to the most complex sensations of feeling, and from the most normal to the most pathological emotional reactions." Affective reactions can spread out across different time-scales, ranging from sustained states (e.g., moods) to fleeting reactions (e.g., startle). They can vary in their observable nature, eliciting changes in a person's physiology, cognition, and behavior. Negative affective states can be closely associated with stress (e.g., they often co-occur, can include changes in norepinephrine levels, and can result in similar physiological changes), but a distinction is that while affective states tend to be defined by the changes in physiology, cognition, conscious experience, or behavior that they evoke, stress is more commonly defined by the depletion of resources created and the strain placed on the organism (see Butler, 1993).

Within the context of understanding how memories are modulated by affective reactions, researchers have primarily focused on dimensional models that parse affect into underlying components. There are multiple different dimensional models (e.g., circumplex model: Russell & Barrett, 1999; positive activation-negative activation: Watson & Tellegen, 1985; vector model: Bradley Greenwald, Petry, & Lang, 1992; see Rubin & Talarico, 2009 for comparison of accounts in the context of memory). What they share in common is that they parse affective reactions into *arousal* or *intensity* (degree of change in physiological state or alertness) and *valence* (degree of pleasure or displeasure).

In this chapter, we use *emotion* as a synonym for a short-lived affective reaction. Yet it is important to note that in some writings, *emotion* is reserved to denote a conscious experience of feeling while *affect* is used for a range of physiological or behavioral changes that do not result in conscious awareness (see Gendron & Barrett, 2009 for a historical review of definitions and models of emotion, affect, feelings, and related constructs).

Box 2. Explaining Mood-Congruency Effects. Three primary hypotheses have been put forth to explain mood-congruency effects. Bower (1981) proposed that mood acts as a central node in an associative network such that, when the mood is experienced, the associated nodes become active, making related material more readily accessible for memory encoding or retrieval. The affect-as-information model (reviewed by Clore et al., 2001; Schwarz, 2012) proposes that individuals use their affective states as a diagnostic tool for making evaluating judgements. This process can lead to mood-congruent biases in the way that information is interpreted or remembered. A third view minimizes the uniqueness of the affective experience, suggesting that it is not the mood but the semantic content of the experience that can prime related content; by this account, mood congruency may be akin to semantic priming (Rholes, Riskind, & Lane, 1987; Higgins, Rholes, & Jones, 1977; Mayer et al., 1990). These debates parallel many that are ongoing within the field of affective science, in trying to distinguish when it is the *experienced affect* that is driving an effect versus the *cognitions that accompany the affective state*. In one sense, the dichotomy is a false one, because changes in cognition can be a key feature of an affective reaction. But in another sense, the debate is a critical one because it puts front-and-center the question of whether an outcome is uniquely caused by an affective reaction or mediated by other factors that may also arise in the absence of an affective reaction.

Box 3. Memory modulation by affective response is more than memory modulation by affective knowledge. Sometimes, participants will have a measurable change in affective state, i.e., an affective reaction, caused by a briefly-presented stimulus: Perhaps participants see a photograph of a snake and, as a consequence, experience a change in heart rate, or a sweat response, or experience another facet of an orienting or startle response. But other times, especially in laboratory settings, individuals may be aware of an affective stimulus, yet that stimulus may not elicit any measurable affective reaction. For instance, when participants see the word “cry” presented on-screen, they may retrieve negative concepts associated with the word, and be able to rate the word as a negative stimulus, but they may not experience any affective reaction of their own. Kensinger (2004) discussed these latter effects on memory as “valence only” effects, distinguishing them from effects more likely to be tied to the internal affective reactions triggered by stimuli. When memory benefits arise for these “valence only” stimuli, the benefits seem attributable to the same cognitive processes that would benefit memory for any type of stimulus, including elaboration, organization, and autobiographical association. While these cognitive processes also can modulate memory for information that elicits an affective reaction (Talmi, 2013; Talmi & McGarry, 2011), they are less likely to be the complete explanation for the patterns of affective memory performance that result and are especially unlikely to account fully for delay-dependent effects of affect on memory.

