

Emotional Cognition

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Volume 44

Emotional Cognition: From brain to behaviour
Edited by Simon Moore and Mike Oaksford

Emotional Cognition

From brain to behaviour

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Emotional Cognition

An introduction

Simon C. Moore and Mike Oaksford

There has been a marked shift in the perceived role of emotion in human behaviour. Plato sought to dispel the detrimental influence of emotion on human reason and the Stoics went as far as proposing training programmes to achieve this (Birley 1987). In contrast, recently Goleman (1996) has advocated developing our emotions as a means to intelligent behaviour. Although the contrast between reason (good) and emotion (bad) has significantly diminished since Plato's day, the importance of emotional processing in human cognition has yet to penetrate all areas of Cognitive Psychology. One reason for this situation is that the goal of cognitive theory is to develop formal computational models of cognitive processes. But such well-defined models are rare in the area of emotional effects on cognition. *Emotional Cognition* seeks to address this imbalance by presenting a collection of papers on computational models of emotion. To fully understand how we think *Emotional Cognition* makes a unique contribution to the emotion-cognition debate it is necessary to consider some of the background history.

Perhaps the most influential contribution to the emotion debate in modern times was Darwin's *The Expression of Emotions in Man and Animals* in 1872. Darwin suggested that there were fundamental emotions that found their expression in overt behaviour in animals *and* in humans. In so arguing, Darwin led to the view of the universality of emotion and that emotions were part of the natural order of things: biological systems expressed emotion as part of their natural context. For Darwin, there was no involvement of the 'higher' functions of reason, those functions that the earlier philosophers tried to protect from the influences of emotion, in expressing an emotion. Emotion was a remnant of our pre-sapient inheritance. For Darwin, it was enough to describe emotion in this irreducible form, without attending to its antecedents.

For example, ‘hate’ affected behaviour and, following Plato, cognition was not involved in driving one to act on that hatred. Emotion and cognition were still regarded as separate, unrelated, processes when William James published his seminal paper ‘What is an Emotion?’ (James 1884).

For James, we feel sad because we cry. The sensation of tears on the face constitutes the emotion of sadness. Our perception of visceral changes, the interaction between the body and the context it was in, determined how we felt. Our heart beating fast, perspiration, an increased rate of respiration, a flushed face, these were the building blocks of our emotions. James’s thesis, together with C. G. Lange’s similar ideas, led researchers to seek out the bodily changes associated with our emotions (e.g. Ekman, Levenson, & Friesen 1983; Lang, Greenwald, & Bradley 1993). However, a consequence of this research was that emotion was further separated from the mind. Emotion was reduced to a sort of visceral sensation, akin to hunger, and divorced from thought and reason. Although this research has contributed enormously to our understanding of emotion, theories of how emotions and cognition interacted were still lacking. One reason may be related to a legacy of the behaviourist paradigm that cognitive psychology replaced.

The Behaviourism of the early to mid-twentieth century sought to examine *observable* behaviour and in so doing removed the topic of emotion from inquiry completely. Whereas cognitivism implicated the thoughts and beliefs of an organism as determinants of its actions and experiences, behaviourists only dealt with the objective and the observable. Yet Behaviourism left research in cognition an important legacy: methodological behaviourism. It is still the objective and the observable that informs much cognitive theorising. For example, reaction times and participant choices are still the primary data that serve as the bedrock of cognitive theories and both can be precisely measured. Emotion, however, is still seen as subjective and somehow inaccessible to accurate measurement. In emotion research there has been a tendency to assume some measurable aspect of the environment is in direct correspondence with the intensity of an elicited emotion: fear is talked of as ‘fear of a dog.’ Thus the emotion ‘fear’ is equated with a measure of the dog’s dangerousness and a measure of the action carried out to avoid that danger. Dangerousness and behaviour are measurable, but it seems there is no role for felt emotions, which still remains penetrable only to subjective measures.

An influential development in recent years has been research into the neuroanatomical substrates of emotion and cognition. This research has exploited more sophisticated imaging equipment that has allowed insight into the hardware of the mind and an increased interest in the relation between the mind

and the brain. This hardware approach has circumvented some of the measurement problems associated with emotion. Even though we do not know precisely how happy or sad someone is, at least we could see differential activation in the brain. For example, Damasio (1994) argues that reason and emotion go hand in hand, without one we would not have the other and suggests this interaction occurs in the frontal lobes. Whereas LeDoux (1994) has documented the specific neuroanatomical circuits involved with the representation of fear and has implicated the amygdala. Both LeDoux and Damasio's work, amongst others, has brought emotion and cognition back together. However, they have done so only by utilising one approach: by looking at how the hardware of the brain relates to the interaction of emotion and cognition. This is only part of the story.

Contemporary cognitive psychology assumes a computational approach. Computational explanation, according to Marr (1982), involves three interacting levels of explanation. At the computational level, the functions that the cognitive system needs to compute are specified. Such theories are constrained to be both normatively justified and descriptively adequate. At the algorithmic level, the cognitive processes that compute these functions, and the representations over which they operate are specified. Finally at the implementational level, the actual hardware in which the algorithms are implemented is outlined. Relating cognition-emotion interactions only to brain function deals only with this last level of providing a computational explanation. Marr originally proposed that it was a logical priority to sort out the computational level first, as only with this level in place, would one know what algorithms to look for and what kinds of brain mechanisms would be needed. These days, these levels are usually thought of as non-autonomous and mutually constraining. So it is useful to know something of the computationally relevant aspects of the hardware of the brain as they might constrain the possible algorithms that can be implemented and may influence their complexity profiles, e.g., how long they take to compute a given function. *Emotional Cognition* seeks to provide a more rounded picture of computational approaches to emotion and cognition by looking also at the algorithmic and computational levels. We hope, therefore, that *Emotional Cognition* presents a broader and more complete picture of the relation between cognition and emotion from a cognitive psychological, and hence computational, perspective.

In keeping with Marr's framework, the chapters in *Emotional Cognition* cross the different levels he proposed with many contributors, although starting from one or other position, also speculating on how their work might be extended into the others. The book begins with Buchanan and Adolphs (*The*

Role of the Human Amygdala in Emotional Modulation of Long-Term Declarative Memory) mechanistic account of the role of the amygdala in the emotional modulation of long-term declarative memory. It makes perfectly good sense to remember aspects of the environment that lead to a happy or sad experience: you might wish to avoid events that made you sad and seek out those that make you happy. Unsurprisingly, there is a large literature that shows that long-term memory is modulated by emotion (e.g. Christianson 1992). Buchanan and Adolphs address how emotion influences the way that material is stored in relation to the current emotional state. In so doing they review what is currently known about the physiology of emotion and memory, providing important insights into this complex relationship.

Killcross and Blundell (*Associative Representations of Emotionally Significant Outcomes*) consider the amygdala's role in acquiring associative representations of emotionally significant outcomes. The amygdala has long been regarded as a central component of emotion (LeDoux 1992) and they suggest that the amygdala plays a vital role in the formation of a representation that integrates sensory and motivational properties of goals or rewards. They further explicate the nature of these representations and how they are formed in an associative-cybernetic model of instrumental action.

Under the right circumstances, using backward masking, it is possible to show someone an emotive picture without them being consciously aware of what they have been shown. Even under these circumstances people appear to have some representation of the emotional content of that picture (Ladavas, Cimatti, Del Pesce, & Tuoizzi 1993). This would suggest that evaluative processes may be located very early in information processing and may be a fundamental aspect of how we see the world. Fulcher's chapter (*Neurons with Attitude*) examines how stimuli are evaluated and incorporates a detailed neural network model of how these evaluations are learnt, one that defines the subject matter and makes testable predictions. The key to Fulcher's account is the observation that evaluative information is extracted quickly and without awareness.

