CHAPTER 1

Emotion and Memory

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INTRODUCTION

Although more than a decade has passed since September 11, 2001, most adults will have no problem remembering what happened on that date; by contrast, most of those same adults will have no memory of what happened on the previous day. It is well established that we are less likely to forget emotional events than we are to forget more mundane experiences. Yet, despite this consensus, there continues to be active research and debate about fundamental questions regarding the links between emotion and memory: How does the nature of the emotional reaction affect memory? Which details of an emotional experience are most likely to be retained? What neural processes enable these interactions between emotion and memory, and over what time course do they operate?

In this chapter, we first focus on how two different aspects of an emotional reaction—its valence and arousal—affect the way that the events are remembered. We then turn to a discussion of the time course of those effects, describing how emotion can affect the sequence of processes engaged during encoding and retrieval as well as the processes that unfold over time as memories are consolidated. In each of these sections, we review findings from behavioral, neuroimaging, and psychophysiological studies, because it is from the combination of these methods that many of the key insights regarding emotion and memory have been revealed. We conclude with a brief discussion of three debates that are ongoing in the field: the role of the amygdala in emotional memory, the effects of emotion on memory accuracy, and the effects of emotional appraisals and reappraisals on memory.

HOW VALENCE AND AROUSAL AFFECT MEMORY

Often when we think about an emotional reaction, we think about the physiological reactions elicited, such as our sweaty palms and pounding heart as we are about to make our way onstage in front of an audience. Indeed, much of the research examining the effects of emotion on memory has focused on the influences of this arousal dimension (Mather & Sutherland, 2011; Yonelinas & Ritchey, 2015), building on decades of research using animal models to reveal the neural circuitry implicated in arousal-based modulation of memory (see McGaugh, 2015, for a review). Yet the pleasure or displeasure stemming from an event also can be a powerful predictor of how that event will be remembered. In this section, we describe the influences of these dimensions of arousal (physiological and subjective reactivity) and valence (pleasure or displeasure; see Lang, Greenwald, Bradley, & Hamm, 1993; Russell, 1980, for discussion of these dimensions).

Separable Influences of Valence and Arousal

The emotional events that we experience often elicit shifts in valence and arousal. In other words, as compared to a neutral state, emotional events tend to evoke pleasure or displeasure as well as subjective and physiological arousal. Although shifts in both dimensions often occur when emotion is elicited in real-world contexts, in laboratory settings the influences of these dimensions can be distinguished. Most commonly, this is achieved by selecting stimuli that elicit shifts in one primary dimension or by matching stimuli on one dimension (e.g., valence) and then examining how a change in the other dimension (e.g., arousal) affects memory.

In a series of studies, Kensinger and Corkin (2003, 2004; see Kensinger, 2004, for a review) demonstrated that the presence of either the valence or the arousal dimension (i.e., a change from neutral in either direction) was sufficient to elicit memory enhancements (Kensinger & Corkin, 2003): Words that evoked changes in arousal but not valence ("high-arousal stimuli") were remembered better than words that elicited neither changes in arousal nor valence, and a similar memory benefit also was revealed for words that evoked changes in valence but not arousal ("valence-only stimuli"). A memory advantage for valenced stimuli, regardless of their arousal, has also been demonstrated using a large corpus of linguistic stimuli (Adelman & Estes, 2013), confirming that shifts in the valence dimension are sufficient to elicit memory benefits. Importantly, however, the mechanisms underlying the valence-only and high-arousal enhancements appear to differ: Kensinger and Corkin (2004) noted that high-arousal stimuli were remembered well even when attention was divided during encoding, whereas memory for the valence-only stimuli was dramatically reduced when attention was divided. In fact, under conditions of divided attention, memory for the valence-only stimuli was no longer greater than memory for neutral words, and the memory enhancement for high-arousal stimuli remained intact (Kensinger & Corkin, 2004).

These behavioral results pointed to dissociable mechanisms supporting the memory benefits for high-arousal and valence-only stimuli and suggested that the memory benefits for the former may occur relatively automatically and the memory benefits for the latter may be linked to more controlled encoding processes. This conclusion is generally consistent with evidence from event-related potentials (ERPs), which suggests arousal is processed faster than valence (Jhean-Larose, Leveau, & Denhière, 2014; Recio, Conrad, Hansen, & Jacobs, 2014; Styliadis, Ioannides, Bamidis, & Papadelis, 2015). In terms of memory encoding, across a range of paradigms, arousing stimuli have been remembered well even when attention is divided (Kern, Libkuman, Otani, & Holmes, 2005; Steinmetz, Waring, & Kensinger, 2014), although the effect may be stronger for negative stimuli than for positive stimuli (Kang, Wang, Surina, & Lü, 2014). Moreover, associations between pairs of high-arousal stimuli can be formed rapidly (Murray & Kensinger, 2013b) and remembered better than neutral stimuli even when attention is divided (Maddox, Naveh-Benjamin, Old, & Kilb, 2012). Debates continue about whether these memory enhancements for high-arousal information occur automatically or whether the processing of that information may be prioritized at the expense of other concurrent processes (Pottage & Schaefer, 2012). But importantly, even if a prioritization explanation is correct, it still appears that the prioritization itself occurs relatively automatically. For instance, high-arousal stimuli typically attract attention and resources (see Bröckelmann et al., 2011; Schmidt, Belopolsky, & Theeuwes, 2015) even when participants are instructed to attend to other concurrent tasks or to ignore those stimuli (see Iordan, Dolcos, & Dolcos, 2013, for a review). Memory enhancements for valence-only stimuli, by contrast, appear to be linked to additional engagement of the same types of controlled, elaborative processes that typically support memory. Thus, when attention is divided, these benefits disappear (Kang et al., 2014; Kensinger & Corkin, 2004), and older adults, who have difficulty engaging elaborative encoding processes show less memory enhancement for valence-only stimuli than for high-arousal stimuli (Kensinger, 2008).

Neuroimaging (functional magnetic resonance imaging; fMRI) studies have provided further evidence of this dissociation. Memory for high-arousal stimuli is linked to engagement of the amygdala at encoding (Kensinger & Corkin, 2004; Mickley & Kensinger, 2008; Steinmetz, Schmidt, Zucker, & Kensinger, 2012) and to correlations between amygdala and hippocampal activity (Fastenrath et al., 2014; Kensinger & Corkin, 2004; Leal, Tighe, Jones, & Yassa, 2014; Richardson, Strange, & Dolan, 2004). By contrast, memory for valence-only stimuli are linked to additional engagement of the same prefrontal cortex (PFC) and hippocampal processes that support memory for neutral information (Kensinger & Corkin, 2004; Steinmetz & Kensinger, 2009).

