CHAPTER

5

Encoding and Retrieval from Long-Term Memory

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Revisit and Reflect

You're walking down a hall. Coming toward you, at a distance of about 50 feet, are two people walking together. You recognize one of them immediately: you know her name, you met her at a political rally last term. On that occasion you discovered that you grew up in the same city and share a liking for Italian food. Her companion looks familiar, you have a vague sense you've met before, but you can't place him—you can't think what his name is, where you might have met, or any details about him. But now, as you all meet, he greets *you* by name. Your embarrassment at not knowing his name grows when the conversation reveals that he remembers you from an encounter only two weeks ago, just before you both took a physics exam. How is it that you can recall clearly a conversation you had months ago, and have no recollection of another that apparently took place relatively recently?

This chapter considers the nature of long-term memory, first describing two classes of long-term memory systems, declarative and nondeclarative. We then focus on the mechanisms that encode, consolidate, and retrieve declarative memories, consider how and why our memories are sometimes inaccurate, and explore why we sometimes forget. We conclude with a discussion of the forms of nondeclarative memory that allow the past to unconsciously shape our current thinking and actions. We specifically address five questions:

1. What are the characteristics of declarative and nondeclarative memory systems?
2. How do we encode new declarative memories, what processes affect encoding efficacy, and what brain mechanisms build these memories?
3. How are episodic memories retrieved, and why is it that sometimes what we retrieve is not an accurate reflection of our past?
4. Why do we sometimes forget?
5. What are the forms of nondeclarative memory, and how do they influence our behavior?

1. THE NATURE OF LONG-TERM MEMORY

The ability to remember the people, places, and things encountered in the course of daily life is a fundamental form of cognition that guides behavior. The frustration experienced in situations such as the hallway meeting described serves as a brief reminder of our dependence on **memory**, the internal repository of stored information. As we shall see in this chapter, memory relies on a set of processes by which information is encoded, consolidated, and retrieved. Although the consequences of memory failure are sometimes limited to social embarrassment, that is not always the case: memory is essential to the functioning and even the survival of human and other animals. Without memory, we could never learn from our experience and would operate aimlessly, without plans or goals. Motor skills and language ability would be lost. Even the sense of personal identity we all possess would be gone.

The kind of memory involved in these situations is **long-term memory**, information that is acquired in the course of an experience and that persists so that it can be retrieved long after the experience is past. As we will see, some forms of long-term memory can be consciously retrieved, so that we can use our remembrance of things past to guide present thought and action. William James (1890) described this kind of memory as "the knowledge of a former state of mind after it has once dropped from consciousness." By contrast, other forms of long-term memory influence our present thinking and behavior while operating outside awareness. In such instances, past experience unconsciously affects the present. Progress in understanding long-term memory has come from behavioral investigations of people with intact memories as well as of patients with memory deficits. Insights into the operation of memory also have come from lesion and recording studies in animals and neuroimaging studies in humans.

1.1. The Forms of Long-Term Memory

Theorists believe that there are multiple forms of long-term memory that differ in their basic information processing properties and in the brain structures that support them (Figure 5–1). These various forms of memory are thought to fall into two general classes, described as declarative and nondeclarative. **Declarative memory** (also known as **explicit memory**) refers to forms of long-term memory that can ordinarily be consciously recollected and "declared," or described to other people, such as memory for facts, ideas, and events. Declarative memory encompasses **episodic memory**, the memory of events in our own personal past, and **semantic memory**, our general knowledge about things in the world and their meaning, a distinction proposed by Endel Tulving in 1972. Tulving defined episodic memory as the conscious knowledge of temporally dated, spatially located, and personally experienced events or episodes.

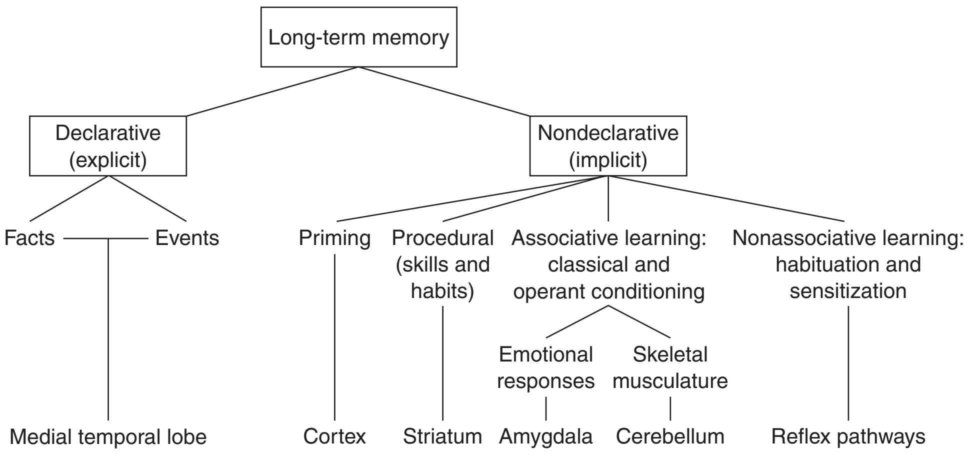


FIGURE 5–1 The organization of long-term memory

Forms of long-term memory can be classified as either declarative (explicit) or nondeclarative (implicit). Declarative and nondeclarative memory depend on different brain regions.

(Kandel, E. R., Kupferman, I., and Iverson, S. 2000. Learning and Memory. In: E. R. Kandel, J. H. Schwartz, and T. M. Jessell (eds.) *Principles of Neural Science,* pp. 1227–1246. New York: McGraw-Hill, Fig. 62-4. Reprinted with permission.)

He defined semantic memory as knowledge about words and concepts, their properties, and interrelations (Tulving, 1972). We are aware of the contents of both kinds of memory, but a difference between them is context, or the lack thereof. Episodic memory, which supports memory for individual life events, has a context: when you recollected details about one of the people you met in the hall—her political views, her tastes in cuisine—you engaged in a kind of "mental time travel" to your earlier meeting, and you were aware that the information you possessed about her was bound to that particular autobiographical experience. But when you retrieve your semantic memory of, say, the main ingredients of Italian cuisine, that memory is not bound to the specific context in which you acquired that knowledge because you likely accumulated the knowledge across multiple experiences in a variety of contexts. Tests that assess declarative memory are termed **explicit memory tests** because they require the retrieval of an explicit description or report of knowledge from memory. Declarative memory is highly flexible, involving the association of multiple pieces of information into a unified memory representation; thus, we may have different routes to retrieval of a given memory. Both forms of declarative memory, episodic and semantic, depend on the operation of the medial temporal lobes.

Nondeclarative memory (also known as **implicit memory**) refers to nonconscious forms of long-term memory that are expressed as a change in behavior without any conscious recollection. Tests of nondeclarative memory—termed **implicit memory tests**—do not require description of the contents of memory, but rather reveal memory *implicitly* through observed changes in performance, such as the gradual acquisition of a motor skill. In comparison to declarative memory, nondeclarative memory tends to be more restricted in the ways that this knowledge can be retrieved. The various forms of nondeclarative memory do not depend on the medial temporal lobe structures that are important for declarative memory. Rather, the various forms of nondeclarative memory are implemented in different brain regions (see Figure 5–1).

1.2. The Power of Memory: The Story of H.M.

Much of the research describing and classifying types of long-term memory has a very human foundation in the experience of a patient known as H.M. The pattern of catastrophic memory deficits observed in this man initiated a revolution in our understanding of memory, revealing that our ability to encode and retrieve new episodic and semantic memories depends on a particular set of brain structures in the medial temporal lobes—the hippocampus and surrounding entorhinal, perirhinal, and parahippocampal cortices (Figure 5–2). The story of H.M. highlights the centrality of memory to our mental lives, and shines a spotlight on the powerful role the medial temporal lobes play in documenting our experiences.

When he was 7, H.M. had a bicycle accident that left him unconscious for 5 minutes. By the age of 10, he was suffering minor epileptic episodes that ultimately progressed to include major seizures. For more than a decade, H.M.'s life was increasingly disrupted by his constant seizures: he had to drop out of high school for a time and had to quit working while he was in his twenties. Because the seizures could

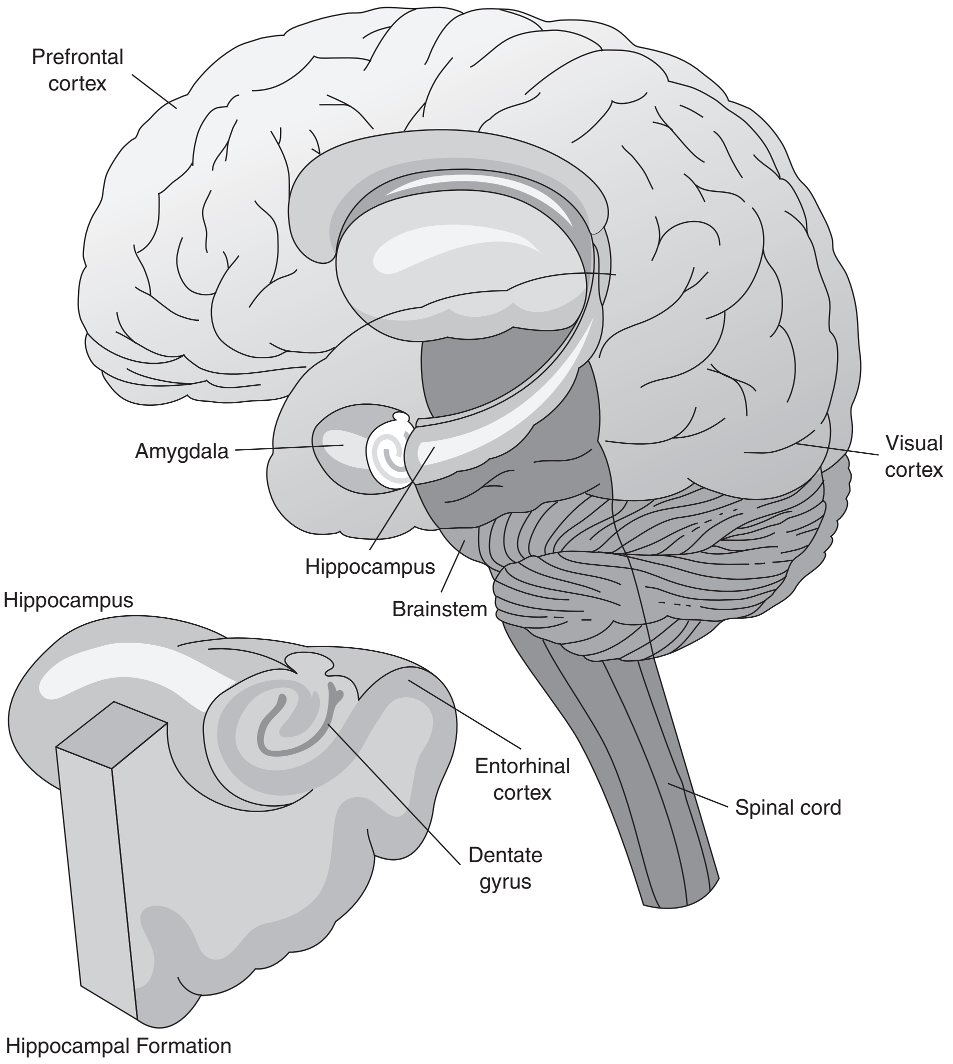


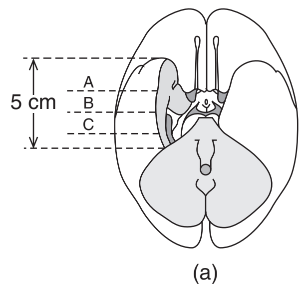
FIGURE 5–2 The medial temporal lobe structures of the human brain, which are critical for declarative memory

The hippocampus is a structure located deep in the medial portion of the temporal lobe. Information flows into the hippocampal formation from the surrounding medial temporal cortices, including the entorhinal cortex.