This issue is examined further by Winkielman, Schwarz and Nowak (*Affect and Processing Dynamics*) who suggest that perceptual fluency, the amount of effort put into processing information, may be responsible for eliciting an emotion. Evaluation, which involves the emotions, is a way of coming to understand the world (Plato was wrong, we do not come to understand the world through reason alone). This is an important issue as it subtly moves research away from the view that emotion is some post hoc reaction to our delibera-

tions towards the view that emotion is related to how we come to understand the world.

Are feelings emotions? This is an important question, examined by Prinz (*Somatic Appraisals and Emotional Consciousness*), and directly relates to the claim that emotion is separate from cognition. It does seem reasonable to assume that emotions are feelings that are in turn sensations. With a change in emotion we are aware of some physiological changes such as an increase in ones heart rate. However, much goes *unfelt*, such as changes in, say the activity of the brain. But what is essential is that none of these changes are paradigmatic of one, and only one, emotion (Boiton 1996; Ekman et al. 1983). So how do we know we are in one emotional state rather than another when so much that constitutes an emotion is outside of our awareness? Prinz presents, at a philosophical/computational level, his AIR theory of consciousness to address this issue.

Beliefs and goals are the mainstay of cognitivism but we live in an uncertain world, one where we are confronted with more and more information. Employing our beliefs to accurately navigate our world and attain our goals, is fraught with difficulty. This difficulty is compounded by the limitations imposed by our cognitive system (Gigerenzer & Goldstein 1996). Oatley and Johnson-Laird (*Emotion and Reasoning to Consistency*) suggest that emotions are elicited when things go wrong and errors are made. Importantly, Oatley and Johnson-Laird place goals and beliefs as central to emotion. This is a marked shift from how emotion was initially conceived by Plato and Darwin (see above). Emotion is now seen as a consequence of cognition, rather than a visceral sensation. Further, Oatley and Johnson-Laird suggest that emotion acts as a heuristic that biases the cognitive system to resolve the inconsistencies with which it is confronted.

According to classical economic theory, the decisions we make are those that maximise our subjective utilities. However, we also have preferences for our emotions and generally prefer to remain happy than experience sadness. This is the focus of Schwartz's (*Expected Feelings about Risky Options*) chapter and he makes the claim that people can gauge how they will feel given some decision and that these anticipated feelings influences their choice. What is more, he presents data suggesting people are swayed by how they anticipate they will feel as much as the objective returns given some option. Although intuitive, we often invest considerable time and money securing our happiness, this is at odds with traditional economic theory.

Although decision theory is also central to Busemeyer, Townsend and Stout's chapter (*Motivational Underpinnings of Utility in Decision Making*) they

use an extension of decision field theory (Busemeyer & Townsend 1993) to examine the influence of emotion on decision-making. Decision field theory represents an important extension of decision theory, which assumes our perceived utilities are static and fixed. In contrast, decision field theory makes the intuitive claim that our perceived values vary under differing circumstances, levels of consumption and so forth. Using decision field theory, Busemeyer and Townsend examine decision-making in a variety of experimental contexts and hypothesise that emotional plays an important role in determining the decision-makers subjective utilities.

Moore and Oaksford (*An Informational Value for Mood: Negative Mood Biases Attention to Global Information in a Probabilistic Classification Task*) examine how emotion can be represented in relation to a classification task. In this empirical chapter they present data suggesting that negative mood biases visual attention towards information located at low visual spatial frequencies under conditions of maximal uncertainty. They further suggest that, and contrary to the view that mood has no information value compared to emotion, one effect of mood may be to act as an attentional weight in the dimensional representation of information, one that has its strongest effect under conditions of uncertainty.

Ashby, Valentin and Turken (*The Effects of Positive Affect and Arousal on Working Memory and Executive Attention*) examine the effects of positive affect and arousal on working memory and executive attention via a neural network model of the hardware involved in creative problem solving tasks (Dunkers Candle Task, Remote Associates Task and a words association task). To achieve this they consider a wide range of normally disparate literatures. For example, dopamine has long been associated with emotion (Schildkraut & Kety 1967) and positive mood has been associated with creativity (Isen 1987). To determine the relationship between mood, behaviour and the brain they propose a neural network model that captures the behavioural effects of dopamine (associated with more positive moods) and show how the model can account for the effects of mood on behaviour.

Goal states are an important feature of many of the chapters in this volume. Gray and Braver's chapter (*Integration of Emotion and Cognitive Control: A Neurocomputational Hypothesis of Dynamic Goal Regulation*) deals with rewards and punishments and their relationship to approach and withdrawal goals. Starting with a psychologically plausible account of why we should avoid punishment and approach rewards they posit an informal computational model whereby emotion prioritises one or other of the two goal states (approach and withdrawal). Drawing on research on the anatomical substrates of

working memory (Smith & Jonides 1999) their computational model is then applied to research on the neuroanatomical substrates of emotion and cognition. They suggest that different emotions serve to prioritise different goal states and suggest how this relationship is realised anatomically.

As a whole, *Emotional Cognition* attempts to present the reader with an up to date overview of the current state of emotion and cognition research that is striving for computationally explicit accounts of the relationship between these two domains. Many different areas are covered across a range of cognitive research, from the neurosciences through mathematical models to philosophy. We think that the emergence of such an integrative, computational, approach in emotion and cognition research is an exciting development. And we hope that this collection will stimulate even more research in the same vein.

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The role of the human amygdala in emotional modulation of long-term declarative memory

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It seems obvious that some events are better remembered than others are. The emotional salience of a situation often determines the subsequent memory for that situation. Ultimately the role of emotion is to support survival and well-being in an organism's interactions with the environment (Adolphs & Damasio 2000). There would seem to be survival value in creating stronger associations during emotional situations – it would be adaptive for an organism to remember the location of a water source or a predatory attack over less relevant information. The nervous system has evolved mechanisms that facilitate the formation of emotional memories in the service of survival. The neural basis of emotional memory has been studied extensively in animal models. Examination of the neural basis of human emotional memory is a relatively recent endeavor that has been fostered by interdisciplinary research in the field of cognitive neuroscience. A major thrust of this research has been a focus on the role of the amygdala in the formation of long-term declarative memory for emotionally arousing material. This chapter will focus on the role of the human amygdala in the formation of long-term emotional declarative memories. Following an introduction to the effect of emotion on human long-term declarative memory, we will review neurobiological studies that have used the lesion method, functional neuroimaging and pharmacological probes in the investigation of emotional memory.

Throughout the history of the study of emotions and memory there has been controversy concerning the nature of the association between these phenomena. The psychodynamic concept of repression states that memories associated with negative emotional states are not remembered as well as emo-

tionally neutral memories. This repression was proposed as a mechanism to shield the conscious mind from emotional trauma. Contrary to this view, research illustrates that emotional memories are not repressed at all, but are more vivid and better recalled than memories which are not associated with emotion (Schwartz & Reisberg 1991). So-called flashbulb memories are an example of this enhancement of memory for emotional events (Brown & Kulick 1977). This phenomenon is characterized by a heightened sense of vividness and clarity regarding an individual's personal experiences upon hearing emotionally activating news. In spite of the enhanced clarity of the memory trace, these memories are not necessarily accurate (Schmolck, Buffalo, & Squire 2000).

Two lines of evidence are relevant to the discussion of flashbulb memories as a modulation of memory by emotion. The first came out of animal research and is known as the Easterbrook hypothesis (Easterbrook 1959). This hypothesis proposes that emotional arousal causes a narrowing of the range of attention (or range of cue utilization in Easterbrook's terminology) such that low arousal would lead to a greater amount of information taken in, including relevant and irrelevant information. Conversely, high arousal should lead to a narrowed focus of attention to relevant cues, resulting in improved memory performance for highly salient cues and less to peripheral cues due to the exclusion of distraction. This would suggest an attentional mechanism whereby more attention is focused on one aspect of a situation leading to improved memory for that aspect and diminished memory for those details in the periphery.