Combined Influences of Valence and Arousal Dimensions

Although these prior studies demonstrate that the presence of either valence or arousal is sufficient to elicit memory enhancements, in everyday life, these dimensions tend to co-occur. Events that are highly valenced are also arousing, and vice-versa (see Bradley & Lang, 1991; Lang, Bradley, & Cuthbert, 2008, for distribution of stimuli in this two-dimensional space). Extensive research has therefore focused on the combined influences of valence and arousal on memory: How is memory affected when events are highly arousing and also pleasant or unpleasant?

Decades of research has confirmed that these emotional events are more likely to be remembered than neutral ones and can have a shallower forgetting curve than emotional items. Among the first demonstrations of this memory enhancement were demonstrations of “flashbulb memories,” the subjectively vivid memories formed when events are surprising and emotionally evocative (Brown & Kulik, 1977; see Holland & Kensinger, 2010, for a review of emotion and autobiographical memory). Indeed, everyday memories and flashbulb memories may be similarly detailed at first, but over time, confidence for memory accuracy remains high for flashbulb memories whereas confidence decreases over time for everyday memories (Talarico & Rubin, 2007). In other words, people tend to be overconfident in the accuracy of their flashbulb memories, but objective accuracy itself is not enhanced over everyday memories. Despite the term *flashbulb memory,* the authors recognized that “a flashbulb memory is only somewhat indiscriminate and is very far from complete. In these respects, it is unlike a photograph” (Brown & Kulik, 1977, p. 75). This conjecture has been upheld by myriad studies, revealing that valence and arousal do not result in memory enhancement for all event details. Rather, some details are remembered better when events elicit shifts in valence and arousal, but many other details are not. There continue to be debates about the best way to characterize the types of details that are remembered best (e.g., Bennion, Ford, Murray, & Kensinger, 2013; Levine & Edelstein, 2009; Mather & Sutherland, 2011; Yonelinas & Ritchey, 2015), but in a general sense, the effects of arousal on memory appear to be best described as selective enhancements.

Many of these selective enhancements have been attributed to amygdala engagement. Individuals with damage to the amygdala show neither the enhancing nor the impairing effects of arousal on memory (e.g., Adolphs, Tranel, & Buchanan, 2005; Strange, Hurlemann, & Dolan, 2003). Many fMRI studies have confirmed a link between amygdala engagement and successful encoding of emotional events (for a meta-analysis see Murty, Ritchey, Adcock, & LaBar, 2010). The amygdala is activated as attention is drawn toward salient, novel stimuli, and amygdala activity is greater during the processing of emotional items that are subsequently remembered than during the processing of items that are subsequently forgotten (reviewed by Hamann, 2001; LaBar & Cabeza, 2006). Amygdala activity does not correspond with subsequent memory for all details of an arousing event, however, consistent with the idea of selective enhancements (Kensinger, Addis, & Atapattu, 2011; Kensinger & Schacter, 2006). For instance, increased amygdala activity at encoding is associated with an increasingly vivid memory at retrieval but not with retention of an increasing number of contextual details (Kensinger et al., 2011; Waring & Kensinger, 2011).

These selective enhancements can occur relatively automatically (Steinmetz et al., 2014) and are not dependent on how overt attention is focused (Steinmetz & Kensinger, 2013). In fact, the use of controlled, PFC-based encoding strategies can sometimes help to broaden the types of details that are remembered about emotional events (e.g., Kensinger, Garoff-Eaton, & Schacter, 2007; Steinberger, Payne, & Kensinger, 2011; Waring & Kensinger, 2011; Waring, Payne, Schacter, & Kensinger, 2010). These results are consistent with the proposal that some of the arousal- and amygdala-mediated effects on memory may occur relatively automatically.

Separable Influences of Positive and Negative Valence

So far, this chapter has defined the effects of valence as those that occur when there is a change from neutral valence. But research has demonstrated that it is not just the magnitude of the change that matters but also the direction of the change: Many of the mnemonic effects of valence depend on whether that change is in the direction of pleasantness or in the direction of unpleasantness. Negative events often are remembered with a greater subjective vividness than positive events, whereas positive memories often are associated with a feeling of familiarity (Dewhurst & Parry, 2000; Ochsner, 2000). In the laboratory, participants are better able to remember the visual details of negative stimuli (e.g., which weapon they saw), but they have a harder time remembering the visual details of positive stimuli (e.g., which cake they saw; Kensinger, Garoff-Eaton, et al., 2007). This difference extends to autobiographical memories: Individuals have an easier time remembering the details of games or elections that were associated with a negative outcome (preferred team or candidate lost) than with a positive outcome (preferred team or candidate won; Holland & Kensinger, 2012; Kensinger & Schacter, 2006).

These valence differences likely relate to the fact that, even when items are equated for arousal, different sets of neural regions are recruited during the processing and encoding of negative compared to positive stimuli. Although converging evidence suggests that the amygdala is engaged for all salient stimuli, regardless of valence (e.g., Blackford, Buckholtz, Avery, & Zald, 2000; Liberzon, Phan, Decker, & Taylor, 2003; Sander, Grafman, & Zalla, 2003), negative valence may lead to greater recruitment of sensory regions, and positive valence may lead to greater recruitment of PFC regions (reviewed by Kensinger, 2009) and midline regions (Ritchey, Bessette-Symons, Hayes, & Cabeza, 2011). More specifically, the encoding of negative images tends to be associated with greater fusiform activity and with greater connectivity between the fusiform and amygdala (Kark & Kensinger, 2015) than does the encoding of neutral or positive images (reviewed by Kensinger, 2009). Conversely, the processing of positive items often is associated with greater recruitment of medial and lateral PFC regions and parietal regions than negative items (reviewed by Kensinger, 2009; see also Ritchey et al., 2011). These findings have been corroborated in a number of fMRI studies, and a recent repetitive transcranial magnetic stimulation (rTMS) study also provided partial support for this distinction, revealing that facilitation of left dorsolateral PFC processes improved memory for positive, but not for negative, stimuli (Balconi & Cobelli, 2015).

Why might these processing differences exist? There are multiple levels at which this question can be answered. At one level are theories regarding the adaptive nature of brain function (Friston, 2010), which could suggest that different types of emotions prepare the person for different forms of action and thus bias different modes of cognitive processing (Schwarz & Clore, 1996; Storbeck, 2012; Storbeck & Clore, 2005). Indeed, another level of evidence reveals that positive and negative emotions are associated with different forms of processing: Positive affect supports gist-based and relational processing (our ability to connect incoming information with what we know already), whereas negative affect leads to a reduction in relational processing and instead enables item-specific or referential processing (Storbeck & Clore, 2005), which can become intensified under conditions of high arousal (Storbeck & Clore, 2008). Importantly, although much of this research has examined the effects of sustained moods on cognitive processing, the literature reviewed in this section has highlighted similar effects with relatively short-lived emotional reactions to specific stimuli. Thus, valence may be able to rapidly bias the way in which incoming information that is arousing is processed and stored in the brain (see Figure 1.1).