(From Squire, L. R. and E. R. Kandel. Memory: From *Mind to Molecules,* p. 111. © 2000 Larry R. Squire & Eric R. Kandel. Reprinted with permission of the authors.)

not be controlled by medication, at 27 H.M. underwent bilateral removal of the medial temporal lobes, thought to be the site where his seizures originated. The surgery excised the hippocampus, amygdala, and much of the surrounding medial temporal cortices (Figure 5–3). The surgery effectively brought H.M.'s seizures under control, but it was immediately clear that this positive outcome was accompanied by an unexpectedly devastating loss of memory (Corkin, 1984; Scoville & Milner, 1957).

Tests of H.M.'s cognitive abilities reveal that his deficit is highly specific, as his intelligence and some memory functions are relatively preserved. For example, when presented with a short list of numbers and asked to remember them for 30 seconds, H.M. performs as well as those with intact medial temporal lobes. This observation indicates that *working memory* (discussed in Chapter 6), information that is maintained over a period of seconds or minutes, does not depend on medial temporal lobe structures. H.M. also has preserved long-term memory for information acquired well before his operation. He remembers his name and former occupation, and he retains a command of language, including vocabulary, indicating a preservation of previously



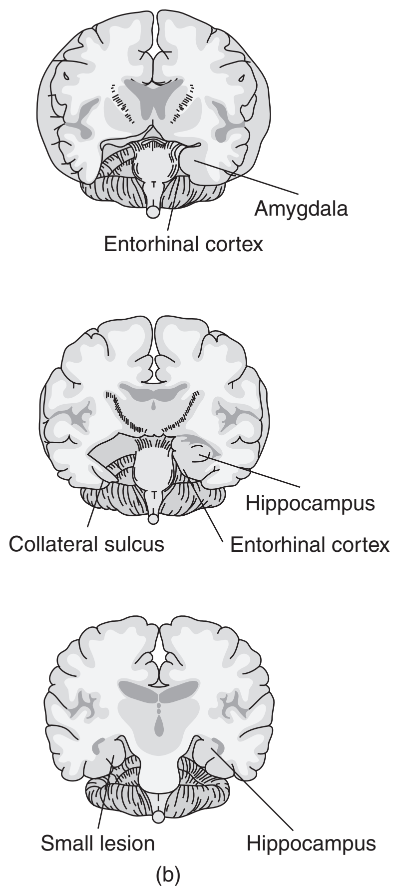


FIGURE 5–3 **H.M.'s medial temporal lobe surgery**

(a) A diagram of the brain, in ventral view (i.e., looking up from the bottom), showing the longitudinal extent of H.M.'s temporal lobe lesion. (b) Cross sections (seen from the front, with the locations of slices identified in panel a) showing the estimated extent of surgical removal of areas of H.M.'s brain. (Note the lack of brain tissue at the bottom left side, in fact the surgery was bilateral, but here the left side of the brain is shown intact to illustrate the structures that were removed.)

(Corkin, S., et al., 1997. H. M.'s medial temporal lobe lesion: findings from magnetic resonance imaging. *Journal of Neuroscience, 17,* 3964–3979.)

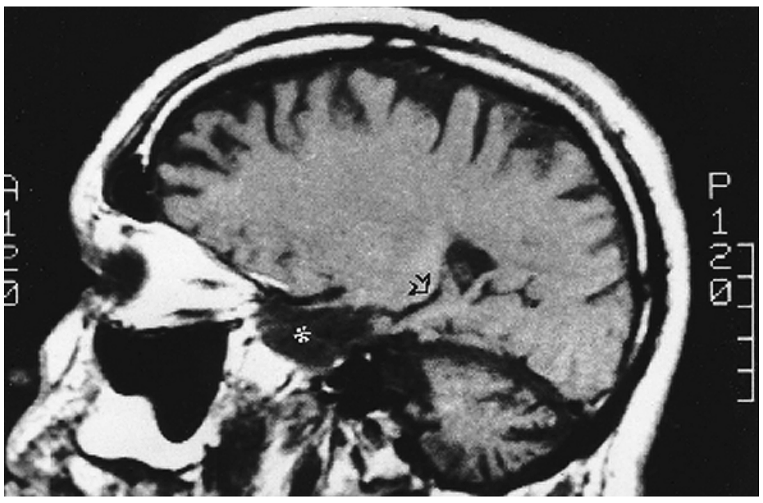


FIGURE 5–3 (contd.)

(c) An MRI scan of a parasagittal (i.e., seen from the side) section from the left side of H.M.'s brain. The resected, or removed, portion of the anterior temporal lobes is indicated by the asterisk. A remaining portion of the hippocampal formation is indicated by the open arrow.

(Corkin, S., Amaral, D. C., Gonzalez, R. C., Johnson, K. A., and Hyman, B. T. 1997. H.M.'s medial temporal lobe lesion: findings from magnetic resonance imaging. *Journal of Neuroscience*. Copyright © 1997 by the Society for Neuroscience. Reprinted by permission.)

acquired semantic memory. Remote episodic memories are also spared: he can recall childhood events in detail, including riding in a car with his parents when he had his first major seizure on his 16th birthday.

However, even though some memory functions are preserved, to this day H.M. suffers from a severe **anterograde amnesia**, the inability consciously to remember information encountered *after* brain damage. Thus, although H.M can briefly retain a short list of numbers (because his working memory is intact), he will immediately and completely forget them as soon as the information is lost from working memory. This catastrophic forgetting reveals an inability to form, retain, and retrieve new episodic memories. In essence, H.M. is frozen in time, and has been since the 1950s—he is unable to update his personal life narrative because of his inability to remember his daily experiences. H.M. himself has eloquently described this outcome:

> Right now, I'm wondering. Have I done or said anything amiss? You see, at this moment everything looks clear to me, but what happened just before? That's what worries me. It's like waking from a dream; I just don't remember (Milner, 1966).

Extensive testing indicates that H.M.'s anterograde amnesia is global; that is, he cannot consciously remember new events irrespective of their content or modality.

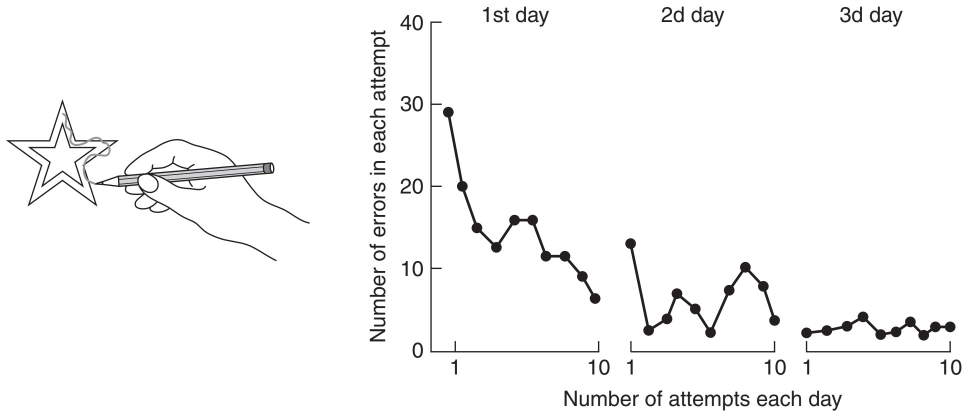
He cannot remember the people, places, and objects he sees, even after repeated encounters. He rapidly forgets both face-to-face conversations and songs heard on the radio, he cannot remember where he lives or who cares for him, and he even has difficulty recalling what he has eaten. It is clear that his amnesia does not reflect a perceptual deficit or a generalized impairment in intelligence; rather, H.M. suffers from a domain-general memory deficit. Moreover, H.M. has been unable to form new semantic memories following his surgery (an indication not appreciated until the late 1980s). Thus, when his semantic memory was tested for phrases such as "flower child" that had entered the language after his surgery but to which he had been repeatedly exposed, H.M. did not know their meanings (he guessed that "flower child" meant "a young person who grows flowers") (Gabrieli, Cohen, & Corkin, 1988). His anterograde amnesia applies to both episodic and semantic knowledge (O'Kane et al., 2004).

H.M. also demonstrates some **retrograde amnesia**, the forgetting of events that occurred *before* the damage to the brain. An important aspect of H.M.'s retrograde amnesia is that it is *temporally graded:* The closer an event had occurred to his surgery, the more likely it is to have been forgotten. In particular, he has greater difficulty remembering experiences that had occurred during the 11 years immediately preceding his surgery than in recalling more remote experiences from his childhood. This pattern of forgetting indicates that memories do not permanently depend on the medial temporal lobes; if this were the case, then even H.M.'s remote memories should have been forgotten. That remote memories were retained suggests that *over time* some process appears to lodge information in memory so that it remains even after medial temporal lobe damage. Nonetheless, the pattern of preserved working memory and impaired long-term memory following H.M.'s surgery is a powerful demonstration that the medial temporal lobes are critical for long-term memory (Squire, Stark, & Clark, 2004).

1.3. Multiple Memory Systems for Long-Term Learning and Remembering

The impact of the study of H.M. continued. Following the understanding that long-term memory depends on the medial temporal lobes, further tests of H.M.'s memory abilities initiated a second landmark insight into the organization of memory: the medial temporal lobes are not necessary for *all* types of long-term memory. Although suffering profound deficits of episodic and semantic memory after removal of his medial temporal lobes, H.M. nevertheless was able to form and retain other types of long-term memories.

The first evidence to this effect came in the 1960s with the observation that H.M. could acquire new motor skills at a normal rate, and that his level of long-term retention of these new skills was comparable to that of healthy controls (Milner, 1962). For example, H.M. was able to learn the skill of "mirror tracing." Given a picture of a star drawn with a double outline, H.M. was to draw a third outline of



(a)

(b)

FIGURE 5–4 **H.M. shows improvement on tasks involving the learning of skilled movements**

(a) The task: to trace between two outlines of a star while looking at his hand in a mirror. (b) The graphs plot, over three days, the number of times during each attempt that he strayed outside the outlines as he drew the star. As with neurologically healthy participants, H.M. improved considerably across the multiple attempts, but he had no conscious recollection that he had ever performed the task before.

(Adapted from Brenda Milner, Larry R. Squire, and Eric R. Kandel, Cognitive neuroscience and the study of memory, *Neuron* 20 (1998): 445–468, Fig. 2. Found in Squire, Larry R. and Eric R. Kandel. Memory: From Mind to Molecules. W.H. Freeman and Company, New York, 2000, pg. 13. Reprinted with permission from Elsevier.)

the star between the two already present—while looking only at the reflection of his hand and the star in a mirror (Figure 5–4). This task requires the remapping of visual perception onto motor actions because of the mirror-reversed nature of the visual input. Tested over a period of days, his improvement in performance—a measure of learning—was similar to that of participants with no memory deficit. H.M. became increasingly adept each day, tracing the star more quickly and more accurately, but at the outset of each day he had no conscious recollection of ever having done it before. These observations provided a clear demonstration that different kinds of long-term memory can be distinguished in amnesia.