The second line of evidence is derived from human research on eyewitness testimony (Loftus 1979). The emotional nature and memory demands of eyewitness testimony make it an externally valid means of examining the effect of emotion on memory. A common phenomenon reported anecdotally is known as the 'weapon focus.' The prototype of this phenomenon involves an eyewitness to a crime focusing primarily on the weapon used by the perpetrator to the exclusion of other aspects of the incident. This fits with the Easterbrook hypothesis in that it involves an increased memory for one aspect of a situation and diminished memory for peripheral details.

What aspect of emotion is most important for the modulation of declarative memory? Evidence so far indicates that it is primarily emotional arousal, as opposed to valence (or pleasantness). Some psychological theories of emotion have argued that valence and arousal are two orthogonal factors that may capture the entire spectrum of basic emotions (Lang, Greenwald, Bradley, & Hamm 1993; Russell 1980; Russell & Bullock 1985; Russell, Lewicka, & Niit 1989). Several studies have shown that emotions, as depicted both in facial expressions and in verbal labels, can be represented in a two dimensional space

with valence and arousal as orthogonal axes (Lang et al. 1993; Russell 1980; Russell & Bullock 1985; Russell et al. 1989). Using this framework, studies have shown that stimuli are remembered better the more emotionally arousing they are (Bradley, Greenwald, Petry, & Lang 1992; Hamann, Cahill, & Squire 1997). These findings have led to the hypothesis that it is emotional arousal, and not valence, that is the major factor contributing to how well material is encoded into declarative memory. This hypothesis has been directly tested by manipulating arousal, either pharmacologically (Cahill, Prins, Weber, & McGaugh 1994) or through the use of a specific context (Cahill & McGaugh 1995) in normal human subjects. In the remainder of the chapter the term 'emotional memory' will be used to describe the effect of emotional arousal during encoding on subsequent recollection of the arousing materials.

The aforementioned examples illustrate the complexity of the relationship between emotion and memory. The experience of emotion appears to modulate memory by alternately enhancing or impoverishing memory performance depending upon the details involved in the test of memory. It would seem that the experience of flashbulb memories are at odds with the position espoused in the Easterbrook hypothesis and the phenomenon of weapon focus (Heuer & Reisberg 1990). Flashbulb memories are thought to be vivid due to the inclusion of a great many peripheral details, which is just the opposite of the Easterbrook/weapon focus claim which states that memory for peripheral details is reduced while central information is enhanced. Heuer and Reisberg (1990) suggest that while emotion leads to vivid recollections, these recollections may not be accurate and could be the result of post-hoc reconstructions of the emotional event. This contention is consistent with Loftus' work on the fallibility of eyewitness testimony (Loftus 1979).

Heuer and Reisberg (1990) designed an experiment to assess the impact of emotional arousal on both central and peripheral memory. In the study, subjects watched a series of slides accompanied by a narrative. Each participant was randomly assigned to either the neutral or arousing version of slides. In the neutral version, the slides featured a story about a boy and his mother going to visit his father at a garage. The arousal version also features a story about a boy and his mother visiting the father at work, however in this version, the father is a surgeon at a local hospital and several of the slides feature graphic portrayals of surgery scenes. The slides were roughly matched for structure and layout. The participants were not told that their memory for the slides would be tested, instead they were told that the purpose of the experiment was to assess heart rate responses to the different slide presentations. A third group of participants, however, saw the neutral slides and was told to attempt to memorize the details

of the slides. Participants were asked to return two weeks later at which time a surprise memory test was given. The memory test consisted of both recall and recognition questions regarding central and peripheral material contained within the two slide presentations. Results showed that those in the arousal group had increased memory for both central and peripheral aspects of the slide presentation compared to those who watched the neutral slides.

Additionally, the arousal group showed increased memory compared to the memorizing group in peripheral details. The authors discuss this finding as a contrast to the idea that the arousing material may have been more interesting and therefore, more time would have been spent thinking about the material. The memorizing group were those most likely to rehearse the information that they saw prior to memory assessment, and yet their performance on recall of peripheral details was worse than the arousal group. These data fit with the data on flashbulb memories, but do not support the claims of the Easterbrook hypothesis. This study illustrates that both central and peripheral details of an emotional situation are better remembered than details from a neutral situation.

Cahill and McGaugh (1995) point out a possible confound of these findings in regard to the effect of emotional arousal on memory. In the Heuer and Reisberg (1990) study, participants in the emotional arousal group were exposed to stimuli that were not presented to the other group. It is therefore possible that the differences in memory performance between groups may be due to different features of the stimuli other than their emotional content (differences due to story effects versus emotion effects). Cahill and McGaugh designed a study to address this possible confound (Cahill & McGaugh 1995). All participants were exposed to the same slides (similar to the slides from the arousal condition in the Heuer and Reisberg study), different only in narration, to create two different stories, one neutral and one arousing. The only difference between the two conditions consisted of the narration during the middle phase of each slide presentation. In the neutral condition, the narration describes the son watching his father conduct mock surgery during a disaster drill at the hospital. In the arousal condition, the boy is badly injured on the way to the hospital and a surgeon attempts to save the boy's life. Graphic pictures of surgery in the neutral condition were described as being an actor made up to appear badly injured, whereas the arousal condition narration described the slides as actual surgery on the boy. As in the earlier study, participants returned two weeks later expecting to see a new set of slides, but were presented with an unexpected memory test consisting of recall and recognition questions. Results of this study showed that both groups had identical performance for the neu-

tral portions of the slide narration. The arousal group, however, had markedly increased performance for the arousal portion of the narration both in free recall and recognition tests compared to the neutral group. Additionally, participants who reported greater emotional reaction to the emotional slides also showed better performance. The authors interpret these findings as showing a specific effect of emotional arousal on subsequent memory performance.

Findings from these studies illustrate that emotionally arousing stimuli – including both central and peripheral details – are better remembered than neutral stimuli. A question that arises from these results is: What are the neurobiological underpinnings of emotional memory?

Neurobiology of emotional memory

By virtue of its position in the brain, the amygdala has been the focus of much interest as a possible site of learning and memory for many years (Squire 1987). It was originally thought to play an integral role in the formation of declarative memories. More careful study has revealed the role of the amygdala to be separate from the traditional ‘medial temporal lobe memory system’, which includes the hippocampus and adjacent cortex (Murray 1992; Zola-Morgan, Squire, Alvarez-Royo, & Clower 1991; Zola-Morgan, Squire, & Amaral 1986). There is now evidence, however, that the amygdala plays a modulatory rather than an essential role in declarative memory formation. This evidence is derived from a model of the amygdala’s role in memory formation derived from animal research (McGaugh 2000). In this model, the amygdala is part of a neurobiological system – including stress hormones – that regulates the formation of memory for emotionally salient events via its influence on other brain structures – including the hippocampus and caudate/putamen (Packard & Teather 1998). Within this model, the amygdala is not the site of memory storage, but is involved only in the formation of memories. Also according to this model, the amygdala is not involved in the retrieval of memories – emotional or otherwise – but only in modulating initial encoding and consolidation of memories. While the specifics of this model are controversial (Cahill, Weinberger, Roozendaal, & McGaugh 1999; Fanselow & LeDoux 1999), both animal and human research supports the idea of a selective role of the amygdala in the formation of emotionally significant long-term memories. Additionally, there is evidence that the amygdala is involved in storage of non-declarative emotional memory, for example auditory fear conditioning (Maren 2000).