Box 4. Putative shared mechanisms support the encoding of emotional and self-relevant information. There is clear overlap between the experiences of emotion and self-relevance (Fossati et al., 2004; Herbert et al., 2011; Skowronski et al., 2015); in fact, some theories of emotion postulate that self-relevance must be present for emotion to arise (Lazarus, 1991). It recently has been proposed that there is overlap not only in the experience of self-relevance and emotion but also in the processes that enable these experiences to become encoded into memory: Gutchess and Kensinger (2018) propose a shared-processes model for the encoding of emotional and self-referential material. This model is supported by a few empirical findings. Behaviorally, there can be sub-additive effects on attention and memory when combining emotion with self-relevance. For instance, Grilli, Woolverton, Crawford, and Glisky (2018) presented older adults with emotional and neutral vignettes under different encoding conditions that varied in self-relevance. They revealed an EEM when encoding conditions were not self relevant (participants counted syllables or semantically elaborated on sentences). But when the encoding context was self-relevant (participants reflected on personal meaning), there was no longer an EEM. This pattern is what would be expected if there are shared processes leading to successful encoding within each domain. Overlap is also suggested by neurophysiological and neuroimaging research. In an ERP study, Fields and Kuperberg (2012) showed increased amplitude in the late positive potential (LPP), which typically is enhanced for emotional stimuli (Hajcak et al., 2012), for neutral content encoded in a self-relevant compared to a non-self-relevant neutral content. There was no further enhancement for self-relevant emotional content, once again suggesting a sub-additive pattern of self-relevance and emotion. Coupled with neuroimaging research suggesting that emotion and self-relevance engage overlapping circuitry within medial prefrontal cortex (Glisky et al., 2019), these results suggest that self-relevant and emotional information may show prioritized encoding due to their recruitment of shared neural mechanisms.

Box 5. Future directions: EEG and neural oscillations in the study of affective memory. Some of the most exciting work using EEG to study memory in recent years has focused on the role of neural oscillations. Such oscillations are not always phase-locked to stimuli and can therefore be obscured by the averaging process that creates ERPs, but increased computing power and advances in time-frequency analysis techniques have opened exciting new possibilities for studying the contributions of oscillations to cognition. Neural oscillations may play a particularly important role in memory. For example, single-cell and local field potential recordings show that theta is a prominent rhythm in the hippocampus and may play a key role in long-term potentiation (Buzsaki, 2002). In the human scalp EEG, theta (~4-7 Hz, generally frontally distributed) is the most consistent index of memory encoding processes, and is thought to represent cortex-hippocampus interactions (Hsieh & Ranganath, 2014; Nyhus & Curran, 2010). More generally, oscillations have been suggested to be key to the ability of the brain to form temporary networks and link information across regions of the brain. Such binding is a key feature of episodic memory (Fell & Axmacher, 2011; Nyhus & Curran, 2010) and is likely modulated by emotion (Bowen, Kark & Kensinger, 2018; Yonelinas & Ritchey, 2015). Thus, oscillatory analyses may provide important insights into the mechanisms by which affect modulates memory.

As analysis approaches continue to advance, more complex relations to memory are uncovered. For example, examination of cross frequency coupling suggests that the linking of the amplitude of neural spiking in gamma bands (>30 Hz) to the phase of the theta wave may be particularly important for memory formation (Hanslmayr, Staresina, & Bowman, 2016). Much of this research is in its infancy and the field is in the process of trying to reconcile diverse and sometimes contradictory results (e.g., Hanslmayr et al., 2016; Hanslmayr & Staudigl, 2014). In this chapter, we do not discuss time-frequency EEG and oscillations because little research has examined the role of neural oscillations in affective memory. However, this is likely to be a rich area of research as the contributions of oscillations to memory become clearer.

Box 6. The importance of using neutral retrieval cues to isolate effects of affect on memory retrieval. One complication of using recognition tasks to study affective memory retrieval—as is done in the vast majority of ERP and fMRI research—is that the effects of processing the retrieval cues have to be disentangled from memory-related processes. This can create large challenges when emotionally salient cues are used to trigger affective memories but neutral cues are used to trigger neutral memories. For example, in the ERP literature, the component most commonly modulated by emotion at the time of retrieval is a parietally-distributed late positive potential (LPP) that is very similar to the parietal positivity associated with recollection in the memory literature (Citron, 2012; Hajcak, Weinberg, MacNamara, & Foti, 2012). This overlap can make it impossible to distinguish effects of emotion processing from effects of memory. More generally, emotionally arousing stimuli may lead to physiological arousal and valenced stimuli may affect processing styles (Clore & Huntsinger, 2007), such that differences in memory retrieval are due to properties of the cue rather than the underlying memory.