The observation of intact skill learning following his surgery prompted careful reassessment of H.M.'s memory abilities, as well as those of other amnesic patients who suffered similar declarative memory deficits following damage to the medial temporal lobes. Investigations revealed that there is a whole class of long-term memories—now described as nondeclarative (implicit) memories—that operate outside awareness and that are preserved in the face of medial temporal lobe damage. For example, Warrington and Weiskrantz (1968, 1974) showed that amnesic patients could indirectly manifest evidence of recent learning in a perceptual domain. In their experiments, amnesic patients and controls were shown a list of words, such as ABSENT, INCOME, FILLY. Memory for the words was then tested.

However, instead of asking participants to recall or recognize the words on the list, Warrington and Weiskrantz instructed them simply to try to complete word beginnings (or "word stems"), taken from the original list, to make complete words (for example, ABS_____ could be completed to make either ABSENT or ABSTAIN). With these instructions, which made no explicit reference to the original list, both amnesic patients and controls were more likely to complete the word stems to make words that had been initially presented (ABSENT, not ABSTAIN). The presence of such a *priming* effect—which in this case is an increased likelihood of generating a particular response (for example, ABSENT) related to a stimulus previously presented—with amnesic patients was subsequently clarified. Graf and colleagues (1984) showed that amnesic patients demonstrate normal priming when the test instructions are to complete each word stem with the first word that comes to mind, but their performance is impaired when the instructions are to complete each stem by recalling a previously presented item.

Such reports of intact priming following medial temporal lobe damage indicate that the long-term memory capabilities of amnesic patients are not limited to motor skills such as mirror tracing. Amnesic patients are able to improve their performance on certain perceptual and conceptual tasks, even though they demonstrate deficient episodic memory for the earlier encounter with the material. Considerable evidence indicates that episodic memory and priming obey different underlying principles even in neurologically healthy people. We revisit such nondeclarative memory in more detail in the final section of this chapter.

Comprehension Check: ✓

1. What are the differences between declarative and nondeclarative memory?
2. What are the two forms of amnesia?

2. ENCODING: HOW EPISODIC MEMORIES ARE FORMED

Some of life's episodes, central or trivial, may be remembered so well that we can accurately bring back to mind tremendous detail, even after considerable time has elapsed—you remember with pleasure an Italian dinner you shared with the friend you just met again in the hall. Other experiences may be poorly remembered or, worse yet, irretrievably lost—what *is* that guy's name? He's not in my physics section, is he?

What determines whether an experience will be remembered or forgotten? Early experimental studies of human memory in the late 1800s investigated this puzzle. Research during the past century has demonstrated that a complete understanding of how memories are formed requires appreciation of the many cognitive and neurobiological processes that constitute the three stages of memory processing—encoding, consolidation (the modification of representations in memory so that they become stable), and retrieval—and the interactions among these different stages.

Encoding is the term used for the various processes by which information is transformed into a memory representation. These processes are set in motion at the time of the experience, forming a mental representation that records some aspect or aspects of it. All forms of memory, declarative and nondeclarative, begin with encoding. But because episodic memory records the unique history of each person's life, it seems a suitable starting point for our discussion of how encoding works.

One way to uncover the fundamental properties of encoding is to try to determine what strengthens the process. This approach has revealed that encoding is influenced by a number of factors, including the degree to which we attend to information and the extent to which we "elaborate" on its meaning. **Elaboration** involves interpreting information, connecting it with other information, and mulling it over. Other influences that strengthen encoding are conscious retrieval of the information, and practice that is "distributed," or spaced out, in time. As suggested by studies of patients with amnesia, the medial temporal lobes play a critical role in episodic encoding. Neuroimaging and clinical data also indicate that the frontal lobes contribute to attention and elaborative processing and thus affect encoding.

2.1. The Importance of Attention

You're not alone if you've said things like "Where did I put my glasses?" or "Tell me *again* the name of the new teaching assistant!" This kind of forgetting of everyday events is not likely to be either an indication of a poor memory or a harbinger of decline with age. Many instances of forgetting are simply the natural consequences of ineffective encoding of an experience into episodic memory in the first place.

One of the more obvious and consequential reasons for poor encoding is failure to attend to an event while it is happening. When your attention to information is divided, for example because you are distracted, encoding is weaker and later attempts to remember are likely to fail. You may have forgotten where you put your glasses because you're still trying to remember the name of the physics student you saw in the hall. And you may have forgotten his name because when you met the first time your attention was focused on the impending physics exam.

The role of attention in encoding has been explored in the laboratory. In one set of experiments (Craik et al., 1996) participants were instructed to try to remember 15 auditorily presented words under one of two conditions. In the *full-attention* condition, participants were not given any task other than to try to remember the words. In the *divided-attention* condition, during word presentation participants were also instructed to monitor the position of an asterisk on a computer screen and press one of four buttons as the location changed. Participants remembered on average 9 of the 15 words when encoding was performed under full attention, but only 5 words when encoding was performed along with the secondary task. Many other experiments have revealed equally compelling evidence that attention is necessary for effective encoding.

Neuroimaging studies indicate that the pattern of neural activation during encoding under conditions of full attention differs from that when attention is divided. In one study, the brains of participants were scanned, using PET, while these people tried to encode category–exemplar pairs (for example, POET–BROWNING) (Shallice et al., 1994). This encoding was conducted while participants performed either an "easy" or a "difficult" secondary task, with "easy" defined as "requiring less attention." There were two significant findings. First, the behavioral performance of the "easy task" group was better than that of the "difficult task" group. Second, the brain images showed that regions in the left frontal lobe were more active when encoding was accompanied by the easy secondary task, indicating that the frontal lobes support the ability to attend during learning, and in so doing, affect episodic encoding (Uncapher & Rugg, 2005).

2.2. Levels of Processing and Elaborative Encoding

Evidence that attention is central to encoding might seem to suggest the conclusion that *intent* is required for effective memory formation. But not so fast: although intent to encode can motivate attention, intention per se is not required for effective encoding. Encoding is an automatic by-product of attending to and processing a stimulus (Craik & Lockhart, 1972). What influences encoding efficacy is the way the stimulus is processed, not the reason that processing was performed.

2.2.1. Levels-of-Processing Theory: Argument and Limitations

Consider the various kinds of cognitive operations you could perform when meeting someone for the first time. Looking at that person's face, you might observe some aspect of the structure of its appearance. Or you might note the phonology—the speech sounds—of the person's name. Or you might *elaborate* on conceptual details you learn at this first meeting, a political viewpoint, for example, relating it to your own. In this sense, elaboration consists of generating additional information.

Levels-of-processing theory draws on the fact that there are various aspects of any given stimulus that can be attended and processed. In this view, encoding is seen as a direct by-product of stimulus processing, the processing of particular aspects of a stimulus leaving a corresponding residue in the system that can guide later remembering. Different aspects of stimulus processing are thought to correspond to different levels of analysis that range from a "shallow" or superficial level of perceptual analysis to a "deep" (i.e., elaborative level) of semantic (i.e., meaning-based) analysis that actively relates incoming information to knowledge already stored in memory (Figure 5–5).

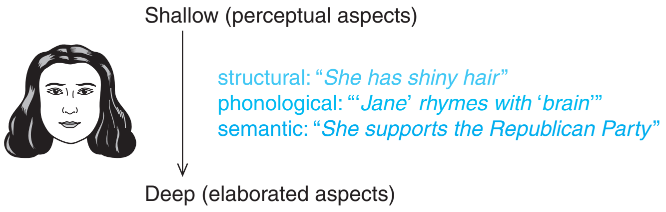


FIGURE 5–5 Levels of processing illustrated

According to levels-of-processing theory, different aspects of stimulus processing are thought to correspond to different levels of analysis, ranging from a "shallow" level of perceptual analysis to a "deep" level of semantic analysis.

According to the theory, encoding efficacy heavily depends on the level of processing performed on a stimulus, with deeper processing producing a stronger, more durable representation and thus increasing the likelihood that the stimulus will be remembered.

Many behavioral studies have supported the hypothesis that episodic memory benefits from "deep" (i.e., elaborative) processing. In one of these studies (Craik & Tulving, 1975), participants viewed words and made one of three decisions about each word. For some words, participants were to say whether the words were in uppercase or lowercase letters—a "shallow" structural condition. For a second set of words, participants were asked whether each rhymed with a target word—an "intermediate" phonological condition. For words in a third set, participants were to decide whether each was a member of a particular category—a "deep" semantic condition. Consistent with the levels-of-processing hypothesis, a later memory test revealed that the percentage of words from each set that was subsequently recognized as having been studied differed markedly for the three sets: 78 percent of the words were recognized following "deep" encoding, 57 percent following "intermediate" encoding, and just 16 percent following "shallow" encoding. Episodic memory substantially benefits from elaboration of the meaning of a stimulus or event at the time it is encountered. Levels-of-processing theory suggests that the stimuli and events that we are likely to remember best are those that we actively process for meaning. Your recollection of meeting someone who also grew up in Des Moines, likes the same kind of food you do, and is a supporter of the Republican party is clear and detailed because of the elaboration provided by links to other representations of information already in memory and shared in conversation.

As in the Craik and Tulving (1975) experiment, most studies testing levels-of-processing theory have used instructions that reveal **incidental learning**, learning that occurs not as the result of a purposeful attempt but as a by-product of performing a task. In these instructions participants are not explicitly directed to learn, but rather are asked to perform a particular task with stimuli. Because participants are unaware that memory for the stimuli will be tested, they do not intentionally try to learn, and learning is incidental to performance of the task. The phenomenon of incidental learning helps us understand just how it is that we can remember our everyday experiences, which, after all, we don't usually deliberately attempt to encode into memory. It is unlikely that you tried to encode your meeting with your political bedfellow when it first occurred. Nonetheless, you do remember it, because encoding occurs whenever we process or attend to a stimulus or event while it occurs. (You didn't try to encode your first meeting with the physics student, either—but more to the point, you didn't particularly attend to it, so the encounter left only a weak memory, and you had difficulty remembering the event.)

Levels-of-processing theory has provided much insight into the processes that lead to episodic encoding, and thus it has considerable explanatory power. But the theory has a number of limitations. For example, as Shakespeare put it in another context, "Who hath measured the ground?" There is no way of measuring the "depth" or quantifying the "level" of processing required by a particular encoding task other than its impact on memory. The lack of an independent measure of depth makes it difficult to test the theory.

A more central question concerns interpretation: do levels-of-processing effects reflect differences in the strength and durability of encoding, or differences in which aspects of a stimulus are selected for encoding and the correspondence between the kind of processing performed at encoding and that performed at retrieval? Some investigators believe that the question is not one of level but of match between what is encoded and what is tested at retrieval. If retrieval demands recovery of semantic details about a past experience, then semantic processing at encoding will be more effective because it increases the likelihood that semantic aspects of the stimulus or event will be stored in memory; but if retrieval demands recovery of perceptual details, then perceptual processing at encoding will be more effective for the complementary reason. This principle—that processing at encoding is most effective to the extent that that processing overlaps with the processing to be performed at retrieval—is known as **transfer appropriate processing** (Morris et al., 1977).

In an important study testing the levels-of-processing and transfer-appropriate-processing perspectives, Morris and colleagues (1977) had participants encode words by making a rhyme decision or a semantic decision about each word. During retrieval, memory was probed in one of two ways. A task requiring recognition of words that had been previously studied revealed the standard levels-of-processing effect (superior memory following semantic encoding). By contrast, a task requiring recognition of words that rhymed with previously studied words revealed superior memory following rhyme encoding. The level of processing does not necessarily affect the strength or durability of the encoded memory, but rather influences *what* is encoded. Encoding processes yield superior memory to the degree that the features attended and processed during encoding overlap with those being sought at retrieval. For a more detailed discussion of this landmark work, see the accompanying *A Closer Look* box.