While our review will focus on emotional memory in humans, we briefly mention studies in animals. A large literature from such studies has demonstrated that the amygdala critically influences both the acquisition and the expression of emotional memories. Much of the evidence to support this claim comes from studies of motivated learning, using both appetitive as well as aversive stimuli. In these experiments, clear evidence has been obtained that the behavioral expression of emotionally motivated learning depends on the integrity of the amygdala during a narrow and highly specific window of time (McGaugh 2000). Notably, the amygdala appears to play a critical role immediately after acquisition of the behavior, and for some time thereafter. These findings have been interpreted as evidence for the amygdala's role specifically in the consolidation processes of motivated learning that are influenced by emotional arousal, a finding also consistent with studies in humans (see below; McGaugh 2000). Direct manipulations of neural activity in the amygdala with reversible pharmacological lesions have shown that the amygdala exerts its modulatory effect on secondary structures, such as the hippocampus, that are directly involved in memory consolidation (McGaugh & Izquierdo 2000; Packard & Teather 1998; Roozendaal 2000).

Lesion studies of emotional memory

As with most brain-behavior relationships, our primary source of information on the role of the amygdala in human behavior has come from patients with specific lesions. This pattern holds true for the relationship between the amygdala and emotional declarative memories as well. While selective bilateral lesions of the amygdala are rare, the few cases that have been reported are illustrative. In addition to bilateral temporal lobectomies, two disorders have been described that result in the bilateral destruction of the amygdala: 1) Urbach-Wiethe disease and 2) Herpes simplex encephalitis. Urbach-Wiethe disease (also known as lipoid proteinosis) is a rare hereditary disorder characterized by the deposition of hyaline material in the skin and mouth areas, and is associated with bilateral mineralization of medial temporal lobe structures in about half of the cases. Herpes simplex encephalitis is an inflammation of neural structures following viral infection. While this disease may result in widespread pathology throughout the nervous system, its earliest pathology almost invariably includes the amygdalae. Additionally, unilateral temporal lobectomy is commonly employed in the surgical treatment of intractable epilepsy. Here we

report on studies of long-term declarative memory of emotional events from subjects with both bilateral and unilateral amygdala damage.

One of the cases of bilateral amygdala damage that has been best characterized was originally reported by Tranel and Hyman (Tranel & Hyman 1990). The patient (SM046) had been diagnosed with Urbach-Wiethe disease. Computerized tomography (CT) and magnetic resonance imaging (MRI) confirmed the mineralization of both amygdalae, as well as minimal damage to anterior entorhinal cortices, but no other structural abnormality. Neuropsychological evaluation of this patient revealed normal general intellect, language and verbal memory function. These results are in stark contrast to the profound declarative memory impairment following hippocampal damage (Squire 1987). Follow-up research with patient SM046 and others with amygdala damage has highlighted the modulatory role in declarative memory formation played by the amygdala. While no explicit tests of emotion or emotional memory were originally documented, later work with this patient (described below) has addressed her emotional memory function.

The results of a conditioning study conducted by Bechara and colleagues (Bechara et al. 1995) illustrate the separable roles of the amygdala and hippocampus in the memory formation. The ability of patient SM046 to show conditioned autonomic responses to conditioned stimuli (CS) paired with an aversive sound (unconditioned stimulus; US) was tested in comparison to a patient with bilateral hippocampal damage as well as a patient with bilateral damage to both amygdalae and hippocampi. Results illustrated that while SM046 was impaired in the production of conditioned autonomic responses to the CS, she was able to form declarative memories for which stimulus was paired with the aversive sound. The patient with hippocampal damage displayed the opposite pattern, showing no declarative knowledge of the CS-US contingency, but exhibiting normal conditioned autonomic responses to the CS presentation. The patient with damage to both amygdala and hippocampus failed to form either associative or declarative memories during the task. In this study, declarative memory for the CS-US contingency was not dependent on the amygdala. While both the amygdala and hippocampus are necessary for the 'normal' performance of these tasks, bilateral damage to either structure results in a dissociable pattern of deficits.

Markowitsch and colleagues have examined emotional memory formation in two patients with Urbach-Wiethe disease (Markowitsch et al. 1994). Both patients showed bilateral mineralization of the amygdala. Neuropsychological evaluation revealed that while neither patient had a general impairment of declarative memory, they were slightly impaired on several specific tests of

memory (e.g., Auditory Verbal Learning). Memory for emotional material was similarly depressed, with one patient (C.P.) showing more impairment than the other (B.P.). Specifically, in a word stem completion task of previously presented emotional or neutral words, C.P. remembered the neutral words better than the emotional words, while B.P. showed roughly equivalent performance for neutral and emotional stimuli, as compared to control subjects who tend to remember the emotional stimuli better. Similarly, in a recognition test of previously presented emotional pictures, C.P. recognized neutral pictures better than emotional pictures in contrast to normal controls who showed enhanced recognition performance of the emotional materials. This study was one of the first to examine the relationship between emotional memories and the amygdala using the lesion method. Subsequent work has refined the experimental stimuli and conditions in order to better address this relationship.

Two studies have provided a follow-up experiment, all using the same task in rare patients with selective bilateral amygdala damage (Adolphs et al. 1997; Cahill et al. 1995). Subjects completed a task that shows a reliable effect of emotional content on memory performance in normal human participants, the 'Reisberg Task' mentioned earlier (Cahill & McGaugh 1995; Heuer & Reisberg 1990). In the task, participants are presented with 12 slides with an accompanying narration. The slides depict a mother and son going to visit the boy's father at a local hospital. While on route to the hospital, they are involved in a traffic accident and the boy is rushed to the hospital where a surgeon attempts to save the boy's life. The story of the slides and narration may be divided into three phases: phase 1 contains non-arousing material (e.g., the boy and mother on their way to the hospital), phase 2 contains emotionally arousing material (scenes of surgery), and phase 3 again contains neutral materials (mother leaving the hospital). Participants were told only to pay close attention to the slides, but no mention of a memory test was made. All studies found a similar impairment in subjects with bilateral amygdala damage. For example, in the study by Adolphs et al. (1997), immediately after viewing the slides, subjects were asked to rate their emotional reactions to the story; all subjects rated the story equally on this measure. Twenty-four hours after exposure to the slides, memory for the stimuli was tested using a multiple-choice questionnaire. While normal participants remembered slides from phase 2 significantly better than the other two phases, neither amygdala damaged patient showed this pattern. Specifically, the one slide remembered best by the control participants (a slide showing the surgically reattached legs of a car-crash victim) was the slide on which the two patients deviated most from the controls' scores (see Figure 1). The pattern of impaired facilitation of memory for emotionally

arousing material in the face of otherwise normal overall memory performance in subjects with bilateral amygdala damage contrasts sharply with the performances given by amnesic subjects. Subjects with hippocampal or diencephalic amnesia are impaired in their overall memory performance, but show a normal (albeit smaller absolute magnitude) enhancement when the subject matter is emotionally arousing (Hamann et al. 1997).

Using the same task, Adolphs and colleagues examined the pattern of emotional memory performance following unilateral amygdala damage (Adolphs, Tranel, & Denburg 2000). Eight subjects with unilateral amygdala damage consequent to temporal lobectomy (6 left; 2 right), 9 brain damaged controls with no damage to the anterior temporal lobe, and 7 normal controls participated in the study. In this experiment, each slide in the story was rated on scales of emotional valence, arousal, unusualness, and complexity. There were no group differences in slide ratings. As in the previous study, both normal con-