Future Directions: Interactive Effects of Valence and Arousal

There is still relatively little research examining the interactive effects of valence and arousal, yet the extant research suggests that these interactions are important to consider. A number of studies have revealed that the effects of arousal on memory can differ when information is of positive valence rather than of negative valence (Ford, Addis, & Giovanello, 2012; Mickley Steinmetz, Addis, & Kensinger, 2010). Moreover, there is suggestive evidence for distinct neural processes supporting the interaction of valence and arousal (Styliadis et al., 2015; Wang et al., 2015). The effects of pleasant or unpleasant valence can also be affected by the arousal of the information (Greene, Flannery, & Soto, 2014; Simola, Le Fevre, Torniainen, & Baccino, 2015). Although the literature is insufficient to create a systematic explanation for these interactive effects, these studies demonstrate the importance of considering both dimensions together in future research.

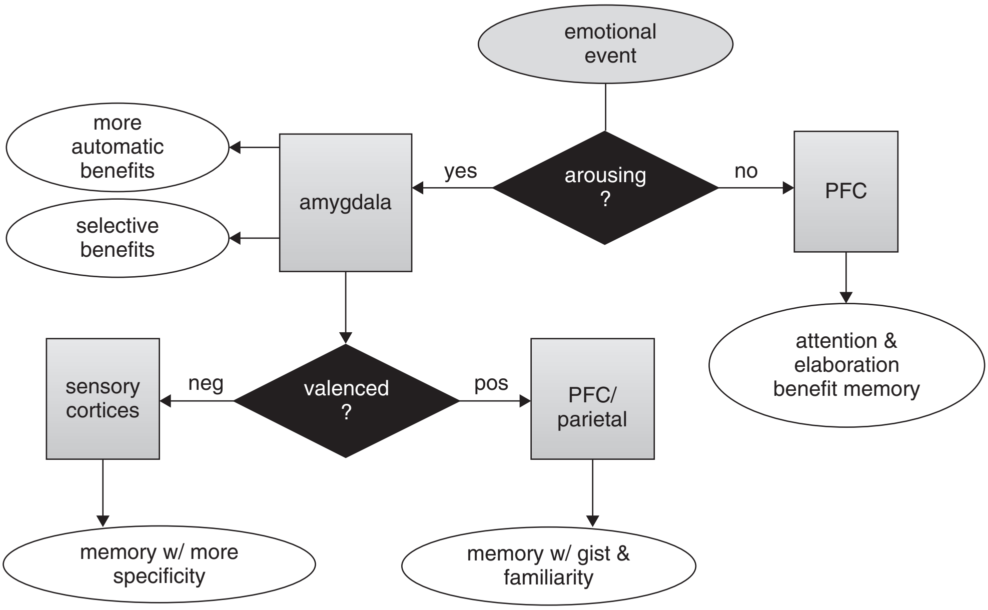

Figure 1.1 Overview of the modulatory influences of arousal and valence at encoding.

TIME COURSE OF THE EFFECTS OF VALENCE AND AROUSAL ON MEMORY

Valence and arousal influence memory from the moment stimuli are perceived, influencing the way they are encoded, stored, and retrieved. In this section, we examine the effects of valence and arousal on emotional memory across various time courses. We begin by zooming in to examine how valence and arousal affect the rapid processing of information during encoding and retrieval. Then, we gradually zoom out in time. We review evidence for effects of emotion on memory retrieval during an initial search phase—during which a memory is accessed—and a subsequent elaboration phase—during which the information retrieved during the initial search is expanded on in further detail. We explore how the effects of arousal and valence unfold as the time between an encoding event and later memory retrieval progresses from minutes to years. Last, we examine encoding-to-retrieval interactions; we highlight that what happens during encoding can affect downstream retrieval processes and present evidence for the flexibility of when emotion can prioritize information.

Valence and Arousal by the Millisecond: Effects at Encoding and Retrieval

When stimuli elicit valence or arousal, processing differences are noticeable within a few milliseconds of their presentation. Word processing studies have suggested that arousal effects might serve as an early "alert system" that precedes the evaluation of valence (Jhean-Larose et al., 2014, Recio et al., 2014). The presence of arousal also leads to earlier memory-related signatures: Dolcos and Cabeza (2002) demonstrated that positive and negative high-arousal stimuli (relative to neutral stimuli) were associated with earlier subsequent-memory effects (see Paller & Wagner, 2002; Wagner, Koutstaal, & Schacter, 1999, for discussion of these effects). Specifically, over centro-parietal electrodes, subsequent-memory effects for emotionally arousing stimuli were greater than for neutral stimuli at a relatively early epoch (400 ms–600 ms).

Although Dolcos and Cabeza (2002) focused on memory for high-arousal stimuli, a recent ERP study assessed subsequent-memory effects for high-arousal and low-arousal negative stimuli. Yick, Burrato, and Schaefer (2015) reported that high- and low-arousal negative images were associated with enhanced subsequent-memory effects as compared to neutral stimuli, but the high-arousal stimuli elicited enhanced effects earlier in the encoding time course. These results are generally consistent with those of Dolcos and Cabeza (2002) and suggest rapid, preferential processing of high-arousal negative stimuli. Interestingly, Yick and colleagues noted that the emotion-enhanced subsequent-memory effects occurred based on item memory and regardless of whether the source (context) memory was accurate but that the effect was even stronger when the item and source were remembered. This pattern is generally consistent with the selective memory enhancements conveyed by emotion, discussed later in the section “Time Course of Memory Retrieval: Effects of Emotion on Memory Search and Elaboration.” In Dolcos and Cabeza (2002) and Yick et al. (2015), the effects of emotion on subsequent-memory signatures co-occurred with behavioral memory enhancement for the emotional stimuli. In fact, Yick et al. (2015) interpreted their results within a hybrid model for attention (Pottage & Schaefer, 2012), whereby high arousal enhances pre-attentive processes, sustained attention, early and late perceptual processing, and sensory information integration, whereas low-arousal negative emotion enhances more controlled processes. By contrast, when behavioral enhancements of memory have not been present, ERP studies have not always revealed effects of emotion on subsequent-memory signatures (Galli, Wolpe, & Otten, 2011; Koenig & Mecklinger, 2008). This pattern of results suggests that the modulation of early memory signatures may reflect the preferential processing and encoding of emotional information so that emotional enhancements occur when those early signatures are modulated by emotion.