A related idea, proposed by Tulving and Thompson (1973) and referred to as the **encoding specificity principle**, states that our ability to remember a stimulus depends on the similarity between the way the stimulus is processed at encoding and the way it is processed at test. For example, if the word *bank* is interpreted as meaning "the side of a river" rather than "a financial institution" at encoding, then remembering will be superior if at retrieval *bank* is interpreted as "the side of a river."

2.2.2. The Brain, Semantic Elaboration, and Episodic Encoding

Because semantic processing tends to yield higher levels of memory performance (on standard tests) than does nonsemantic processing, it is reasonable to ask whether brain regions that are more active during semantic processing tasks are regions that support encoding processes that influence learning. A series of studies measured brain activity of participants while they encoded words under semantic or perceptual processing conditions (Gabrieli et al., 1996; Kapur et al, 1994; Wagner et al., 1998;

A CLOSER LOOK

Transfer Appropriate Processing

We consider the landmark work of C. D. Morris, J. D. Bransford, and J. J. Franks, reported in a 1977 paper titled "Levels of Processing versus Transfer Appropriate Processing," *Journal of Verbal Learning and Verbal Behavior, 16,* 519–533.

Introduction

The investigators hypothesize that the level of processing at encoding does not influence later memory performance in isolation, but rather later memory depends, at least in part, on the overlap between the processing engaged at encoding and at retrieval. Put another way, transfer appropriate processing proposes an interaction between encoding and retrieval, leading to the prediction that memory performance will be better when encoding processing overlaps with (and thus transfers to) retrieval processing.

Method

The investigators tested their hypothesis by examining the memory performance of undergraduate participants, using an experimental design that combined two encoding tasks (*semantic* and *rhyme*) with two retrieval tasks (*standard recognition* and *rhyming recognition*).

All participants studied 32 target words embedded in sentences. For all words, a sentence was initially read aloud by the experimenter, with the target word missing from the sentence (for example, "The _____ had a silver engine."). Following each sentence, a target word was presented to the participant, who had to decide whether the word fit the sentence. There were two types of sentences, *semantic* and *rhyme,* with 16 words studied in each type. For semantic sentences, participants had to decide whether the target word was semantically consistent or inconsistent with the sentence (TRAIN would be consistent with the example sentence, whereas APPLE would not be). For rhyming sentences (for example, "_____ rhymes with legal"), participants had to decide whether the target word was phonologically consistent (EAGLE) or inconsistent (CHAIR).

Following encoding of the 32 target words, memory was tested using either a *standard recognition* test or a *rhyme recognition* test; half the participants received the standard and half received the rhyme test. In the standard test, the 32 target words and 32 unstudied words were presented one at a time in a random order. Participants responded "yes" if they recognized the test word as having been studied, and "no" if they did not. In the rhyme test, participants were presented a random ordering of words that rhymed with the studied words and unstudied words that did not. Participants responded "yes" if they recognized the test word as rhyming with a studied word, and "no" if they did not.

By having two study conditions and two test types, the experimental design resulted in four critical conditions that combined encoding (semantic/rhyme) and test (standard/rhyme): semantic + standard test, semantic + rhyme test, rhyme + standard test, rhyme + rhyme test.

Results

The data of interest are the percentage of test trials on which participants correctly recognized either studied words (standard test) or rhymes of studied words (rhyme test), correcting for erroneous responses to unstudied words or to nonrhymes of studied words. The analysis focuses on memory for items that were consistent with the sentence context at encoding, and the key question is how performance varied across the four critical encoding + test conditions. The results are plotted in the following table:

	Standard Test	Rhyme Test
Semantic encoding mode	84%	33%
Rhyme encoding mode	63%	49%

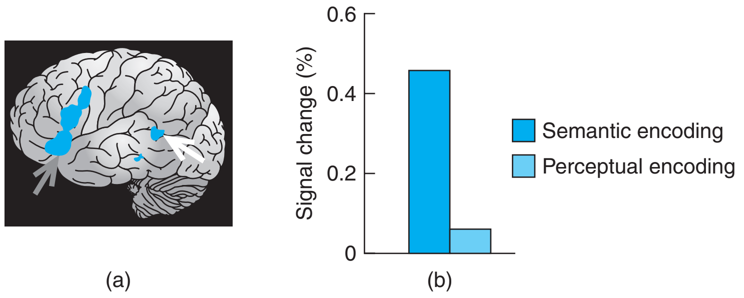
These data reveal a striking interaction: when memory is probed using the standard test, performance is clearly better following semantic than following rhyme encoding, whereas when memory is probed using the rhyme test, performance is clearly better following rhyme than following semantic encoding.

Discussion

The transfer-appropriate-processing hypothesis is supported by the observed interaction: processing at encoding is particularly effective to the extent that it overlaps with processing at retrieval. These data support the interpretation that level of processing does not influence encoding strength per se, but rather influences what is encoded. When processing at study fosters encoding of information that will be desired at retrieval, then that processing will be particularly effective in enhancing later memory performance.

2005). Greater activation in the left inferior frontal lobe was observed during semantic compared to perceptual processing, and a similar pattern was observed in the left lateral and medial temporal lobes (Figure 5–6).

An interesting correspondence suggests itself. We know from the studies involving "easy" and "difficult" secondary tasks that divided attention diminishes left frontal lobe activation and episodic encoding during **intentional learning**, learning that occurs as the result of a purposeful attempt (Shallice et al., 1994). We also know that during *incidental learning* left frontal lobe activation is diminished at shallower levels of processing. This overlap of brain regions engaged during intentional and



(a) (b)

FIGURE 5–6 Brain activation in perceptual and in semantic processing

(a) The left inferior frontal cortex (*gray arrow*) and left lateral temporal cortex (*white arrow*) are active when we attend to and elaborate on the meaning of stimuli.

(Wagner et al. (2001). Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron,* 31, 329–338 (Fig. 3b). Reprinted with permission from Elsevier.)

(b) When data are plotted, the graph shows that left frontal activation (expressed as signal change) is greater during semantic than during perceptual processing of words.

(Wagner et al. (2000). Task-specific repetition priming in left inferior prefrontal cortex. *Cerebral Cortex,* 10, 1176–1184. Reprinted with permission of Oxford University Press.)

incidental learning is consistent with the idea that intention per se does not determine learning. Rather, intentional learning affects encoding to the extent that it motivates elaboration and thus leads to processing at a deeper level.

To assess more precisely how experienced events are transformed into memories, researchers have sought to obtain tighter links between memory behavior and brain activity. A particularly powerful approach measures brain activity at encoding and correlates the results with participants' later successful or unsuccessful recollection. The key contrast is between neural responses during the encoding of events that are later remembered and neural responses during the encoding of events later forgotten. By identifying brain activity at the moment when memories are born, this method reveals neural responses that predict the mnemonic fate of an experience—that is, whether it will be remembered or forgotten.

A functional magnetic resonance imaging (fMRI) study using this approach scanned participants while they made semantic judgments about a series of words (Wagner et al., 1998). Participants' memory for the words was later tested and correlated with the fMRI encoding data. Analysis revealed greater activation in the left inferior frontal and medial temporal lobes during the encoding of words that were later remembered compared to words that were later forgotten (see Figure 5–7 on Color Insert C). Further, the regions predicting subsequent memory were those previously identified as showing a levels-of-processing effect. A related study of visual learning (Brewer et al., 1998) revealed a similar pattern, but this time in the right frontal lobe and both medial temporal lobes. These data indicate that greater engagement of frontal lobe attentional mechanisms increases encoding efficacy, with the left frontal lobe supporting the encoding of words and the right frontal lobe the encoding of nonverbal stimuli. These frontal lobe attentional processes appear to interact with medial temporal lobe learning mechanisms during effective learning.

2.3. Enhancers of Encoding: Generation and Spacing

The circumstances of the initial encounter with information influence the strength of encoding, as we have seen: it makes a difference if you're paying attention, it makes a difference if, at the time, you elaborate. Research has also uncovered other factors that enhance the strength of the encoded representation. One way makes use of the *generation effect,* where episodic learning is better if we can generate the target information from memory compared to when the information is presented to us by another person. The other employs the *spacing effect,* where encoding across multiple study trials with the same information is optimal following a particular pattern of temporal sequencing of the study trials.

2.3.1. The Generation Effect

Flashcards. You may have used them in elementary school: 9 × 7 = ? on one side of the card, 63 on the other. Medical students use them to learn diagnostic symptoms, chemistry students use them to learn the formulas of compounds and alloys, language students use them to learn vocabulary. Formula on one side of the card, compound name on the other. And rather boring they are.

But the flashcard approach to learning is a highly effective way to learn, and there is an important reason why: the act of retrieving or generating information from memory is a powerful enhancer of encoding. "Generating" here does not mean "creating;" rather, it emphasizes the idea of active production of the information rather than passive study.

The term generation effect describes the observed phenomenon that you are more likely to remember information you retrieve or generate (during study) than information that you simply receive and attempt to "memorize." Thus you are more likely to remember the 12 cranial nerves from flashcards, which demand action on your part, than from studying a list. The effect is an experimental demonstration of the generally accepted idea that we often learn best by doing.

The generation effect was first described following an experiment (Slamecka & Graf, 1978) in which participants learned word pairs in one of two ways. In the "read" condition, word pairs were presented and participants decided whether the second word was a synonym of the first (as in UNHAPPY–SAD) or a rhyme of it (as in PAD–SAD). In the second learning task—the "generate" condition—participants were to generate a synonym (from, say, UNHAPPY–S_____) or a rhyme (from, say, PAD–S_____). Following learning, when participants were tested for memory of the second word (given the first word as a cue), two effects were revealed. Memory was better after semantic encoding, which depended on the meaning of the words, than after phonological encoding, which considered only their sound; this was a levels-of-processing effect. Further, overall memory was better when participants were asked to generate the second word themselves than when this word was presented by the experimenter and they had simply to read it (Figure 5–8).

Generating information from memory is thought to be a more powerful encoding event than merely processing externally presented information because both elaboration and greater attention are required for generation. Support for this interpretation comes from neuroimaging experiments, which have demonstrated that the left frontal lobe region, which shows a levels-of-processing effect, is also more active when generating than when reading words (Petersen et al., 1988). Transfer appropriate processing further suggests that generation is a particularly effective way to learn because the processes that are engaged during the initial generation at encoding are likely to overlap with those required to generate the information from memory at retrieval.

2.3.2. The Spacing Effect

Should you go over and over an idiom translation, or a chemical formula, flipping the card over and back time after time, and only eventually move on to the next item to be learned? Or should you go through a number of cards, and then go through them all again? The first approach, in which many trials with the same stimulus are undertaken without interruption, is known as massed practice; the second, in which the trials with the same stimulus are separated by other stimuli, as distributed practice. Which is more effective for learning?

READ conditions:	
Synonym	UNHAPPY–SAD
Rhyme	PAD–SAD
GENERATE conditions:	
Synonym	UNHAPPY–S____
Rhyme	PAD–S____

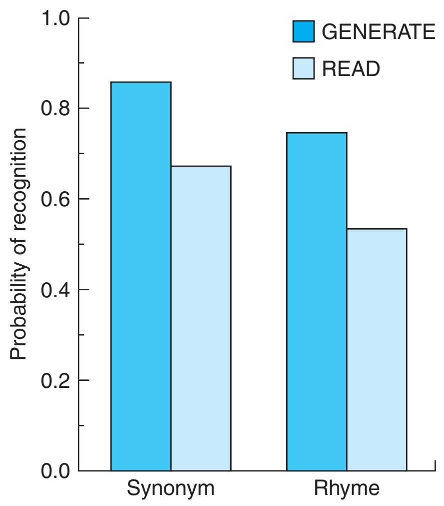


FIGURE 5–8 The effects of generation and processing level

Participants studied words by either reading presented words or generating words in response to a cue. In both the READ and GENERATE tasks, words were processed for meaning (synonym) or phonology (rhyme). As shown in the graph, the probability of later remembering the studied words was facilitated both by generation and by a deeper level of processing (synonym as opposed to rhyme, which was appropriate for the type of test).