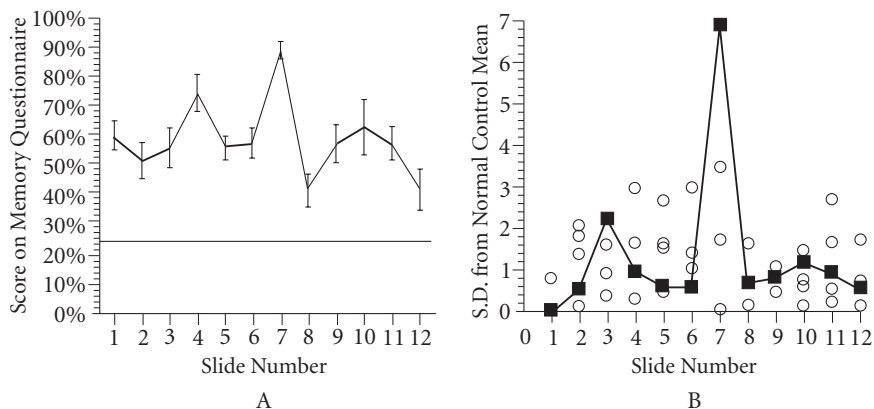


Figure 1. Bilateral damage to the human amygdala impairs declarative memory for emotionally arousing material. Subjects were shown a series of 12 slides that varied in emotional arousal. Slide 7 was the most arousing slide, showing surgically reattached legs of a car-crash victim. *A*, Data from seven normal control subjects, showing memory score on a questionnaire about each slide. Chance is at 25% (solid line). *B*, Data from six brain-damaged control subjects with no damage to amygdala (circles) and from subject SM (solid line), plotted as differences from the control data, SM differed most from controls on the most emotional slide, an impairment not shown by any of the brain-damaged control subjects. (Reprinted from Adolphs, Cahill, Schul, & Babinsky. Impaired declarative memory for emotional material following bilateral amygdala damage in humans. *Learn Mem* 1997; 4: 291–300. Copyright ©1997 Cold Spring Harbor Laboratory Press.)

trols and brain damaged controls showed enhanced memory for phase 2 of the slide/narrative story, specifically for the most highly arousing slide. This pattern was also found for the 2 subjects with right amygdala damage. Those subjects with left amygdala damage, however, failed to show enhanced memory for this slide, showing the same pattern as previously reported for subjects with bilateral amygdala damage. These findings suggest a role for the left amygdala in the consolidation of declarative memory for emotionally arousing stimuli.

Further studies have addressed the role of unilateral amygdala damage in the formation of memory for emotional words. Phelps and colleagues examined emotional memory formation in 26 subjects following unilateral temporal lobectomy (Phelps, LaBar, & Spencer 1997). In experiment 1, subjects were presented with a list of 27 words (9 positive, 9 negative, and 9 neutral) while skin conductance responses (SCRs) were recorded. A surprise recall test was administered 1 minute after the presentation of the word list. Results illustrated that the left temporal lobectomy group had the worst recall of the word list, but this effect was not statistically significant. Each group recalled the negative and positive words better than the neutral words, but there was no difference among the groups in terms of the pattern of slide recall. The authors noted that the words used in the negative ('victim') and positive ('comedy') categories were perhaps not salient enough to produce the emotional arousal necessary to show any group differences in emotional memory performance. In fact, the SCR data illustrated that the neutral word category elicited a greater response than did either emotion word category. In light of these findings, these investigators report a subsequent study designed specifically to address the role of the arousal dimension in memory consolidation (LaBar & Phelps 1998). In this follow-up study, 22 temporal lobectomy patients (10 left, 12 right) were presented with a list of 40 words (20 arousing, 20 neutral). The arousing words chosen in this study consisted of 'profanities, sexually explicit words, and words depicting social taboos.' These words were successful in producing increased SCRs and were rated as significantly more arousing than neutral words in controls and in both temporal lobectomy groups. Free recall for the words was assessed both immediately and at 1 hour post-encoding. The results were assessed in terms of 'forgetting rates' between the immediate and delayed free recall tests. Only the control group showed a differential forgetting rate for the arousing versus neutral words, showing increased recall for the arousing words at the delayed recall test. Both the right and the left temporal lobectomy group showed decreased memory for the arousing words at delayed recall. Consistent with the two previously reported studies, the left temporal lobectomy group showed the poorest levels of recall; their performance was significantly worse

than both controls and the right temporal lobectomy group. This effect was not, however, specific to emotionally arousing material, as the left temporal lobectomy group showed reduced overall performance, but not a specific impairment on memory for emotional stimuli. While these results are consistent with previous research showing a left-hemisphere dominance for verbal memory, they do not address a specific role of the right or left amygdala in memory for verbal versus visual emotional stimuli.

A recent study in this lab has attempted to address this issue (Buchanan, Denburg, Tranel & Adolphs 2001). Participants consisted of 20 subjects with unilateral amygdala damage following temporal lobectomy for treatment of epilepsy (11 left, 9 right) and 25 brain damaged controls with unilateral lesions outside the temporal lobe. Additionally, 35 normal control subjects were recruited for participation. Participants were tested on two days, on the first session 15 pictures differing in emotional salience (5 pleasant, 5 unpleasant, 5 neutral) were presented along with a one-sentence verbal narrative description (e.g., accompanying a picture of two parents with their new twin babies was the narrative: 'After the babies were born, both parents were very happy, although a bit exhausted.'). During picture presentation, SCRs were recorded. Subjects were told to watch attentively while the emotional responses to the stimuli were recorded, no mention of a follow-up memory test was made. Twenty-four hours after the first session, subjects' memory for the slides was assessed with free recall, multiple choice and 4-alternative forced choice recognition tests. Within both free recall and multiple choice tests, memory for both narrative and picture information was assessed. The recognition test assessed only recognition of visual detail. Results illustrated that the group with left amygdala damage was specifically impaired on memory for emotional narratives relative to memory for neutral narratives. Interestingly, this group was not impaired on memory for emotional picture information. The right amygdala group, on the other hand, were impaired on visual recognition memory; however this impairment was not specific to emotional pictures. These findings support a role of the left amygdala in the processing of verbal emotional stimuli and a role of the right amygdala in processing visual emotional stimuli, corroborating previous work describing the separable language versus visuospatial processing roles for the left and right hemispheres, respectively. These data replicate previous work illustrating a deficit in verbal emotional memory in individuals with left amygdala damage (LaBar & Phelps 1998; Phelps et al. 1997) while illustrating a lateralized pattern of the amygdala's influence on emotional memory. Future work should further examine the lateralization of amygdala involvement in the processing of emotional memory (Cahill et al. 2001).

Neuroimaging studies of emotional memory

Functional neuroimaging has provided another tool with which to examine the role of the human amygdala in the formation of emotional memories. Several recent studies have been able to test specific hypotheses derived from both animal research and studies in humans with amygdala lesions using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI).

The first study to examine the role of the human amygdala in the formation of emotional memories using functional neuroimaging was conducted by Cahill and colleagues (Cahill et al. 1996). Healthy participants viewed emotionally arousing and neutral videos during PET scanning. Three weeks later, participants were asked to recall all the information that they could remember from each video. As expected, participants recalled significantly more information from the emotionally arousing video than from the neutral video. Correlation analyses revealed a significant positive correlation between the glucose metabolic rate of the right amygdala and the number of emotional film clips recalled ($r = 0.93$). Further analyses showed no such association with recall of neutral film clips. These findings suggest that the amygdala is activated during the encoding of emotionally arousing events and is involved in the translation of these events into long-term memory. A follow-up study corroborated the finding that amygdala activity is not involved in the formation of declarative memory for nonemotional material (Alkire, Haier, Fallon, & Cahill 1998). This study did, however, document an association between hippocampal activity and the formation of memory for a nonemotional word list. These two studies further illustrate the dissociation of memory functions between the hippocampus and amygdala, and highlight a specific role of the amygdala in the formation of emotional memories.

Two recent studies have extended these findings to show an association between bilateral amygdala activity during encoding and memory for both emotionally pleasant and unpleasant stimuli using both PET (Hamann, Ely, Grafton, & Kilts 1999) and fMRI (Canli, Zhao, Desmond, Glover, & Gabrieli 1999). The study by Hamann and colleagues additionally tested the emotional specificity of the amygdala's influence on memory by including a stimulus category of interesting and memorable pictures. These interesting pictures included a chrome rhinoceros and a scene from a surrealist painting. Presumably, if the amygdala is involved in general memory enhancement, then amygdala activity should be associated with memory for memorable yet nonemotional stimuli. Results from this study illustrate that while these interesting pictures were better remembered than neutral and pleasant pictures at 4 weeks

after encoding, this enhancement was unrelated to amygdala activity that was specifically related only to memory for aversive and pleasant stimuli (a finding also consistent with studies in monkeys, which have failed to find any effect of amygdala lesions on the von Restorff effect – enhanced memory for especially unusual or distinctive stimuli in a set; (Parker, Wilding, & Akerman 1998). These results highlight the specific role of the amygdala in the enhancement of memories for emotionally significant material.