Arousal and valence affect the timing not only of encoding processes, as just described, but also of retrieval processes. In order to avoid confounds between the emotionality of a retrieval cue and the emotionality of the memory target, many paradigms have used neutral prompts to cue memories of emotional events (e.g., Maratos, Allan, & Rugg, 2000). In one such study, Righi et al. (2012) presented participants with images of faces with happy, fearful, and neutral expressions at study. During the test, participants were presented with the same faces, but this time all of them conveyed a neutral expression. The novel aspect of this study was that there were no emotional stimuli presented at retrieval (all expressions were neutral), so any ERP effects that differed based on study history (i.e., the studied facial expression) would be because of memory for emotional stimuli and not a reaction to an emotional cue. The researchers found that, compared to faces studied with a happy or neutral expression, recognition of faces previously studied with a fearful expression elicited a number of ERP markers of enhanced perceptual processing and visual attention capture (e.g., a greater early positive [P] component appearing 100 ms after the stimulus [P100]; Carretie, Hinojosa, Martin-Loeches, Mercado, & Tapia, 2004; Mangun, 1995), and of implicit memory (e.g., a larger early fronto-central effect and a reduced negative [N] signal appearing 170 ms after the stimulus [N170]; see also Jaeger & Rugg, 2012; Smith, Henson, Rugg, & Dolan, 2005, for evidence of implicit effects). Because the behavioral data demonstrated faster reaction times during recognition of previously fearful faces compared to previously happy or neutral faces, these effects were interpreted to reflect rapid decoding of threat-related retrieval cues. Another study (Jaeger, Johnson, Corona, & Rugg, 2009) also reported early modulation of ERP effects during recognition of neutral objects previously shown on an emotional background compared to a neutral background; after a 10-minute and a 24-hour study-test delay, effects of the emotional context were apparent within 200 ms of the presentation of the retrieval cue. Interestingly, the polarity and spatial distribution of the emotion effects reversed between the shorter and longer delay, which could reflect changes in the memory trace because of consolidation processes.

Together, these electrophysiological studies highlight the spatiotemporal dynamics of the effects of valence and arousal on encoding and retrieval processes and suggest that stimuli with high intrinsic motivational salience (i.e., high-arousal negative or threat-related stimuli) appear to have rapid and privileged access to encoding and retrieval processes. As we describe next, however, the effects of valence and arousal are not circumscribed to these earliest phases of retrieval. Rather, the effects appear to begin early but to have downstream effects on the way the retrieved information is monitored and elaborated. Figure 1.2 summarizes the time course of emotional memory effects across multiple phases of memory.

Time Course of Memory Retrieval: Effects of Emotion on Memory Search and Elaboration

Memory retrieval has been demarcated into at least two phases: an initial search phase during which a memory is accessed and a later event elaboration phase during which the retrieved memory is maintained in mind and the details of the event are further expanded on (Conway, Pleydell-Pearce, & Whitecross, 2001). Specifically, the information retrieved during the initial search phase serves as a retrieval cue to bring further information and fine-grained details to mind during elaboration. For instance, try to remember the last time you went to the movie theater. On hearing the cue *movie theater,* a controlled search process can use your world knowledge (e.g., nearby movie theaters) and personal semantic knowledge (e.g., favorite movie genre) to narrow the search space. Then, on selecting the content (e.g., saw the latest Pixar film *Inside Out* with Kat and Corey at the Cineplex), an elaboration process can expand on the internal details (e.g., you cried during the movie) and external details of the events (e.g., it was a going-away party for Kat; you downed a bucket of popcorn before the previews were even finished). Monitoring processes also come online to detect erroneous details (e.g., you actually saw the movie at the Odeon because it was closer to Kat's house). Search and elaboration processes can repeat iteratively as additional details are recovered and expounded on (St Jacques, Kragel, & Rubin, 2011).

The distinction between these phases has been corroborated in neuroimaging studies (Daselaar et al., 2008; Ford, Morris, & Kensinger, 2014; St Jacques et al., 2011; see Cabeza & St Jacques, 2007; Holland & Kensinger, 2010, for reviews). In these studies, the search phase is triggered by the presentation of a retrieval cue, whereas the elaboration phase begins once participants have accessed the memory. Consistent with the ERP studies, there has been compelling fMRI evidence to indicate that emotion affects the memory search process. For example, Daselaar et al. (2008)