(Slamecka, N. J., and Graf, P. The generation effect: Delineation of a phenomenon, *Journal of Experimental Psychology: Human Learning and Memory* 4 (1978): Fig. 2, p. 595 (adapted) from Exp. 2. Found in: Anderson, John R., Cognitive Psychology and its Implications (4th ed.). W.W. Freeman and Company, New York, 1995, p. 192. Copyright © 1978 American Psychological Association. Adapted with permission.)

The German psychologist Hermann Ebbinghaus (1850–1909), whose work laid the foundations for modern experimental investigation of mental processes and particularly memory, was the first to study the effects of massed vs. distributed practice (Ebbinghaus, 1885/1964). In his pioneering experiments, he taught himself meaningless consonant–vowel–consonant syllables (such as WUG, PEV, RIC), using massed practice learning for some items and distributed practice for others. A later test of his memory revealed a **spacing effect**: that is, as Ebbinghaus himself put it, "with any considerable number of repetitions a suitable distribution of them over a space of time is decidedly more advantageous than the massing of them at a single time" (p. 89). So a word to the wise: for more effective encoding, go for distributed practice.

There are a number of reasons for the spacing effect. An obvious one is that when study trials are massed together, we are less likely to attend fully to each presentation. Rather, with each subsequent presentation we are likely to be deluded into thinking we've learned the item, and therefore allocate increasingly less attention to it. Moreover, when trials are spaced, the context in which the stimulus is processed is likely to have changed to a greater degree than in massed practice. The result is a richer memory representation and additional retrieval routes back to the memory. That is, the processing performed for the initial encounter and for repeated trials in massed practice is likely to be highly similar. Distributed practice, on the other hand, fosters greater **encoding variability**, the encoding of different aspects of a stimulus as different features are selected for encoding in subsequent encounters. A stimulus is more likely to be remembered when it is processed in different ways across study trials.

2.4. Episodic Encoding, Binding, and the Medial Temporal Lobe

Encoding information into episodic memory involves attention and elaboration, which rely on the frontal lobes. Damage to the frontal lobes generally impairs episodic memory (Shimamura, 1995) because these cognitive processes are affected. These deficits are modest, however, compared with those resulting from damage to the medial temporal lobes, such as that suffered by H.M. Densely amnesic patients, such as H.M., are as it were "stuck in time" because they are unable to form new episodic memories.

The hallmark of episodic encoding is the binding together of the various features of a stimulus or event into an integrated memory representation (Tulving, 1983). When you first met the people you later encountered in the hall, you encoded various characteristics of each of them (with different degrees of success, for the reasons we've discussed). Perceptual aspects of visual appearance and sound of voice, the spatial and temporal context, phonological encoding of names, and the semantics of your conversation: each was processed by a different neural network in the brain. But in the same way that perception of an apple requires the binding together of disparate features (green color, round shape, sharp smell), memory of a life experience requires the binding together of the disparate elements that make it up: the people and things you encounter, the place and time in which these things are encountered, your thoughts during the encounter. And here is the crux of the problem: how does this binding occur?

The answer lies, literally, in the medial temporal lobe, the area excised in H.M.'s surgery (Squire et al., 2004). This region has been shown to be a convergence zone (a notion discussed in Chapter 4), that is, a region that receives highly processed input from many brain areas (Lavenex & Amaral, 2000; Suzuki & Amaral, 1994) (Figure 5–9). Information about a face, a name, and the context converges on the medial temporal lobe, and this region—in particular, the hippocampus—binds these multiple features into an integrated memory representation (Figure 5–10). Frontal lobe activity involved in attention and elaboration modulates encoding by favoring the processing of particular features, enhancing their input into the medial temporal lobe, and thus increasing the likelihood that those features are bound into the episodic memory representation. But this binding no longer can happen in H.M.'s brain, and he is left without the ability to construct episodic memories.

The anterograde amnesia that follows bilateral medial temporal lobe damage provides critical evidence that this region is necessary for episodic memory. Unilateral medial temporal lobe lesions also produce a deficit in episodic memory,

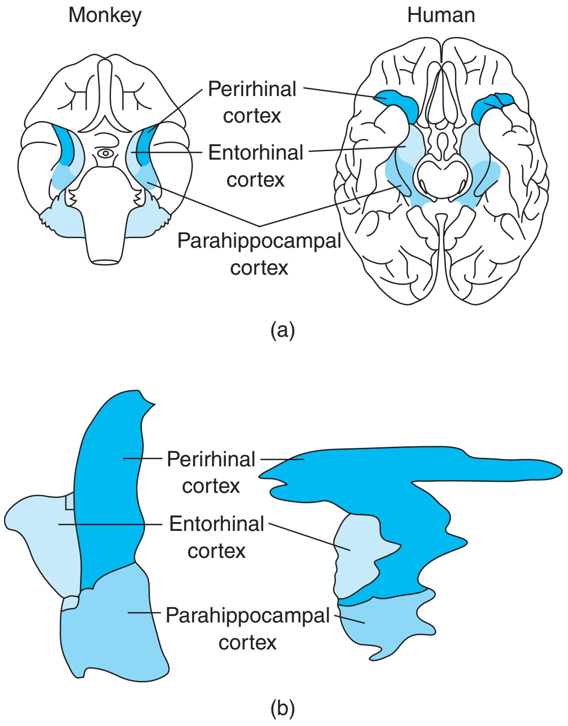


FIGURE 5–9 The medial temporal lobe memory system

(a) Ventral views (i.e., seen from the bottom, looking up) of the monkey and human brain show the borders of the entorhinal, perirhinal, and parahippocampal cortices.

(From R. D. Burwell, W. A. Suzuki, R. Insausti, and D. G. Amaral. Some observations on the perirhinal and parahippocampal cortices in the rat, monkey and human brains. In *Perception, Memory and Emotion: Frontiers in Neuroscience,* edited by T. Ono, B. L. McNaughton, S. Molotchnikoff, E. T. Rolls and H. Hishijo. Elsevier UK, 1996, 95–110, Fig. 1. Reprinted with permission from Elsevier.)

(b) Unfolded two-dimensional maps of these cortical areas, which, together with the hippocampal formation, make up the medial temporal lobe memory system on which declarative memory depends. (The brains are not drawn to scale.) The pathways into and out of the medial temporal lobe memory system are believed to be important in the transition from perception to memory.

(From Squire, L. R. and E. R. Kandel. Memory: From Mind to Molecules, p. 111. Originally appeared in Squire L. R., Lindenlaub, E. *The Biology of Memory*. Stuttgart, New York: Schattauer, 1990; 648. Reprinted with permission.)

although of lesser magnitude. Behavioral studies of patients with unilateral lesions indicate that there are hemispheric differences in medial temporal lobe function: lesions of the right hippocampus give rise to greater deficits in nonverbal episodic memory, whereas lesions of the left hippocampus give rise to greater deficits in verbal episodic memory (Milner, 1972). Neuroimaging studies of medial temporal lobe activation in neurologically healthy people have provided convergent evidence: right hippocampal activation is greater during the encoding of unfamiliar faces, whereas left

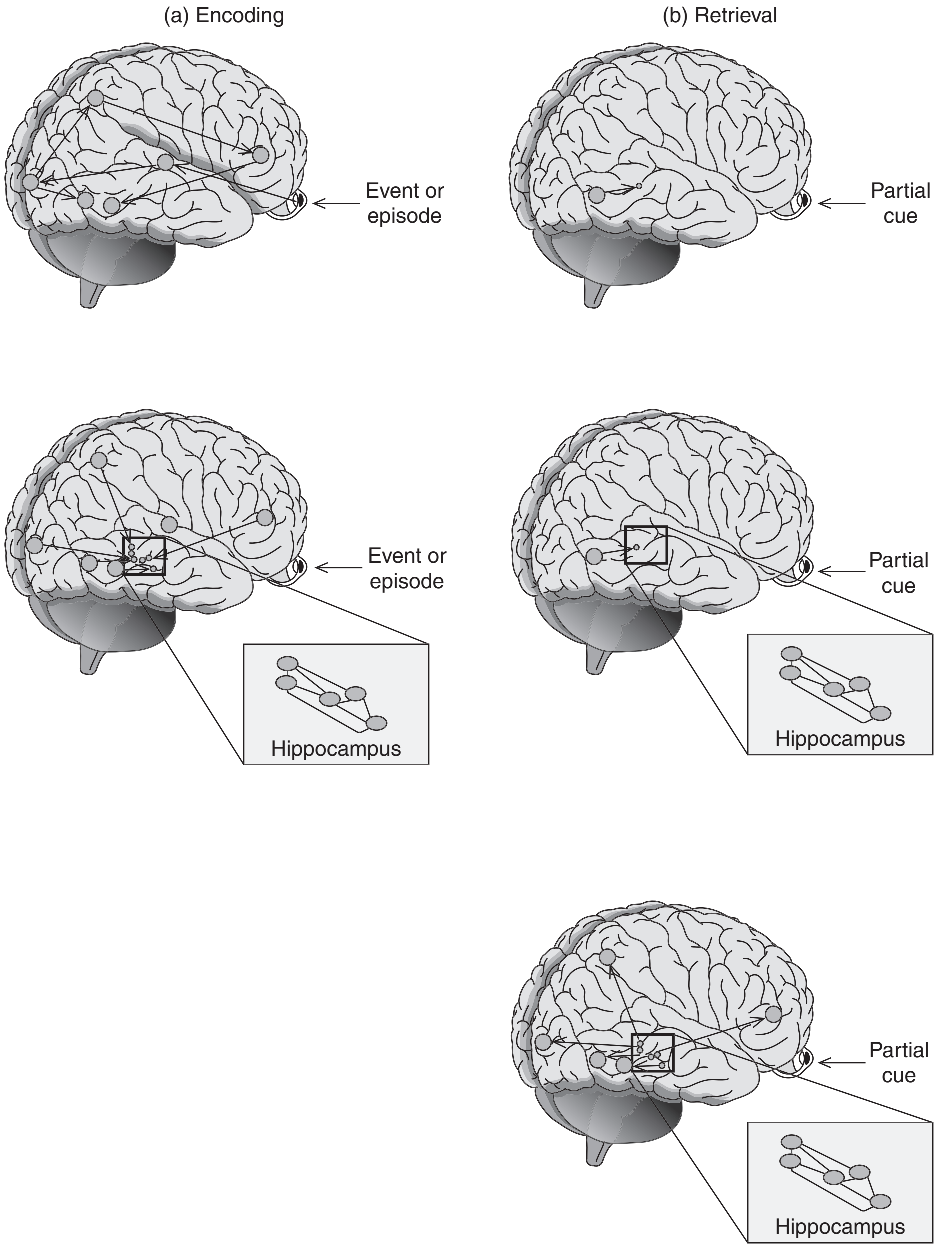


FIGURE 5–10 How the medial temporal lobe contributes to episodic encoding and retrieval

(a) During encoding, aspects of the stimulus or event are processed in different lateral cortical processing areas (*top*). These pieces of information converge on hippocampal neurons, and activated hippocampal neurons are bound together (*bottom*). (b) During retrieval, cues typically hold partial information about a past stimulus or event (*top*). As this partial information converges on the medial temporal lobe, it may trigger pattern completion in the hippocampus (*middle*). This medial temporal lobe process is thought to result in reactivation of information in lateral cortex (*bottom*).

hippocampal activation is greater during the encoding of words (Figure 5–11 on Color Insert D) (Kelley et al., 1998; Powell et al; 2005). Although such conclusions are well documented, it should be emphasized that the verbal and nonverbal mental representations are ultimately bound together within the medial temporal lobes, perhaps partially through cross-hemisphere interactions.