A recent event-related fMRI study has shown that only those stimuli rated as the most emotionally intense are associated with increased amygdala activity and increased memory performance (Canli, Zhao, Brewer, Gabrieli, & Cahill 2000). In this study, 10 female volunteers were exposed to a selection of neutral and emotionally negative pictures while the fMRI response was recorded for each picture. Immediately after viewing each picture, subjects rated their emotional response on a scale from 0 indicating 'not emotionally intense at all' to 3 indicating 'extremely emotionally intense.' Analysis of the fMRI response illustrated that bilateral amygdala activity was correlated with increased ratings of emotional intensity, such that the greater the emotional intensity, the greater the amygdala response. Three weeks later, subjects returned for a surprise memory test in which they were asked to report whether they were certain that they remembered a slide, whether the slide seemed familiar or whether they did not remember the slide. Performance data illustrated that those slides rated as 'extremely emotionally intense' were remembered significantly better than those rated as less intense. Additionally, the degree of left amygdala activation during picture encoding was correlated with subsequent memory for the pictures (see Figure 2). Those pictures that tended to produce the greatest response in the left amygdala were also those that were remembered most often.

Results from lesion studies and neuroimaging investigations would suggest that the amygdala enhances the encoding of emotional stimuli and that this enhancement translates into improved memory performance for these materials. In addition to encoding, long-term memory involves other processes including consolidation and retrieval. The designs of the aforementioned studies have not allowed for the assessment of the role of the amygdala in these other processes of memory for emotional events. Two neuroimaging studies have addressed the role of the amygdala in the recognition of previously presented emotional stimuli (Dolan, Lane, Chua, & Fletcher 2000; Taylor et al. 1998). Taylor and colleagues report a study in which PET scans were taken during the encoding of emotionally unpleasant and neutral pictures and subsequent recognition of these stimuli. Initial encoding of the unpleasant pictures resulted in increased left amygdala activity, but the recognition of these

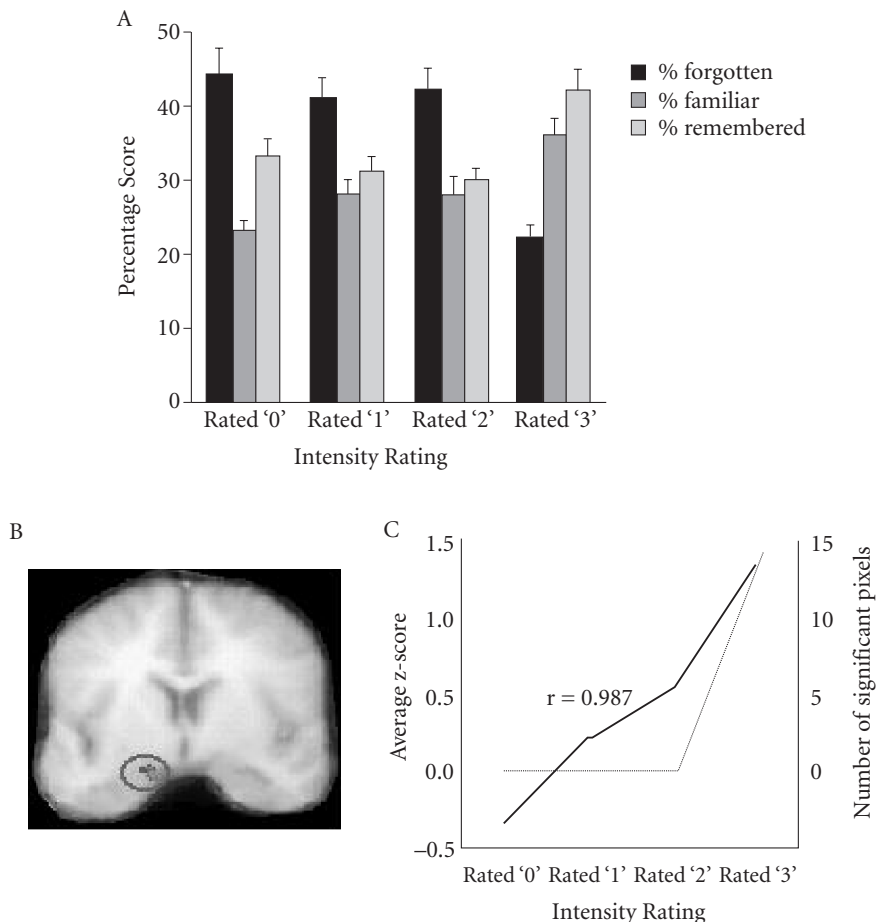


Figure 2. Enhanced emotional memory correlates with amygdala activation to highly emotionally intense stimuli. *A*, Behavioral data on memory performance as a function of subjects' ratings of emotional intensity. *B*, Cluster of significant correlation between amygdala activation and subjects' memory for scenes rated as emotionally highly intense (rated 3). Left side of the image is left side of the brain. *C*, Correlation between left amygdala activation and memory for emotional items increases with greater emotional intensity. Black solid line shows higher z-score averages across the amygdala with higher emotional intensity ratings. Z-scores represent the strength of correlation between amygdala activation and subsequent memory for emotional stimuli. The gray line shows that there were no pixels within the amygdala that reached statistically significant z-score level ($z > 1.96$) for scenes that were rated 0 to 2, but there were 14 significant pixels for scenes that were rated 3. (Reprinted with permission from Canli, Zhao, Brewer, Gabrieli, & Cahill, Event-related activation in the human amygdala associates with later memory for individual emotional experience. *J. Neurosci* 2000, 20 (RC99), 1–5. Copyright ©2000 Society for Neuroscience.)

same pictures did not affect amygdala activity. Areas associated with recognition included prefrontal and anterior cingulate cortices. These findings fit with the aforementioned model of the role of the amygdala in memory formation derived from animal research (McGaugh 2000) which suggests that the amygdala is involved in the acquisition and consolidation, rather than the retrieval of emotional memory. However, a recent study provided some evidence against this model by examining amygdala activity during the recognition of emotional pictures while controlling for the emotional reaction to the pictures (Dolan et al. 2000). Dolan and colleagues presented emotionally pleasant, unpleasant and neutral pictures to subjects prior to a PET scan during which two different tasks were performed: memory and judgment. In the memory condition, recognition for these pictures was tested using a target detection task. The judgment condition consisted of looking at the same pictures as in the memory condition, but instead of indicating recognition the subjects were instructed only to decide whether the pictures depicted indoor or outdoor scenes. Results illustrated increased left amygdala activity during the recognition of emotional pictures compared to the judgment condition. These findings provide some preliminary evidence that in addition to the previously described role of the amygdala in the encoding of emotional memory, it may also play a role in the retrieval of emotional events.

Findings from several of these studies have illustrated different patterns of lateralized amygdala activity in males (Cahill et al. 1996; Hamann et al. 1999) who showed predominantly right lateralized activation versus females (Canli et al. 1999; Canli et al. 2000) who showed left lateralized activation. These gender differences have recently been addressed in a study utilizing both men and women (Cahill et al. 2001) and using identical experimental conditions as previously used with men only (Cahill et al. 1996). Results from this study illustrated the same gender-specific lateralized pattern of activation previously documented across separate studies with right amygdala activity predicting enhanced emotional memory performance in men while in women, left amygdala activity predicted enhanced emotional memory. The authors suggest that these gender differences may reflect different cognitive strategies between men and women in the processing of these stimuli. These intriguing findings clearly warrant the inclusion of gender and laterality as factors in future work on the relationship between the amygdala and emotional memory.