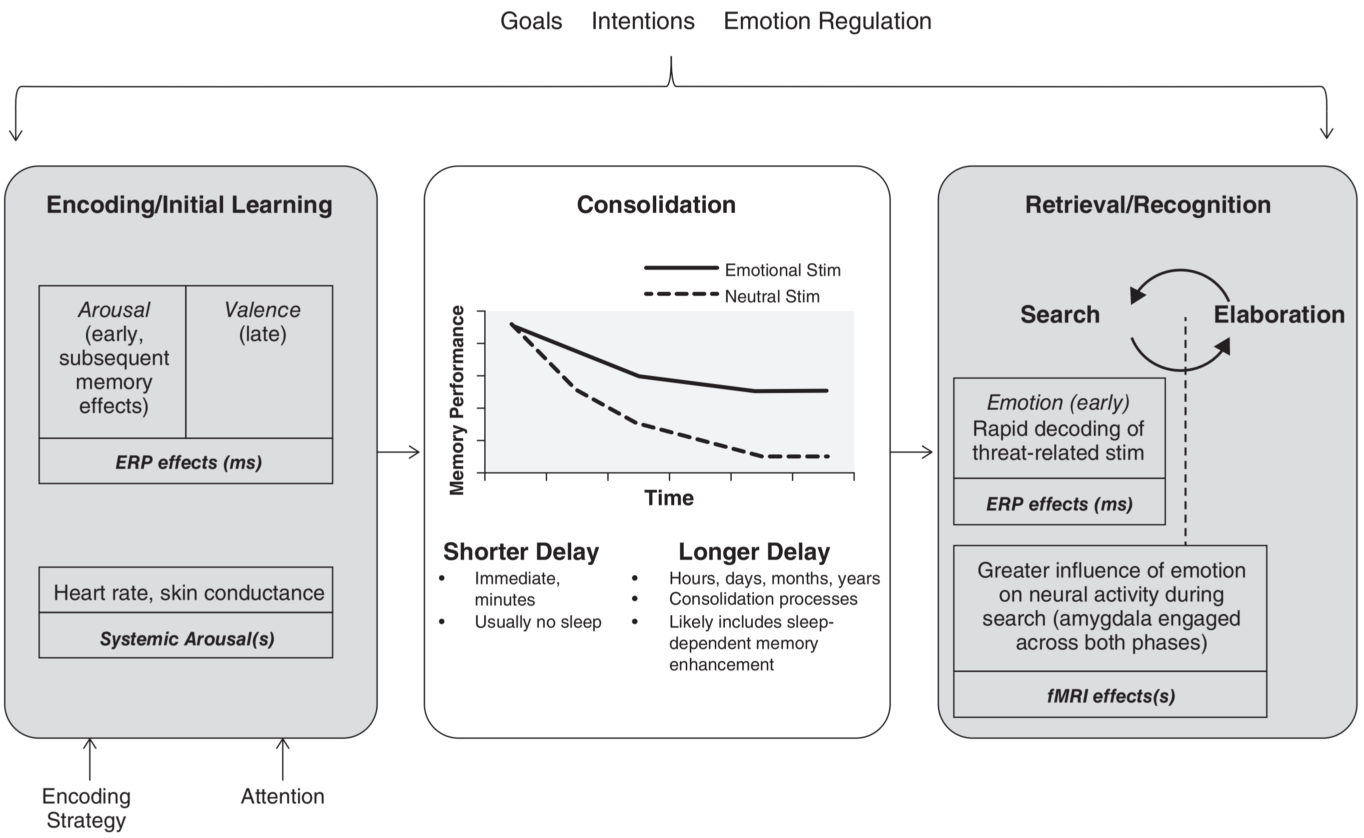

Figure 1.2 Overview of time course of arousal and valence emotion effects on memory, including factors that could influence the effects of emotion at one phase (e.g., encoding strategy or attention allocation during encoding) or across multiple phases (e.g., goals, intentions, and emotion regulation strategies).

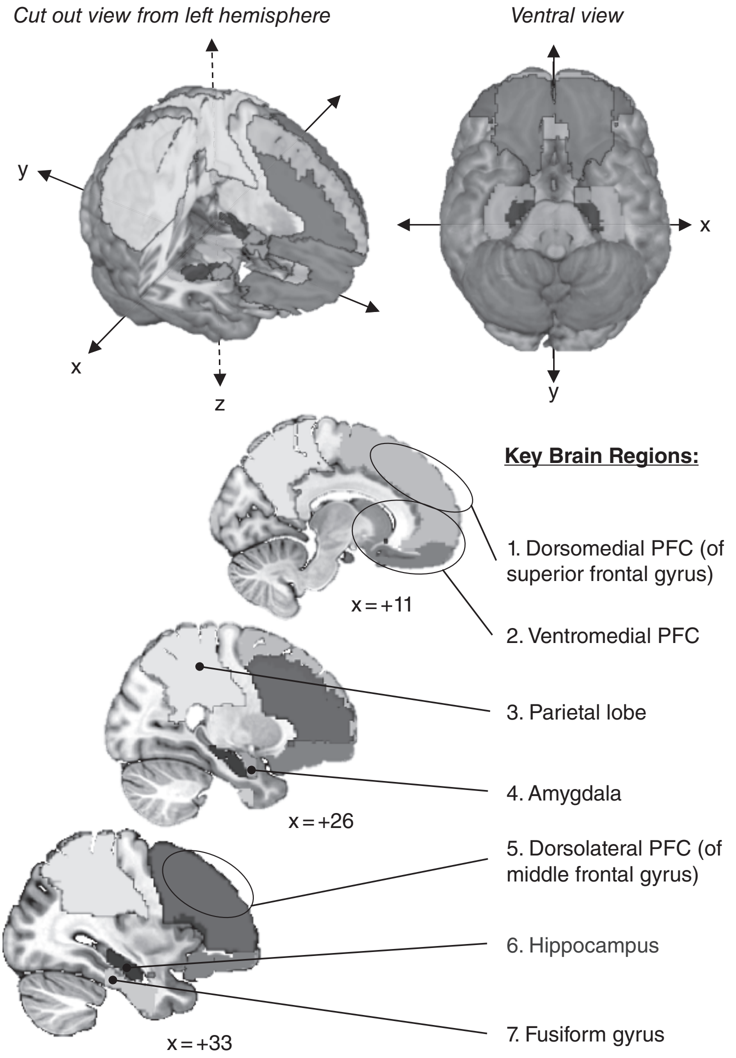

Figure 1.3 Visualizations of key brain regions discussed in this chapter. Color version of this figure is available at http://onlinelibrary.wiley.com/book/10.1002/9781119170174.
Source: 3D maximum probability atlas overlays from Gousias et al. (2008) and Hammers et al. (2003).

distinguished the search from the elaboration phase of autobiographical memory retrieval and provided evidence that emotion had a greater effect on amygdala engagement during the search phase, before people retrieved the memory in full (see Figure 1.3 for depiction of brain regions discussed in this chapter). Similar conclusions were reached by Ford et al. (2014), using an episodic memory retrieval task; even when all retrieval cues were neutral, the emotionality of the memory target had a greater influence on neural activity during search than elaboration. These results suggest that emotion affects, or even guides, the way that details of an experience are retrieved or reassembled in order to reconstruct the past event in memory.

Emotion is also likely to affect the way that memories are elaborated. Memory for emotions themselves is a central and useful part of most emotional memories (Levine & Pizarro, 2004; Wirtz, Kruger, Napa Scollon, & Diener, 2003), and there is evidence that amygdala and medial temporal lobe (MTL) activation may relate to the intensity with which these emotions are reexperienced (Addis, Moscovitch, Crawley, & McAndrews, 2004; Ford & Kensinger, 2016). A study in patients with MTL damage supported the conclusion that the amygdala is involved in memory search and in the elaboration of emotional details of past events. In that study (Buchanan, Tranel, & Adolphs, 2006), patients with MTL damage that spared the amygdala were compared to those whose damage affected the amygdala. Importantly, memories were assessed for events that had occurred when the individuals still had intact medial temporal lobes; thus, anything atypical about their memories could be ascribed to the role of the MTL during retrieval rather than to the encoding or initial consolidation phases. This study revealed that the subset of patients with amygdala damage were less likely to retrieve memories of unpleasant events than were the other patients, corroborating a role for the amygdala in the search and recovery of emotional events. But in addition, when these patients did retrieve unpleasant events, they rated them as less intense than did the other patients. This latter finding suggests that the amygdala may also participate in the reexperience and reconstruction of emotion during retrieval (see Buchanan, 2007, for a review of effects of emotion at retrieval).

Although relatively little research has assessed the effects of valence on memory retrieval, across a few studies, frontal regions have been more active during retrieval of positive memories compared to negative memories. This pattern has been demonstrated in studies of autobiographical memory (Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003) and, more recently, in a study of episodic memory (Ford et al., 2014). This distinction could be tied to the effects of valence discussed previously, with positive memories associated with a more thematic and heuristic form of recall (Monin, 2003; Schwarz & Clore, 1996) and often with a broadening of attention associated with broaden-and-build theories of positive emotions (Fredrickson, 2001). Interestingly, relative to healthy participants, patients with post-traumatic stress disorder (PTSD) have shown greater hippocampus and amygdala activation during the search phase for negative memories compared to positive memories, which might reflect exaggerated early-threat detection to non-traumatic negative memories and less sensitivity to positive autobiographical memories in the PTSD population (St Jacques, Botzung, Miles, & Rubin, 2011). Together, these neuroimaging studies demonstrate that effects of emotion begin during the search for a memory and can vary with the valence of the event.