2.5. Consolidation: The Fixing of Memory

Encoded episodic memories undergo **consolidation**, a process that modifies these representations such that they become more stable over time and ultimately exist independently of the medial temporal lobes. Evidence for consolidation comes from the observation that H.M.'s, and other amnesic patients', retrograde amnesia is temporally graded: following removal of the medial temporal lobes, H.M. could still recall childhood memories, but he had difficulty remembering events that happened during the years immediately preceding the surgery. The preservation of his remote episodic memories implies that older memories are not stored in the medial temporal lobe—otherwise, those memories would have been lost following medial temporal damage. Rather, interactions between the medial temporal lobe and various lateral cortical regions are thought to store memories outside the medial temporal lobes by slowly forming direct links between the cortical representations of the experience (thus obviating the need for the bound representation in the medial temporal lobe). One hypothesis is that memory consolidation in cortex occurs through a process of reinstatement or recapitulation, wherein during sleep and during remembering the medial temporal lobe recapitulates the pattern of activation present during learning, thus strengthening the direct connections across the relevant lateral cortical regions (McClelland et al., 1995; Wilson and McNaughton, 1994). Thus the medial temporal lobes are necessary for retrieving unconsolidated memories but, once consolidated, memories can be retrieved directly from lateral cortical regions (McGaugh, 2000; Squire, 1992).

✓ Comprehension Check:

1. What are the major factors that affect encoding efficacy?
2. How does the medial temporal lobe support encoding and consolidation?

3. RETRIEVAL: HOW WE RECALL THE PAST FROM EPISODIC MEMORY

Our individual remembrances of times past depend on episodic retrieval, the processes by which stored memory traces are subsequently reactivated. It is the phenomenon of retrieval that produces the subjective experience of consciously remembering the past. Episodic retrieval depends on medial temporal lobe processes that support pattern completion, and frontal lobe processes that support strategic retrieval mechanisms.

3.1. Pattern Completion and Recapitulation

Episodic retrieval is a powerful cognitive event that transforms our current mental state such that the present makes contact with and reinstates aspects of the past. Before you unexpectedly saw those people in the hall, it's perfectly likely you weren't thinking about either of them. For reasons we've discussed, you didn't remember one of them very well at all. But simply upon perceiving the face of the other person, your mental state was transformed. The sight of her face was a *cue* that initiated a cascade of processes that brought back to mind a host of details about your earlier encounter. Moreover, you were aware that these retrieved details pertained to a particular moment in your personal past. In essence, it is as if episodic retrieval launched you back in time, to an earlier moment in your life (Tulving, 1983).

How does a retrieval cue—such as the appearance of a face—serve to bring back details about the past? Episodic memories are encoded by binding together the various features of a stimulus or event into an integrated representation, so an episodic memory consists of a conjunction of linked features. Why is this important to retrieval? For two reasons: (1) because any of those features is a possible route to the memory, multiplying the "ways in" to recollection, and (2) because it means we have access to our memories even when we have limited information. When a retrieval cue that corresponds to part of the encoded information, such as sight of a particular face, homes in on the stored representation, other features bound to the representation—a name, a restaurant sign, a conversation—are reactivated (see Figure 5–10). Because in this way a whole is built from linked parts, this retrieval process is known as **pattern completion** (McClelland et al., 1995; Nakazawa et al., 2002).

Perhaps not surprisingly in view of their role in integrating features, the medial temporal lobes are critical for pattern completion (at least for unconsolidated memories). Unconsolidated episodic memories are stored at least in part in the medial temporal lobes, and retrieval of these memories depends on the function of the medial temporal lobe circuit. Neuroimaging studies in neurologically healthy humans have provided evidence for a role of the medial temporal lobes in episodic retrieval. For example, it has been demonstrated that the hippocampus is active during retrieval attempts that yield successful recollection of contextual or event details, but not during attempts that result in retrieval failure (Eldridge et al., 2000).

The notion that episodic retrieval depends on pattern completion has led to the additional hypothesis that retrieval entails **recapitulation**, a reinstatement of the pattern of activations that was present during encoding. Recapitulation is a reversal of the direction of information processing between lateral cortex (where disparate types of information are processed) and the hippocampus (where this information is integrated). During encoding, cortical processing provides inputs to the hippocampus, which binds the inputs into an integrated memory. In retrieval, a partial cue to the hippocampus triggers pattern completion, and the hippocampus projects back to cortical areas and replays the pattern of activation that was present during encoding (see Figure 5–10). (This is similar to the notion of simulation discussed in Chapter 4.)

The pattern completion and recapitulation hypotheses make two predictions. First, if pattern completion occurs in the medial temporal lobes and serves to recapitulate activation patterns, redirecting them to the lateral cortices, then medial temporal lobe retrieval activation should precede the recovery of episodic knowledge. Such retrieval signals preceding knowledge recovery in lateral cortical neurons have been observed in nonhuman primates (Naya et al., 2001). Further, it has been demonstrated that medial temporal lobe lesions in nonhuman primates eliminate cortical knowledge recovery, indicating that medial temporal processes precede and are necessary for reactivating cortical representations (Higuchi & Miyashita, 1996).

The second prediction is that, if episodic retrieval in fact entails the recapitulation of representations that were present during encoding, the pattern of cortical activation during retrieval should resemble that seen at the time of encoding. Neuroimaging studies with human participants have shown patterns of activation in visual and auditory association cortices during the encoding of pictures and sounds that were strikingly similar to those observed during the retrieval of such episodes (Figure 5–12 on Color Insert E) (Nyberg et al., 2000; Wheeler et al., 2000). It seems clear that retrieval entails the recapitulation of encoding patterns. However, what is recapitulated is typically not an *identical* copy of the information that was present at encoding; memory, as we all have had occasion to know, is subject to distortion.

3.2. Episodic Retrieval and the Frontal Lobes

Episodic retrieval involves a complex interaction between the medial temporal lobes and other cortical regions (Johnson et al., 1997; Shimamura, 1995), and considerable evidence indicates the importance of the frontal lobes. In nonhuman primates, disconnection of the frontal lobes from posterior brain structures causes a deficit in the ability to retrieve information associated with a retrieval cue (Tomita et al., 1999). Similarly, human patients with damage to the frontal lobes have particular difficulties in recollecting the details of earlier personal events (Janowski et al., 1989; Schacter et al., 1984). For example, frontal patients have difficulty remembering from whom they learned a new fact even when they can remember the fact itself, thus revealing a specific deficit in recollecting context. (This deficit is called *source amnesia*.) Consistent with these findings, neuroimaging studies of neurologically healthy people have revealed activation in a number of frontal lobe areas when participants are asked to retrieve episodic memories (Buckner & Wheeler, 2001; Fletcher & Henson, 2001; Nolde et al., 1998; Nyberg et al., 1996; Wagner, 2002).

The frontal lobes are important when we develop a retrieval plan, which requires selecting and representing the cues that will be used to probe memory. In addition, when we attempt to remember details of a past experience, there is activation in left frontal lobe regions associated with semantic elaboration (Dobbins et al., 2002). This pattern suggests that we elaborate on retrieval cues, thereby generating additional cues that might trigger pattern completion. The frontal lobes also support mechanisms that resolve competition or interference between competing memories (more than one memory is retrieved from a single cue, and the memories compete to be fully retrieved). Interference during retrieval is a significant cause of forgetting, and studies of patients with frontal lesions indicate that these patients are particularly prone to interference-based forgetting (Shimamura, 1995). Finally, the frontal lobes are important for evaluating or monitoring retrieved information, permitting decisions based on the quantity and quality at what is remembered (Rugg & Wilding, 2000).

3.3. Cues for Retrieval

As with the investigation of encoding, researchers have gained insight into the mechanisms underlying episodic retrieval by noting the factors present on occasions when retrieval is successful. One of the fundamental conclusions reached as a result of this approach is that retrieval is **cue dependent**, that is, it is stimulated by hints and clues from the external and the internal environment—from the state of the world and the state of ourselves. When cues are not available or are not used, attempts at retrieval are less likely to produce pattern completion. Many instances of forgetting occur not because the information sought has been lost from memory but because the cues used to probe memory are ineffective.

Context provides particularly strong retrieval cues, a phenomenon you may have experienced in visiting your old elementary school or standing in the room you had as a child or for old times' sake having a snack at a deli that was a high school hangout. The memories thus produced are stronger and more detailed in such circumstances than when you simply reminisce without cues. This phenomenon reveals a **context-dependent effect** on retrieval: retrieval is typically better when the physical environment at retrieval matches that at encoding (this is similar to the encoding specificity principle). In a particularly creative experiment, the context dependency of retrieval was demonstrated by presenting word lists to four groups of deep-sea divers and testing recall (Godden & Baddeley, 1975). One group both encoded and retrieved the words on shore, another group while under water. The third and fourth groups, however, encoded and retrieved in different contexts (studying the lists underwater and recalling them on shore, and vice versa). The groups that encoded and retrieved in the same physical context had the most successful retrieval (Figure 5–13).

Thus context-dependent effects not only support the idea that retrieval is cue dependent, they also reveal another important characteristic of episodic memory: when a stimulus or event is encoded, features of the physical environment are typically bound into the resulting episodic memory representation, providing another route to recall. If those features are present in the environment at the time of retrieval, they serve as further cues to memory and increase the likelihood of retrieval of other details of the experience. Similarly, aspects of our internal states, as affected by drugs or mood, also are encoded in memory and provide important cues at retrieval. Research has demonstrated **state-dependent effects**—better retrieval when internal states at retrieval match those at encoding—that parallel context-dependent effects. For example, Eich and colleagues (1975) demonstrated that participants who learned a list of words after having smoked marijuana were better

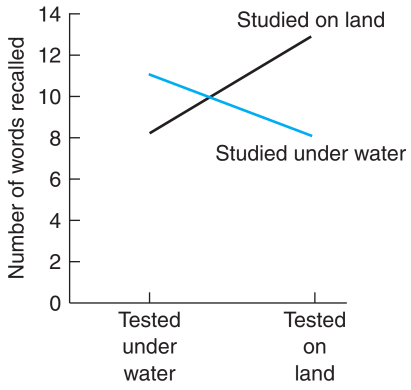


FIGURE 5–13 **Evidence for context-dependent memory**

In a test with deep-sea divers, the mean number of words recalled was affected by the match between the study and test contexts. Performance was better when words were recalled in the same environment in which they were learned.

(Data from Godden, D. R., and Bradley, A. D. 1975. Context-dependent memory in two natural environments: On land and under water. *British Journal of Psychology* 66: 325–331. Reprinted with permission from Elsevier.)

able to recall the words if they smoked again just before retrieval. And if the learning was done without marijuana, retrieval was better without marijuana. As with external environmental features, internal states facilitate retrieval when the internal state at retrieval matches that encoded in memory at the time of the encounter with the stimulus or event. (Participants who did not smoke marijuana at either encoding or retrieval performed the best of all groups: both encoding and retrieval are impaired if you are "under the influence.")