Pharmacology of emotional memory

The effect of drugs on emotional memory has been studied extensively in animals (McGaugh 2000; McGaugh & Izquierdo 2000) and human research on the topic has been accumulating recently (Buchanan & Lovallo 2001; Cahill et al. 1994; O'Carroll, Drysdale, Cahill, Shajahan, & Ebmeier 1999b; van Stegeren, Everaerd, Cahill, McGaugh, & Gooren 1998). Results from animal research have suggested a role of the stress hormones – both epinephrine and glucocorticoids – in the enhancement of memory by emotion. A great deal of work has characterized the influence of these chemicals on memory through pharmacological and neuroanatomical manipulations. This work has led to the postulation of a neurobiological system – involving both the stress hormones and the amygdala – which is active during arousing learning situations to enhance memory for these events (McGaugh 2000). Briefly, both epinephrine and glucocorticoids can enhance memory for aversive events, this enhancement can be blocked either by lesions of the amygdala or specific pharmacological antagonism of either the adrenergic or glucocorticoid system (Roozendaal 2000). It is proposed that the final common pathway of these hormones' influence on emotional memory is through β -adrenergic activation within the basolateral nucleus of the amygdala which regulates memory consolidation via the hippocampus and striatum (McGaugh 2000).

Human research has tested this model, extending the findings on both epinephrine and cortisol (the human glucocorticoid) to declarative memory for emotional materials. The first study to address this issue in humans examined the effects of β -adrenergic blockade on memory for emotionally arousing slides (the same task described previously; Cahill et al. 1994). Results showed that those individuals receiving the β -blocker did not show enhanced memory for the emotionally arousing slides as the placebo group did. There was no effect of the drug, however, on memory for emotionally neutral slides. These findings illustrate that β -adrenergic activity plays a role in the enhancement of memory for emotional stimuli. Follow-up studies using the same task have illustrated that this effect is dependent on central, but not peripheral adrenergic blockade (van Stegeren et al. 1998; O'Carroll, Drysdale, Cahill, Shajahan, & Ebmeier 1999a) and that enhancement of adrenergic function can enhance the emotional-modulation of memory (O'Carroll et al. 1999b). Specifically, O'Carroll and colleagues (1999b) gave participants either yohimbine, a central noradrenergic agonist, or metoprolol, a central noradrenergic antagonist or placebo prior to viewing the slide series. Results showed a modest, but significant increase in emotional memory in those who received yohimbine

and reduced emotional memory performance in those receiving metoprolol. These studies point to a role of central adrenergic activity in the enhancement of memory by emotional events.

A recent study has addressed the role of glucocorticoids in the formation of emotional memory in humans (Buchanan & Lovallo 2001). In this study, separate groups of participants received either 20 mg of cortisol or placebo and viewed both emotionally arousing and neutral pictures. One week later, participants' memories for the pictures was examined using free recall, cued recall and recognition tests. The cortisol group recalled more of the arousing slides compared to the placebo group while the groups did not differ in recall of neutral slides (see Figure 3). Although research has suggested that chronically elevated corticosteroids may impair memory for emotionally neutral materials (Lupien & McEwen 1997), these results suggest that acute elevations in the hormone enhances long-term memory for emotionally arousing stimuli. These findings extend a great deal of animal research which suggests that acute elevation of glucocorticoids can enhance memory performance for emotionally arousing situations (Roosendaal 2000).

Taken together, human studies involving the pharmacological manipulation of epinephrine and glucocorticoids have supported the hypothesis that these compounds are involved in the enhancement of memory by emotion. While these human studies do not directly assess the effects of these compounds on amygdala function, their correspondence with animal research would suggest that the amygdala is a putative site of action in this phenomenon. Future research will no doubt address this relationship.

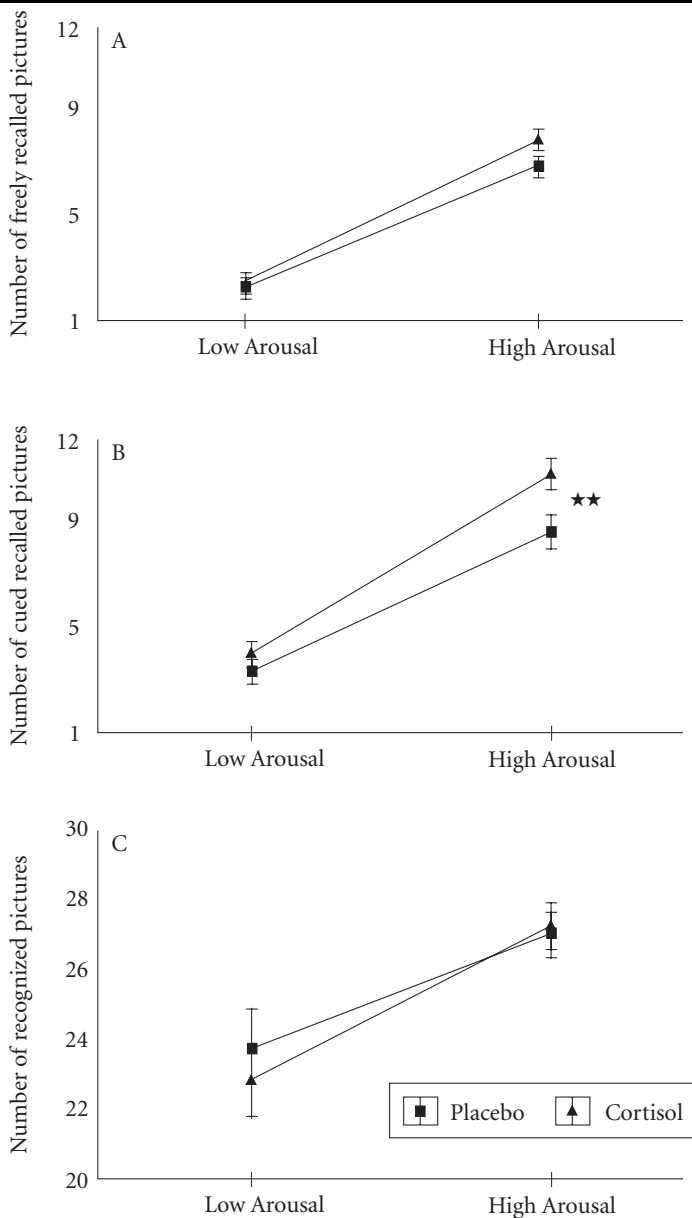


Figure 3. Effects of cortisol and emotional arousal on picture recall and recognition. Subjects who received cortisol (20 mg) recalled more highly arousing material than did the placebo group. A, Correct free recall as a function of a median split of arousal ratings. B, Correct cued recall, ** = significant group difference at $p < 0.02$. C, Correct recognition. (Reprinted with permission from Buchanan & Lovallo, Enhanced memory for emotional material following stress-level cortisol treatment in humans. *Psychoneuroendocrinology* 2001, 26, 307–317. Copyright ©2001 Elsevier Science Ltd.)

Summary and integration

The studies reviewed in this chapter illustrate the complex nature of the role of the amygdala in the modulation of memory by emotion. Findings from lesion studies and neuroimaging work suggest that amygdala activity is necessary for the enhanced memory of emotionally arousing stimuli. Further, pharmacological studies illustrate that both catecholamines and glucocorticoids play a role in emotional memory. What mechanistic role might the amygdala play in facilitating the memory of emotional material? What other brain regions are involved in this process? How do the stress hormones interact? We shall address these questions in this section of the chapter by attempting to place the aforementioned studies within the context of mechanistic animal research and suggest future research that may further elucidate the role of the amygdala in emotional memory.