The Passage of Time Between Encoding and Retrieval: Effects of Consolidation

William James wrote, “An experience may be so exciting emotionally as almost to leave a scar on the cerebral tissue” (James, 1890, p. 670). Indeed, the durability of emotional memories is one of their most compelling features. Although not all details are retained accurately, in the longest test-retest study to date, Hirst et al. (2015) assessed memory up to 10 years after the terrorist attacks of September 11, 2001. They reported maintained consistency and high levels of confidence for canonical features of the memory (e.g., where participants were when they learned of the attack, what they were wearing) between 3 and 10 years after the attacks. These findings corroborate numerous studies of flashbulb memories (Brown & Kulik, 1977) for highly emotional public events, which typically find a decline in consistency and confidence over the first year but stabilization in memory thereafter (Hirst et al., 2015).

It does not take decades to see the selectively beneficial effects of emotion on memory. The neural and behavioral enhancement of memory by emotion can be present even minutes after an event has occurred (Dolcos, LaBar, & Cabeza, 2004; Kensinger & Corkin, 2004; Talmi & McGarry, 2012). However, the beneficial effects of emotion on recollection memory do tend to increase over time (Sharot, Verfaellie, & Yonelinas, 2007; Sharot & Yonelinas, 2008). This delay dependence was first noted by Kleinsmith and Kaplan (1963) and has been corroborated by a number of studies. For instance, Wang (2014) revealed a shallower forgetting curve for negative images compared to neutral and positive images between a 24-hour and 1-week study-test delay, and Quevedo et al. (2003) found enhanced memory for an emotionally arousing slide-show narrative compared to a neutral narrative after a 1 week—but not 1 hour—delay. Similarly, Anderson, Yamaguchi, Grabski, and Lacka (2006) found enhanced memory for negatively arousing scenes (relative to neutral scenes) after a 2-week delay but not at earlier time points.

Often, this delay-dependent effect of emotion arises because memory for neutral items decays at a faster rate over time than does memory for emotional items (LaBar & Phelps, 1998; Sharot & Phelps, 2004). The most likely explanation for the slower forgetting of emotional stimuli is that critical neurobiological consolidation processes take place shortly after learning to stabilize memory for long-term storage (McGaugh, 2000). For example, sleep-based consolidation processes when sleep is initiated shortly after learning—as compared to sleeping after 16 hours post-learning—have been shown to enhance memory for emotional objects after a 24-hour delay (Payne, Chambers, & Kensinger, 2012). These data support a consolidation account, as opposed to an interference account, for emotionally enhanced memory, because all participants were awake for a similar amount of time (for more on the interference hypothesis and sleep-based consolidation see Chapter 4 in this volume).

This slower forgetting curve for emotional items appears to depend on amygdala function (Phelps et al., 1998) coupled with psychophysiological arousal (Anderson et al., 2006; Onoda, Okamoto, & Yamawaki, 2009; Segal, Stark, Kattan, Stark, & Yassa, 2012). For instance, Claire, Sophie, Claudia, Phillippe, and Eliane (2015) reported that, as compared to control participants, a patient with amygdala damage was impaired in the recognition of emotional words after a 1-week—but not 1-hour—delay (see also Phelps et al., 1998).

The amygdala-mediated effects on memory consolidation have been extensively investigated, sparked by the pioneering work by Gallagher and Kapp (1981); Ellis and Kesner (1983); Ledoux, Iwata, Cicchetti, and Reis (1988); and Cahill and McGaugh (1990, 1991). In animals and humans, arousal influences many forms of learning via time-dependent effects of the adrenergic-noradrenergic, cholinergic, and opioid peptide systems—and their interactions—on the amygdala (see McGaugh, 2015, for a recent review).

Electrophysiological studies have shown that stimulation of the amygdala can induce long-term potentiation—patterns of activity that reflect synaptic plasticity related to learning—in the hippocampus (Ikegaya, Saito, & Abe, 1994, 1995) and vice versa (Maren & Fanselow, 1995). Recent work suggests region-specific encoding of the emotional and contextual aspects of fear memory (a form of associative learning resulting from Pavlovian fear conditioning) in the amygdala and hippocampus, respectively, with the medial PFC integrating these emotional and contextual components (Zelikowsky, Hersman, Chawla, Barnes, & Fanselow, 2014). However, although the hippocampus is a clear target for amygdala modulation of memory storage, the amygdala also projects to many different brain regions (Young, 1993) and clearly is not acting in isolation to modulate the durability of emotional memories.

Hints as to the network of regions involved have come from neuroimaging studies examining the processes needed for the creation of durable memories (see Murty et al., 2010, for a quantitative meta-analysis), which reveal not only the engagement of the amygdala but also of PFC and sensory regions. For instance, Steinmetz et al. (2012) revealed activity in the ventromedial PFC, fusiform gyrus, and hippocampus was an equally strong—or stronger—predictor of subsequent memory for emotionally arousing stimuli following a retention delay of 24 hours compared to 30 minutes. By contrast, these regions' ability to predict memory for neutral items dissipated with the longer retention interval. Parallel findings have been revealed at retrieval, with neuroimaging studies showing enhanced recollection ERP effects (Weymar, Low, & Hamm, 2011) and more amygdala and hippocampal engagement (Dolcos, LaBar, & Cabeza, 2005; Kalpouzos, Fischer, Rieckmann, Macdonald, & Backman, 2012) during delayed retrieval of negative events compared to neutral events. Although the role of these regions during encoding and retrieval continues to be debated (see "What Is the Role of the Amygdala in Emotional Memory?"), together these studies begin to suggest mechanisms to support the increased likelihood of retaining emotional memories over time.

Effects of Sleep on Emotional Memory Consolidation

It is not just the amount of time that affects the likelihood of memory retention but also whether high-quality sleep was included within the retention interval. An extensive body of research has shown that the emotional memory advantage is boosted if the study-test interval includes a period of sleep (see Chapter 4 in this volume and also Alger, Chambers, Cunningham, & Payne, 2015; Diekelmann, Wilhelm, & Born, 2009). That boost may be particularly large if the sleep follows soon after the occurrence of the emotional event (Payne et al., 2012).