3.4. The Second Time Around: Recognizing Stimuli by Recollection and Familiarity

A central function of memory is to permit an organism to distinguish between novel stimuli and those that have been previously encountered. The ability to recognize people, objects, and places can be based on two processes: *recollection,* the conscious recall of specific contextual and event details of the earlier encounter, and *familiarity,* the subjective (and unspecific) sense of having previously encountered a stimulus.

The distinction between recollection and familiarity is captured in your experience with those two people in the hall. You remembered one of them clearly, consciously recollecting details about your earlier meeting; on the other hand, you didn't doubt your impression that you'd met the other person before, but you could recollect nothing about him. In the first case, recognition was based on recollection; in the second, on familiarity in the absence of recollection. **Dual-process theories** of recognition assert that both recollection and familiarity can support recognition.

Recollection is thought to depend on the same pattern-completion mechanisms that allow the recall of episodic details associated with a retrieval cue. Familiarity, on the other hand, is thought to emerge from a different process, one that takes account not of detail but of overall similarity. A stimulus is matched against information in memory; if there is a match or a sufficient overlap, we can say "I *know* I've seen you before" without having any specific detail to bring to bear.

Behavioral research has provided compelling evidence that recollection and familiarity are distinct memory processes, with distinct modes of operation (Yonelinas, 2002). For example, recollection is a slower process than is familiarity. Thus, when we are forced to make a recognition decision very rapidly, we are more dependent on assessing the familiarity of a stimulus and less on recollection because recollected knowledge tends to arrive too late to inform our decision (Hintzman & Curran, 1994; Yonelinas & Jacoby, 1994). Also, recollection is particularly dependent on attention at the time of encoding and retrieval: if attention is divided, the contribution of recollection to recognition decisions is markedly decreased (Dodson & Johnson, 1996; Jacoby & Kelley, 1991).

Does neurological investigation support the inferences drawn from behavioral research? Are recollection and familiarity implemented differently in the brain? The medial temporal lobes are known to be crucial for recognition memory, but controversy remains on the question of differential contributions of specific subregions to recollection and familiarity (see Figure 5–9). There is some evidence, from both animal and human studies, that supports the hypothesis that different sub-regions of the medial temporal lobes mediate different memory processes (Brown & Aggleton, 2001). For example, lesions of perirhinal cortex in monkeys yield a more severe impairment in object recognition performance than does damage to the hippocampus (Murray & Mishkin, 1986; Zola-Morgan et al., 1989). Moreover, hippocampal neurons differentially signal memory for the conjunction between stimuli rather than for individual stimuli, whereas perirhinal neurons differentially signal stimulus familiarity (Brown et al., 1987; Sobotka & Ringo, 1993). In humans, studies of some patients believed to have damage limited to the hippocampus have revealed disproportionate deficits in recollection relative to familiarity (Holdstock et al., 2002; Yonelinas et al., 2002; cf. Wixted & Squire, 2004); however, studies of another group of amnesic patients with selective hippocampal damage revealed comparable deficits in recollection and familiarity (Manns et al., 2003a). Human patients with isolated hippocampal lesions are rare, however, and another avenue of investigation is neuroimaging of neurologically healthy people. Initial findings from these studies support the notion that recollection and familiarity differentially depend on hippocampal and perirhinal memory mechanisms, respectively (see the accompanying *Debate* box).

3.5. Misremembering the Past

We tend to regard retrieval as successful when we can say, "Yes, of course I remember that!" (Or even, "Yes, I remember that clearly!") But is what we remember an accurate reflection of past encounters, or is it distorted or even illusory? Almost a

"Remembering," "Knowing," and the Medial Temporal Lobes

DEBATE

The controversy surrounding the relative contributions of the hippocampus and the surrounding perirhinal cortex to recollection and familiarity has recently been explored by neuroimaging of neurologically healthy humans. In one study, hippocampal signals were examined while participants made recognition decisions about previously studied words (Eldridge et al., 2000). The investigators measured recollection and familiarity by asking participants to describe the basis for each recognition decision. Participants were asked to indicate whether each recognition decision was accompanied by "remembering," consciously recollecting particular details about a prior encounter with a stimulus; or by "knowing," feeling confident that a stimulus is familiar but being unable to recollect details about a prior encounter. The important outcome: hippocampal activation was observed during "remembering" but not during "knowing" or forgetting (defined as the inability to recognize a previously encountered item). This pattern suggests that the hippocampus may selectively support recollection (see also, Yonelinas at al; 2005).

Another neuroimaging approach is to measure hippocampal and perirhinal activation at encoding and to test subsequent memory to determine whether the neural encoding signals differentially predict whether recognition will be based on recollection or on familiarity. A study that employed this strategy examined the relation between hippocampal and perirhinal activation during encoding and the ability (1) later to recognize a stimulus as previously encountered (an index of stimulus familiarity) and (2) later to recollect specific contextual details about the prior encounter (an index of recollection) (Davachi et al., 2003). The fMRI data from this investigation revealed that encoding activation in the hippocampus predicted later recollection but was uncorrelated with later stimulus familiarity. In contrast, encoding activation in perirhinal cortex predicted later stimulus recognition but not subsequent recollection. These results suggest that the hippocampus and perirhinal cortex subserve complementary encoding mechanisms that build representations that support later recollection and familiarity, respectively (see also, Ranganath et al., 2004; Kirwan & Stark, 2004). Future neuroimaging investigations, in conjunction with continued study of human patients and of animals with lesions of specific medial temporal lobe structures, promise ultimately to resolve this debate. See figures on Color Insert F and Color Insert G.

century of behavioral research indicates that remembering is often not perfect and suggests why. Memories are occasionally distorted to match our expectations, and sometimes we "remember" events that never occurred. Investigating the similarities and differences between accurate and illusory memories at the neural level provides further insights into the operation of memory. Schacter (2001; Buckner & Schacter, 2005) argues there are multiple forms of memory errors, including *bias, misattribution*, and *suggestion*.

3.5.1. Bias

Experimental analysis of memory distortions began with the work of the British psychologist Frederic Bartlett. In the 1930s, Bartlett had English participants read and then retell complex stories from the folklore of other cultures. He observed that participants frequently misremembered the stories in a number of ways: they noticeably shortened them; they eliminated unfamiliar interpretations; and made the stories more coherent and conventional in the storytelling tradition of their own culture. Adopting a similar approach, Sulin and Dooling (1974) had participants read a brief passage about a violent and unruly young girl; some participants were told that the passage was about "Helen Keller," others that the girl was "Carol Harris." Nowhere in the passage did the words "she was deaf, dumb, and blind" appear. When memory for the story was tested a week later and participants were asked if those words were in the story, half the participants who were told the story was about "Helen Keller" said yes (as opposed to 5 percent of those who thought the story was about "Carol Harris"). These distortions and errors of memory suggest that cultural experience and other background knowledge influence our memories for stimuli and events.

This form of memory distortion is due to *bias,* the inclination toward a conclusion not justified by logic or knowledge. In **belief bias**, such as that observed in the studies just mentioned, background knowledge about the way of the world and personal beliefs unconsciously influences memory to reshape it in a form consistent with expectations.

Bias can operate retrospectively, as well as during encoding. For instance, in one study (Markus, 1986), participants were asked in 1973 to describe their attitudes about the equality of women and legalization of marijuana (and other social issues). A decade later, in 1982, the same participants were asked to rate their *current* attitudes, and also to try to recall their 1973 attitudes. The result? Memory of their 1973 attitudes was more similar to their 1982 beliefs than the beliefs they had in fact expressed a decade earlier; and they apparently sincerely believed they had thought that way all along. Similar **consistency biases**, biases resulting from the often erroneous belief that one's attitudes are stable over time, have been observed in personal relationships: memory for the degree of initial happiness with a relationship is typically distorted by beliefs about the current degree of happiness (Kirkpatrick & Hazan, 1994; McFarland & Ross, 1987). It has been argued that bias of this sort occurs partly because people tend to believe that their attitudes are stable over time, and memories are therefore unconsciously adjusted to bring the past in line with the present (Ross, 1989).

An important implication of memory distortions due to bias is that retrieval is often a reconstructive process—what we retrieve is not always a direct recapitulation of what happened at encoding. In **reconstructive memory**, we reconstruct the past during retrieval rather than reproduce it. We often experience reconstructive memory when our memories for the event are not clear; in such instances we may infer the way things "must have been" from our current thoughts and expectations.

3.5.2. Misattribution

Here's a list of 15 associated words: *candy, sour, sugar, bitter, good, taste, tooth, nice, honey, soda, chocolate, heart, cake, eat, pie* (Deese, 1959; Roediger & McDermott, 1995).

Don't look back at the list, and answer these questions: Was the word *taste* on the list? The word *sweet*? The word *taste* was, and an average of 86 percent of participants said so. The word *sweet* wasn't—but an average of 84 percent of participants said it was. (The false recognition rate for unrelated words, such as *point,* was an average of 20 percent.) What's going on here—beyond the demonstration that it is possible to "remember" something that never happened?

False recognition often occurs when a novel stimulus is similar to stimuli previously encountered. One hypothesis is that, in the example of word lists, seeing each word activates related words, and these related words spontaneously come to mind and thus also are encoded. Then at retrieval, memory for having *thought* the related word is confused with memory for having *seen* the related word. This is an instance of **misattribution**, ascribing a recollection to an incorrect time, place, person, or source (Schacter, 2001). Participants who said the word *sweet* was on the list misattributed self-generated information (their thought of the word) to an external source (the presented word list).

In particular, false recognition occurs when we encounter a stimulus that, although not previously encountered, is semantically or perceptually similar to previously encountered stimuli (Koutstaal et al., 1999). In the example of word lists, *sweet* is semantically similar to the words on the list. In such circumstances, because the stimulus is consistent with the gist of our past experiences, it may elicit false recollection or a false sense of familiarity, leading us to believe that we had encountered the stimulus even though we had not. In essence, the same mechanisms that allow us to remember stimuli accurately that we have encountered can be fooled into signaling memory for a novel stimulus when it is similar to encountered stimuli.

Neuropsychological studies indicate that amnesic patients show lower levels of false recognition than do neurologically healthy people (Koutstaal et al., 2001). This finding suggests that the structures in the medial temporal lobes that support accurate episodic memory are also involved in storing and retrieving the information that leads to false recognition. Neuroimaging studies reveal that the hippocampus is similarly activated during the accurate recognition of previously studied words and the false recognition of related words. However, some studies suggest that accurate recognition and false recognition activate different perceptual processes, an indication that there are subtle but perhaps important differences in the level of perceptual recapitulation underlying true and false memory (Slotnick & Schacter, 2004).

3.5.3. Suggestion

False memories can muddy the waters of criminal investigations, and courtroom testimony based on the memory error of an eyewitness can lead to wrongful acquittal or conviction. Mindful that the fallibility of memory can have serious social and political consequences, researchers have sought to determine whether false memories can be implanted at the time of retrieval by *suggestion,* wherein false or misleading information is introduced after the event or is elicited through the use of leading questions (Schacter, 2001; Loftus, 2005).

In the laboratory, memories have been implanted by asking participants leading questions about an event they had observed in a slide presentation. In a classic experiment, participants watched slides of a car accident and then were asked to remember particular details about the incident (Loftus et al., 1978). The questions used to probe participants' memory introduced new—and false—information. For example, some of the participants were asked, "Did another car pass the red Datsun while it was stopped at the stop sign?" when in fact the slide presentation showed that the car had been stopped at a yield sign. When memory was tested again later, participants who were offered this misinformation were more likely to claim to have seen the car stopped at a stop sign than were those who had not been exposed to misleading information.