In addition to the immediate effect of emotion on survival-related behaviors, enhanced long-term memory of this emotional situation would serve to aid the organism in potential future encounters. Numerous brain structures – including the amygdala, hypothalamus, hippocampus, cingulate, insular, and orbitofrontal cortices, among others – are involved in both the appreciation of and response to emotional stimuli. The various structures involved in this process imbue the emotion-eliciting stimulus with affective properties that, in addition to producing the appropriate response, lead to an enhanced representation of that stimulus as a memory trace. Thus, in response to emotion, the activity of the same brain structures are at the service of both response output and memory formation. That enhanced activity of response systems – autonomic, endocrine and skeletal motor activity – accompanies increased mnemonic representation illustrates the coordinated activity of these brain structures in the service of survival.

The amygdala receives both rudimentary (LeDoux 2000) as well as highly processed sensory information (Amaral, Price, Pitkänen, & Carmichael 1992) that allows for quick and specific activation of response systems that influence behavior and subsequent memory formation. The specific role of the amygdala in this process appears to be that of instigator, the catalyst that initially imbues incoming stimuli with emotional significance triggering other neural regions to react accordingly. This view of the amygdala's role in emotional memory formation fits with its role in classical fear conditioning. In this paradigm the amygdala is involved in the initial formation of the contingency between the biologically meaningful stimulus (US) and predictive stimulus (CS), but once this contingency is established the amygdala is no longer actively involved in

the memory process (Buchel, Morris, Dolan, & Friston 1998; LaBar, Gatenby, Gore, LeDoux, & Phelps 1998; Wilensky, Schafe, & LeDoux 1999). The role of the amygdala in explicit emotional memory formation seems also to be modulatory and time limited: influencing the formation and storage of memory in other brain regions – the hippocampus, caudate and putamen, for example (McGaugh 2000) – while not being involved in the subsequent retrieval of these memory traces.

The role of the amygdala as an instigator of the formation of emotional memories is supported by the aforementioned functional imaging and lesion studies in humans. The lesion studies described suggest that the amygdala is necessary for the enhancement of memory for emotionally arousing stimuli (most specifically the left amygdala due, perhaps, to the verbal nature of the testing procedures). The inactivation of one or both amygdalae (either due to disease or surgery) results in reduced memory for emotionally arousing materials. The nature of these studies do not allow for the assessment of consolidation or retrieval effects, but clearly implicate the amygdala in the encoding of emotional material into memory. Similarly, the functional neuroimaging studies have most consistently pointed to encoding as the memory stage at which the amygdala exerts its effects (although Dolan et al. 1998 also report amygdala activity associated with retrieval). Recent research suggests that both storage and retrieval may be susceptible to modulation by emotion under certain circumstances in which reconsolidation is occurring (Nader, Schafe, & Le Doux 2000; Sara 2000). Regardless of the caveats such as gender and laterality effects (Cahill et al. 2001), and the potential effects of reconsolidation (Sara 2000), the most consistent finding from the discussed studies is an association between amygdala activity during encoding and the enhancement of subsequent memory. The activation of the amygdala would seem to be a potent predictor of memory performance.

In light of the established role of the medial temporal lobe memory system – that includes the hippocampus and adjacent cortex (Cohen & Eichenbaum 1993) – how does the amygdala fit in? The detection and experience of emotion increases the processing of the emotional stimuli by focusing attention and enacting response systems (Frijda 1987; Lang, Bradley, & Cuthbert 1990). The amygdala plays an integral role in this enhanced processing through influence over numerous brain structures including the hippocampus, hypothalamus, brain stem arousal centers, as well as bidirectional connections with neocortex (Amaral et al. 1992). It appears that one pathway of the amygdala's influence is to augment the activity of the medial temporal lobe memory system by imbuing explicit memories with affective tone. Animal research supports

this view by showing that stimulation of the basolateral amygdala enhances long-term potentiation (LTP) – a process widely considered to be a cellular underpinning of memory formation – in both the dentate gyrus (Ikegaya, Saito, & Abe 1995) and insular cortex (Escobar, Chao, & Bermudez-Rattoni 1998). Interestingly, and in relation to the aforementioned role of catecholamines, β -adrenergic blockade within the basolateral amygdala reduces dentate gyrus LTP (Ikegaya, Nakanishi, Saito, & Abe 1997). Human neuroimaging results from Hamann and colleagues (1999) extend this notion by showing that both amygdala and hippocampal activity during the encoding of emotional material was correlated with subsequent emotional memory performance. These findings place the amygdala in a modulatory position of the traditional medial temporal lobe memory system, its activity influencing memory formation only under conditions of emotional arousal.

Another pathway through which the amygdala may influence memory performance is via hormonal output. The previously described pharmacological studies have illustrated the effect of manipulations of both catecholamines and glucocorticoids on emotional memory performance. Direct connections between the amygdala and the hypothalamus mediate the release of both epinephrine and cortisol during emotionally arousing situations (Davis 1997). Following their release, these hormones exert actions throughout the central nervous system and specifically at the level of the amygdala (Honkaniemi et al. 1992; Shepard, Barron, & Myers 2000). A great deal of animal research has focused on the bidirectional nature of the relationship between the amygdala and stress hormones (McGaugh & Izquierdo 2000; Roozendaal 2000). Enhancement of either adrenergic or glucocorticoid activity improves while blockade of these hormones reduces memory performance. The final common pathway of these hormones' effects on memory performance appears to be at the level of the amygdala – specifically via noradrenergic neurotransmission in the lateral/basolateral nuclei (Quirarte, Roozendaal, & McGaugh 1997). As previously mentioned, manipulations of this activity within these nuclei influences hippocampal and cortical function (Escobar et al. 1998; Ikegaya et al. 1997), providing a potential mechanism whereby the actions of these hormones at the level of the amygdala could influence the formation of emotional memories. While human research has yet to show a relationship among stress hormones, amygdala activity and emotional memory, animal research suggests such a relationship and future work will no doubt focus on elucidating this relationship.

In line with the relationship between systemic hormones influencing subsequent amygdala activation, one mechanism through which the amygdala

could influence memory is via perception of the physiological response in the body. Vagal stimulation in both animals (Clark, Krahl, Smith, & Jensen 1995) and humans (Clark, Naritoku, Smith, Browning, & Jensen 1999) results in increased memory performance. Specifically, Clark and colleagues (1999) stimulated the vagus nerve in human patients immediately following verbal learning. This stimulation resulted in enhanced recognition memory for target words previously seen in the encoding phase. While in this experiment the study materials were not emotionally arousing, the authors propose that vagal stimulation resulted in enhanced arousal via influence on the amygdala and thus enhanced memory. In fact, the sensory role of the vagus nerve is proposed to be the mechanism whereby peripherally-released epinephrine – which does not readily pass the blood-brain-barrier – influences amygdala function in the formation of emotional memories (McGaugh 2000). These results illustrate that the influence of the amygdala on memory could occur at multiple stages: (a) through rapid initial responses influencing neural information processing, (b) indirectly via perception of the body's physiological response, or (c) by the experienced feeling of an emotion, even in the absence of an emotional stimulus (for instance, by asking subjects to volitionally induce a particular mood while they are encoding material). Most present studies have not permitted a separation of the emotion depicted in the stimulus, from the emotional reactions and feelings of the subject – the assumption has generally been that emotional stimuli will result in emotional states in the subject. A goal for the future will be to disentangle these issues.

The role of the amygdala in the formation of memories has long been a topic of research and debate in neuropsychology. Research presented in this chapter describes a modulatory role of the human amygdala – in combination with stress hormones – in the formation of emotional memories. This work has grown directly out of basic animal research that has outlined mechanistic models whereby the amygdala may influence memory (LeDoux 2000; McGaugh 2000). Both animal and human research are contributing to a more refined view of the role of the amygdala in long-term declarative memory that will inform our basic understanding of the processes of emotion and memory.

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