Because sleep is thought to selectively preserve memories that have been "tagged" as relevant for the future during encoding (see Bennion, Mickley Steinmetz, Kensinger, & Payne, 2015; Payne & Kensinger, 2011), it makes sense that emotional information may be prioritized over periods of sleep. Indeed, this tagging process may be optimal when arousal levels are high during encoding (Bennion et al., 2015; Cunningham, Chambers, & Payne, 2014). At a neural level, sleep has been shown to facilitate plasticity in the amygdala, hippocampus, PFC, and sensory regions. Although the nature of this facilitation continues to be discussed (Bennion et al., 2015; Cairney, Durrant, Power, & Lewis, 2015; Sterpenich et al., 2014; van Marle, Hermans, Qin, Overeem, & Fernandez, 2013), it seems clear that sleep can alter amygdala connectivity and affect the likelihood of amygdala reactivation during memory retrieval.

To date, most studies examining the effect of sleep on emotional memory have focused on the role of rapid eye movement (REM) sleep (Groch, Wilhelm, Diekelmann, & Born, 2013; Wagner, Gais, & Born, 2001; Wiesner et al., 2015; see Walker, 2010, for an outline of the REM-sleep hypothesis; see van der Helm and Walker, 2011; and for comprehensive reviews, see Alger et al., 2015; Diekelmann et al., 2009). However, enhancing effects of slow-wave sleep (SWS) on memory consolidation are also frequently reported (Ackermann & Rasch, 2014) and have been revealed for emotionally enhanced memories as well as neutral ones (Cairney, Durrant, Hulleman, & Lewis, 2014; Eschenko & Sara, 2008; Groch et al., 2011; Kaestner, Wixted, & Mednick, 2013; Payne et al., 2015). It has recently been suggested that a parsimonious explanation might be that SWS and REM sleep serve complementary functions during sleep-dependent consolidation of emotional memories (Cairney et al., 2015; Payne et al., 2015). In alignment with the sequential hypothesis for the effects of sleep on memory (Giuditta, 1977, Giuditta et al., 1995; and for a more-recent review see Giuditta, 2014), SWS might weaken the dependence of negative memories on the hippocampus before REM sleep preferentially targets negative memories for additional integrative and mnemonic processing. Together, SWS and REM sleep might give rise to the enhancing effects of negative arousal on emotionally enhanced memory (Cairney et al., 2015).

Although the majority of studies have examined the enhancement for negative stimuli (relative to neutral stimuli), recent work has also shown superior sleep-dependent memory consolidation for positive stimuli (i.e., humorous cartoons) (Chambers & Payne, 2014). It will be advantageous for future research to examine whether the effects of sleep on memory unfold similarly for all information with future relevance or whether the emotional memory benefit may be related to unique mechanisms (and see Cunningham, Chambers, et al., 2014, for some evidence). Understanding this issue will be critical for revealing how encoding goals and strategies interact with emotion and can have downstream effects on retrieval, an issue that we expand on in the next section.

Encoding-to-Retrieval Interactions

The effect of emotion on memory retrieval can critically depend on what happened during encoding or consolidation. For instance, the likelihood of retrieving emotional stimuli can be influenced by whether information was intentionally encoded (Chainay, Michael, Vert-Pre, Landre, & Plasson, 2012; Sakaki, Fryer, & Mather, 2014) and by the future relevance of the stimuli (Cunningham, Chambers, et al., 2014). The magnitude of the emotional memory benefit conveyed can also be influenced by the emotion-regulation strategies employed during encoding (Kim & Hamann, 2012) or by the memory-encoding strategy (Murray & Kensinger, 2012). This interdependence is perhaps unsurprising, because retrieval is thought to involve the reactivation of processes that are active during encoding. Indeed, emotional memories are no exception to this rule; studies have demonstrated amygdala reengagement during retrieval of stimuli studied in emotional contexts (Smith et al., 2005) and have revealed that negative valence increases the engagement of ventral visual processing regions during encoding and also the reengagement of those processes during retrieval (Kark & Kensinger, 2015).

Importantly, however, the effects of emotion at encoding do not always parallel those at retrieval. For instance, although there is no doubt that emotionally arousing information benefits from prioritized or facilitated processing during encoding, this facilitated processing does not always result in enhanced memory (see Bennion et al., 2013, for further discussion). As one example, Murray and Kensinger (2012) demonstrated that arousing content enabled participants to more rapidly integrate word pairs (i.e., to form a mental image that incorporated two unrelated items). Participants, however, were *less* likely to remember those arousing pairs over time than they were to remember the neutral pairs. Murray and Kensinger (2013b) argued that the ease of integrating the arousing word pairs may have circumvented the effortful processing that would have translated into a more durable memory trace (see also Murray & Kensinger, 2013a). A related finding was reported by Zimmerman and Kelley (2010): They showed that participants were overconfident when estimating which negative word pairs they would remember. It is likely that participants were fooled by the ease with which they had bound the items at encoding and were biased to believe that this ease would extend to their ability to retain the pairs in memory.

Another example of the interdependence of encoding and retrieval comes from a study by Sakaki et al. (2014), who showed that memory for neutral images seen immediately before emotional images was enhanced if participants were instructed to prioritize the neutral images, but it was impaired if those neutral images were not prioritized. In other words, the encoding orientation influenced the likelihood of later retrieval. The effects of prioritization exist not only when they are apparent at the time of encoding (as in Sakaki et al., 2014) but also when they are revealed during the consolidation period. In a more-recent study, Dunsmoor, Murty, Davachi, and Phelps (2015) demonstrated that neutral memories can be made more durable if conceptually related information later becomes emotionally salient. Together, these studies show that goals and priorities during encoding and consolidation can influence the durability of a memory and the likelihood of later retrieval success.

DEBATES AND OPEN QUESTIONS

The previous sections have noted key conclusions that have been drawn from decades of research into the interactions between emotion and memory, but there are many questions that remain. Here we highlight three of those questions and the debates that have arisen as researchers have tried to answer them.

What Is the Role of the Amygdala in Emotional Memory?

There have been two primary debates that have been ongoing regarding the role of the amygdala in emotional memory. The first relates to the time course over which the amygdala exerts its effects. It is debated whether the amygdala plays a specific role in the consolidation of emotional memories or whether its influence also is related to the initial encoding or the eventual retrieval of those memories. As previously described, there is some evidence to support a consolidation view, in that amygdala engagement appears to be a stronger predictor of memory after longer delays than shorter ones. Indeed, some research has suggested that the amygdala may not be necessary for emotional memory enhancements if memory is tested after a short delay (see Talmi & McGarry, 2012, for discussion). Yet other research suggests that amygdala activation may influence the way that emotional information is prioritized during encoding, biasing attention toward high-priority information (see Mather & Sutherland, 2011). There also are proposals to suggest that the amygdala may facilitate retrieval, working in concert with the hippocampus to support the recollection of emotional events via recapitulation of representations stored in neocortical regions (de Vanssay-Maigne et al., 2011; Fenker, Schott, Richardson-Klavehn, Heinze, & Düzel, 2005). Thus, although there is no doubt that the amygdala is important for the consolidation of emotional memory, questions remain about its role during the encoding and retrieval of that information. Future work, possibly harnessing the high spatial and temporal resolution of intra-cranial recordings, is needed to disentangle whether amygdala activation at the moment of retrieval facilitates successful retrieval itself or if amygdala activation is an emergent property of an emotional reaction to retrieved content. It is also possible that the amygdala plays both roles: Early amygdala activation may guide retrieval and later amygdala activation during retrieval may reflect an emotional reaction to the retrieved memory content.