One way around these issues is to use neutral retrieval cues to cue memory of stimuli of differing valence. These cues can be randomly paired and counter-balanced such that behavioral and neural effects can be compared to the same cues for memories of different valence. In an initial study, Maratos and Rugg (2001) presented sentences that contained neutral critical words within a sentence that was either negative or neutral. When the neutral critical word was re-presented at retrieval, there was a left parietal old/new effect beginning by 500 ms for all old items when compared to new items, but this effect was larger for words encoded in a negative context, suggesting the context may have been recollected to a greater extent for these items.

Other studies have used a similar design with picture stimuli, pairing neutral or emotional photos with a neutral photo or word that is used as a retrieval cue (e.g., Ford, Morris, &

Kensinger, 2014). Some of these studies have found very early-onsetting differences for cues encoded with emotional vs neutral stimuli. For example, Bowen, Fields, & Kensinger (2019) recently reported differences between neutral words that had previously been paired with emotional and neutral images starting at around 200 ms after initial word presentation (see also Jaeger, Johnson, Corona, and Rugg, 2009; Righi et al., 2012). This difference emerged before observed differences between words previously paired with neutral images and new words, and the difference was about as early as any observed old/new effect in the ERP literature, suggesting that the emotional context of encoding can have very early effects on memory retrieval.

Figure Captions

Figure 1. The selectivity of affective episodic memory. Episodic memory is highly selective, with only a subset of information from an experienced event becoming part of a retrieved memory representation. Information that elicits an affective response is likely to be selected for encoding and storage, both due to processes specific to affect and also because that information is likely to be personally relevant, distinctive, or relevant to current goals or states. At retrieval, affect influences the selective pressures; often these will push retrieval toward a focus on affective details, although some retrieval goals (e.g., emotion regulation) can instead push retrieval away from that affective focus.

Figure 2. The types of affective reactions that influence episodic memory encoding.

Figure 3: Emotional modulation of the left parietal old/new effect. The left parietal old/new effect, which is associated with recollection, is often larger to emotional stimuli, especially negative stimuli. Waveforms are from an average of centroparietal electrodes. Scalp maps show the Old –New effect from 500-800 ms (shaded on the waveforms). Adapted with permission from Weymar et al. (2009).

Figure 1.

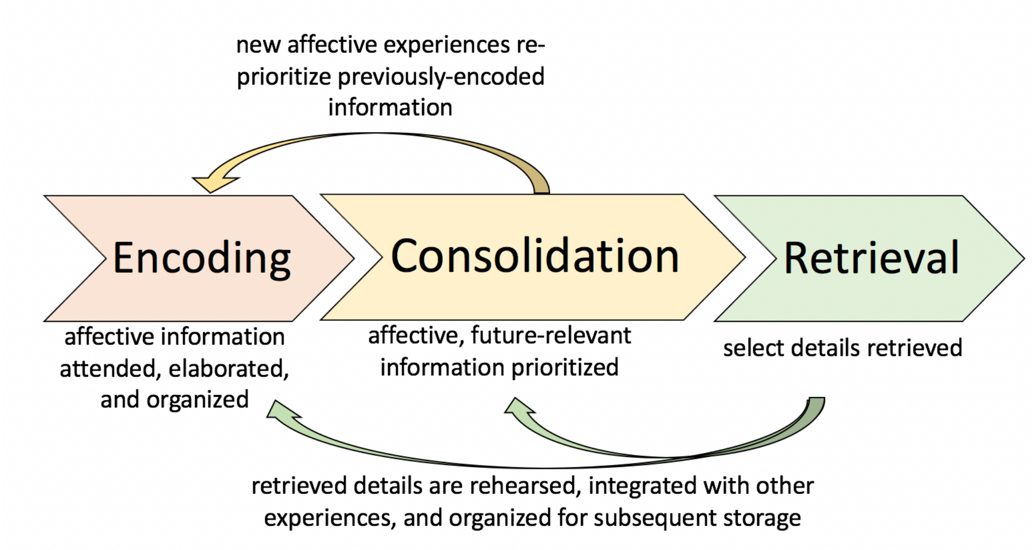

new affective experiences re-prioritize previously-encoded information
Encoding
Consolidation
Retrieval
affective information attended, elaborated, and organized
affective, future-relevant information prioritized
select details retrieved
retrieved details are rehearsed, integrated with other experiences, and organized for subsequent storage

Figure 2.