A second debate relates to how the amygdala influences the consolidation of memory. The traditional view (i.e., modulatory emotional consolidation theory) has been that the amygdala exerts its effects on consolidation through interactions with other MTL regions and specifically the hippocampus (reviewed by Hamann, 2001; LaBar & Cabeza, 2006). This view has been supported by decades of animal research and many studies of human memory. For instance, amygdala activation has been shown to lead to changes in synaptic plasticity within the hippocampus (Ikegaya et al., 1994, 1995; Roozendaal & McGaugh, 1997, 2011), and numerous studies have shown that correlations between amygdala and hippocampal activity predict the memory enhancement for high-arousal stimuli, especially after longer delays (Binder et al., 2012; Fastenrath et al., 2014; Richardson et al., 2004). Yet this view has recently been called into question with the proposal that the amygdala might—in the absence of interaction with the hippocampus—create item-emotion bindings that are resistant to forgetting (Yonelinas & Ritchey, 2015). The authors assert that, if the amygdala were to exert its effects via modulation of the hippocampus, evidence should show enhanced item-context associations of emotional memory and a disruption of emotional-memory longevity following hippocampal damage. However, emotion appears to selectively enhance memory for items, not for their context, and patients with hippocampal damage continue to show a time-dependent enhancement of emotional memory. It is important to note that this newer view posited by Yonelinas and Ritchey (2015) rests on the assumption that the hippocampus does not play a role in item memory but rather functions to bind items and their contexts in support of strong recollection over weaker familiarity (Diana, Yonelinas, & Ranganath, 2007). In contrast with this item-context distinction, other work suggests that the hippocampus supports memory for multi-attribute stimuli, which could include, for example, visual, spatial, and emotional attributes (Wixted & Squire, 2011). Under the latter framework, the hippocampus supports stronger and weak memory for attributes that may or may not be construed as an item or a context. Further work is needed to understand when and how hippocampal involvement enhances the varied constituent parts of emotional memories.

Clearly, further work is needed to clarify the role of the amygdala in emotionally enhanced memory, including the neurochemical mechanisms (e.g., Cahill, Gorski, & Le, 2003; Mather, Clewett, Sakaki, & Harley, 2015; Okuda, Roozendaal, & McGaugh, 1997; Roozendaal, & McGaugh, 2004;) that support the enhancement effect as well as the extent and timing of amygdalae interactions with other MTL structures and cortical regions.

What Are the Effects of Emotional Arousal on Memory Accuracy?

As we discussed previously in this chapter, individuals often report high confidence in emotional memories yet show low consistency over time (Neisser & Harsch, 1992; Schmidt, 2004; Schmolck, Buffalo, & Squire, 2000; Talarico & Rubin, 2003) or only remember select details (for a review, see Kensinger, 2009). Clearly, emotional events do not leave indelible traces. Yet whether emotional arousal provides any benefits to memory for detail has continued to be widely debated.

Some have argued that arousal enhances only the *feeling* of vividness but not the ability to retrieve accurate content (reviewed by Phelps & Sharot, 2008). Relatedly, others have argued that arousal biases individuals to endorse content as having been previously experienced, but it does not enhance the ability to discriminate studied from novel content (Dougal & Rotello, 2007). It is clear that there are conditions in which arousing events are remembered with different qualitative characteristics (e.g., higher vividness) even when those events are remembered at the same rates as neutral memories and with the same, or lesser, objectively measurable detail (reviewed by Kensinger, 2009). But what remains debated is whether arousal *only* enhances these qualitative characteristics.

We suggest the need for future research to attend to two types of factors in order to resolve this debate. First, research must control for confounds between the emotional and nonemotional stimuli. For instance, emotional stimuli are often more interrelated than neutral stimuli, a factor that can inflate the likelihood that participants endorse emotional lures. When this interrelatedness is controlled, emotion may not enhance false memory (Choi, Kensinger, & Rajaram, 2013). Other potential confounds to consider include attention allocation, distinctiveness, and affective state of the participant (see Bennion et al., 2013, for elaboration). Second, research would benefit from considering whether unmeasured memory characteristics may be affecting retrieval decisions. It is likely that participants sometimes report a vivid memory for an event not because they remember its content well, but because they remember their emotional reactions well. These internal details are often not measured yet are likely to influence memory decisions. Relatedly, participants may report a vivid memory because of the *ease* with which a detail comes to mind rather than because of the *quantity* of details that come to mind. In most prior research, only one of these factors has been measured, and usually it has been the latter.

How Do Emotional Appraisals and Reappraisals Affect Memory Patterns?

Arousal and valence are not static and fixed properties of an experience. Emotional regulation strategies can be used in everyday life in order increase or decrease affective reactions to real-world situations (Gross, 1998). Interestingly, use of emotional strategies during the initial experience of an event can have long-lasting effects on memory (Ahn et al., 2015; Hayes et al., 2010). Knowledge acquired after an event can frequently change our feelings toward and appraisal about an event. As these appraisals change, it can be hard for us to remember that we ever felt differently (reviewed by Levine & Safer, 2002). Although these effects are often described in terms of biases and distortions, Levine and Safer (2002) have emphasized the utility of updating our memories to reflect our current conceptions about an event. For instance, if we learn that an argument with a friend was based on a misunderstanding, it is not adaptive for us to continue to reexperience the negative emotions that we felt at the time of the conversation. More generally, if a main purpose of memory is to help us make decisions and behave adaptively in the future, then it makes sense that our memory stores would serve us best if they contained the most up-to-date appraisals of rewards and threats in our environment.

Despite the well-known ability for emotions to change over time, and even to be changed in the moment of an emotional experience (Gross, 1998), relatively little is known about how memory characteristics and the neurobiology of memory consolidation and retrieval are influenced by these reappraisals. For instance, if an event was perceived as negative at the time of its occurrence, but over time is reappraised as neutral, do the retrieval signatures now parallel those for neutral memories, or do some differences remain based on the initial appraisal? The more that we conceive of memory as a dynamic process, the more central these sorts of questions become to our understanding of emotional memory.

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