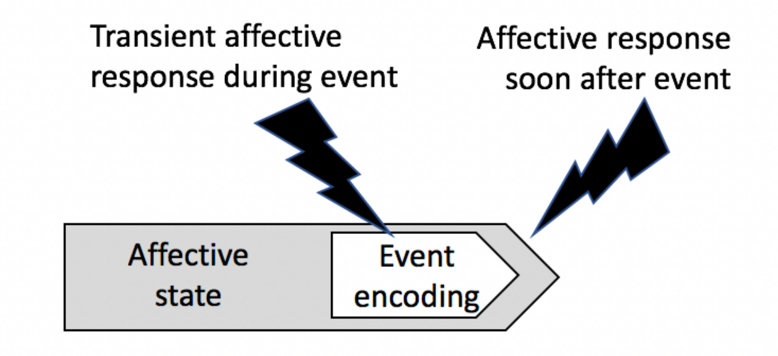
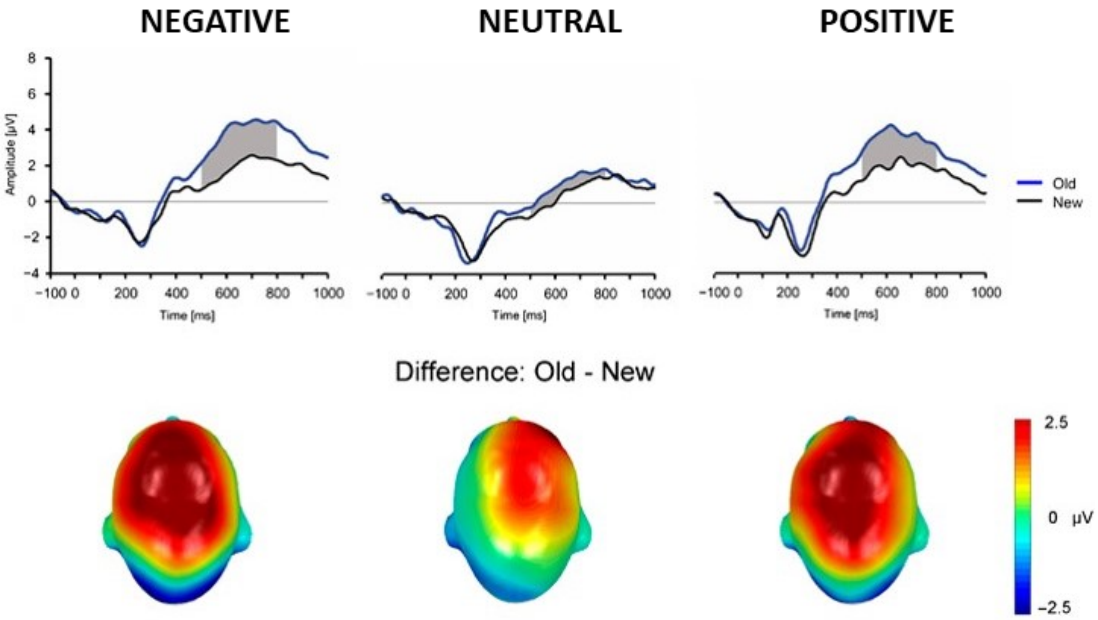

Transient affective response during event
Affective response soon after event
Affective state
Event encoding

Figure 3.


NEGATIVE
NEUTRAL
POSITIVE
Amplitude [µV]
8
6
4
2
0
−2
−4
−100 0
200
400
600
800
1000
Time [ms]
Old
New
Difference: Old - New
2.5
0 µV
−2.5