What accounts for this **misinformation effect**, which produces misremembering of an original event in line with false information (Loftus, 2005)? One hypothesis is that by suggesting false information about a prior event, the misinformation provided in the question serves to overwrite the information that was encoded during the event (Loftus et al., 1978). In this view, information that was once in memory is supplanted by the new misinformation. Alternatively, subsequent presentation of misinformation may lead to misattribution; that is, although the original accurate details remain in memory, when the false details are suggested, the misinformation is also encoded into memory. When later tested, you may remember the accurate information and the misinformation, but fail to remember which was in the original event and which was presented by the questioner. A third account is that, because we often cannot remember details about the past, we are inclined to accept misinformation as accurate when provided by a questioner because we lack memory otherwise; that is, if you cannot remember whether it was a yield sign or a stop sign, you are likely to be inclined to accept the information suggested by the questioner as accurate even if it is not. (This is especially likely to be the case when the questioner is a person of authority, such as a police officer.) Research addressing these alternatives indicates that misinformation distorts memory through a combination of misattribution (i.e., failing to remember the source of false information) and acceptance of suggested misinformation when accurate memory is weak (Lindsay, 1990; McCloskey & Zaragoza, 1985).

In special circumstances we may not only accept suggested misinformation as accurate but may also "remember" other details beyond those suggested by a questioner (Loftus & Bernstein, 2005). Do you remember being taken to a wedding reception as a child and spilling punch on the bride's mother? No? Perhaps you will, if you are subjected to a skilled interviewer; behavioral studies have shown that repeated suggestions about an event that never took place can induce not only acceptance of the memory but also can elicit additional—and wholly imaginary—details (Hyman & Pentland, 1996; Hyman et al., 1995). It appears that inducing people to visualize experiences that never occurred can sometimes lead them to conclude that their representations for what they'd imagined were actually memories of real events. Neuroimaging data support this conclusion: we are more likely falsely to claim to have seen an object that we had simply imagined when our earlier imagination of the object elicited robust activation of brain regions that support object perception (Gonsalves & Paller, 2000).

Comprehension Check: ✓

1. What are the major factors that affect retrieval efficacy and how are memories retrieved in the brain?
2. What are the ways in which memory can be distorted?

4. THE ENCODING WAS SUCCESSFUL, BUT I STILL CAN'T REMEMBER

Noël Coward wrote of a great romance, "What has been is past forgetting." Alas, not true. Although memory processes are operating at every moment of the day, typically we are not aware of the functioning of memory until attempts to remember are met with failure—that is, when we forget.

Forgetting is the inability to recall or recognize previously encoded information. Although some instances of forgetting are due to poor initial encoding, and others are due to the lack of the right cues at the right time, many instances of forgetting result from postencoding mechanisms. These mechanisms interfere with memory, so even if encoding was effective and the cues suitable, attempts to remember may be met with failure, as if the memory were lost.

4.1. Ebbinghaus's Forgetting Function

In his classic work *Memory* (1885/1964), Hermann Ebbinghaus systematically examined how memory for encoded stimuli and events changes as the **retention interval**—the time between encoding and retrieval—increases. He observed that his memory for meaningless, nonsense syllables declined as the retention interval increased (Figure 5–14). Subsequent studies during the decades since Ebbinghaus's report have consistently replicated this pattern. It is now believed that forgetting follows a power law, that is, the rate of forgetting slows with the passage of time: initially very rapid, it

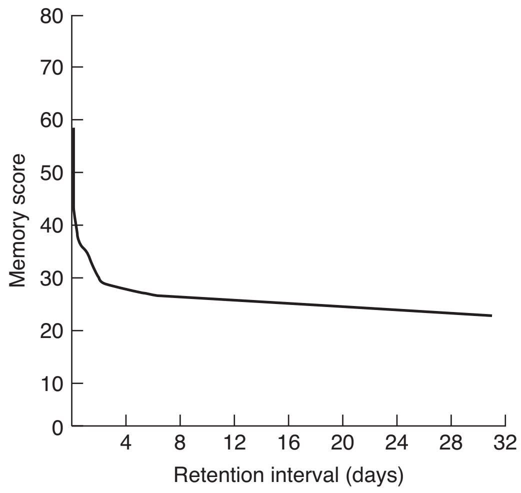


FIGURE 5–14 Ebbinghaus's forgetting function

Initially rapid forgetting is followed by a slow gradual decline.

(Data from Ebbinghaus, Hermann. *Memory:* A contribution to experimental psychology. Dover Publications, Inc., New York, 1964. Reprinted with permission.)

then settles into an extended, slow decline as the retention interval increases (Wixted & Ebbesen, 1991).

Because our ability to remember a stimulus or event systematically declines over time, the earliest theories held that forgetting was caused by the spontaneous weakening of memory representations with time. Such **decay theories** are attractive because they are simple and because they are intuitive. But they don't hold up; there is little direct evidence supporting decay. Indeed, some have argued that time alone cannot be the answer—*something must happen* (Lewardowsky et al., 2004). Consider a fading pair of jeans. Jeans do not fade spontaneously just because they've been around for a while. Their fading reflects a number of mechanisms that occur over time, such as repeated chemical interactions with sunlight and detergent. So it is likely to be for memory: time cannot operate directly on memory representations, which are neurobiological consequences of prior experience. Forgetting must be produced by some mechanism that play out in time.

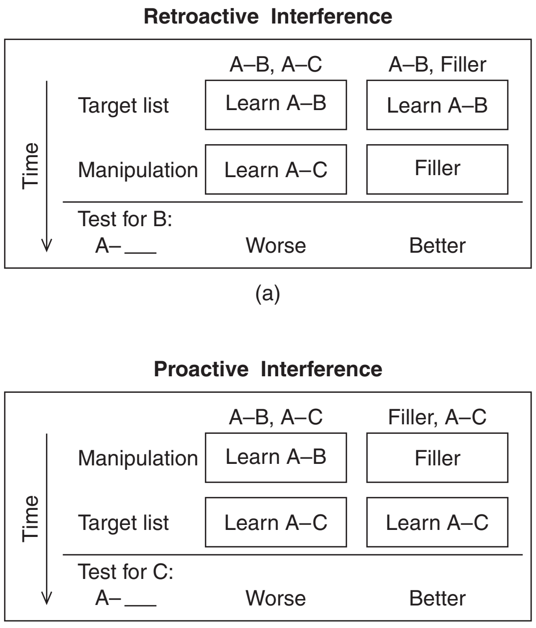
4.2. Forgetting and Competition

Ample evidence indicates that many instances of forgetting are caused by interference. **Interference theories** hold that if the same cue is bound to a number of representations, these representations compete during retrieval, resulting in interference. Newer memories interfere with older ones, and older ones with newer ones; and the result is that neither old nor new stimuli or events are perfectly recalled—even though the information is still in memory, we have forgotten because retrieval attempts have failed.

4.2.1. Retroactive and Proactive Interference

Interference can work both ways: here's an example of **retroactive interference**, in which new learning results in the inability to remember previously learned information (McGeogh, 1942; Melton & Irwin, 1940). You have an old e-mail account, which you used on your home computer, with a password you once used daily; now you're on your school's system, with a new password. The school takes a generous view of personal use of the school account, so you haven't used your old account in some considerable time. But now you need to find some ancient message buried in that e-mail account and *you can no longer remember the old password, because the new password interferes with it.*

Retroactive interference has been demonstrated in the laboratory with pairs of stimuli (Barnes & Underwood, 1959) (Figure 5–15a). All participants first learned random word–word pairings, the A–B pairs. (This stage is analogous to the learning you did when you encoded an association between the concept "password" and a particular combination of characters to gain access to your earlier account.) Some of the participants were then asked to associate a second word (C) with each A word from the original pairs. (This A–C learning is akin to encoding the association between the concept "password" and the characters that make up your school password.) Other participants were not asked to form a second set of word associations, but were given a "filler" task that, although time consuming, did not require learning. Memory was then tested by presenting the A words as retrieval cues and asking



(a)

(b)

FIGURE 5–15 Experimental designs examining retroactive interference and proactive interference

(a) Retroactive interference is shown to produce worse subsequent memory for A–B associations because of A–C associations learned later. (b) Proactive interference is shown to produce worse subsequent memory for A–C associations because of A–B associations learned earlier.

participants to recall the word or words that had been paired with each. The first group, which had to learn A–C as well as A–B pairs, had worse memory for the A–B pairs than did the second group, whose second task did not require learning.

This result eliminated passive decay as a cause: the time between tasks and memory test was the same for both groups, and thus any decay should have been the same. The conclusion then was that the learning of the A–C pairs (or of your new password) interfered with the ability to remember the A–B pairs learned earlier (or your old password). Other research has shown that the degree to which later learned information interferes with memory for earlier learned information depends on the similarity of the two (McGeogh & McDonald, 1931). The more similar the later information is to that learned earlier, the greater the interference and thus the greater the forgetting.

Now let's reverse direction: previously learned information can interfere with memory for information learned later by **proactive interference** (Underwood, 1957). This phenomenon has been explored in the laboratory in the same way as retroactive interference (Figure 5–15b). Here's an example of proactive interference: many people would agree that it is more difficult to remember the location of your car after parking it in a lot that you use regularly than when you park it in a lot you use only occasionally. The many earlier instances of associating your daily lot with a parking location for your car compete—and thus interfere—during attempts to retrieve the memory for the most recent association.

4.2.2. Blocking and Suppression

Memory is associative: encoding entails the formation of associations between different mental representations, such as binding the concept "password" to a particular sequence of characters. Retrieval entails pattern completion: presentation of a retrieval cue (for example, the demand for "password" on a computer screen) reactivates the associated representation (your sequence of characters). Given the fundamental principles of binding and the cue dependence of pattern completion, it becomes clear that interference can lead to forgetting through a number of mechanisms.

Forgetting can be caused by the **blocking** of a memory representation, that is, by obstruction that can occur when multiple associations are associated with a cue and one of those associations is stronger than the others, preventing retrieval of the target information. Many theorists believe that the probability of retrieving a target memory depends on the strength of the association between the retrieval cue and the target representation *relative to* the strength of the association between that same cue and other representations. In the ensuing competition during retrieval, the representation with the strongest association "wins" and is remembered; ones with weaker associations "lose" and are "forgotten". There is an important contrast here to decay theories, which hold that the degraded memory representation is lost; blocking theory emphasizes that the forgotten information still resides in memory, but access to it is temporarily blocked by a dominant competing representation. This weaker representation can be unblocked if a better retrieval cue, one that is more strongly associated with it, is presented.

Blocking likely accounts for many instances of forgetting; the mental representation of the old password, unused for some time, could be considered a weaker representation than the new password, which is used daily (Figure 5–16). The phenomenon is possibly adaptive: it permits the updating of memories so that we remember the information most likely to be relevant (Bjork, 1989).

Blocking also partly explains a striking and counterintuitive characteristic of memory: that the mere act of remembering one stimulus or event can result in the forgetting of another. Suppose you idly start thinking about cataloguing your CDs, and you begin by making a mental list of them. The list grows quickly at first, but very soon your rate of retrieval slows. Your familiarity with all your CDs is about the same, so why should this be? What is happening is a phenomenon called **output interference**, in which the strengthening of memories provided by the act of initial retrieval blocks the retrieval of other memories. Retrieving the names of some of the CDs in your collection serves to strengthen the association between those representations and the retrieval cue; and in turn these newly strengthened representations serve to block access to other CD titles, temporarily decreasing your ability to remember them.

If representations can be strengthened, as by retrieval, can nonretrieved representations be *suppressed*—weakened in absolute, not relative, terms? In other

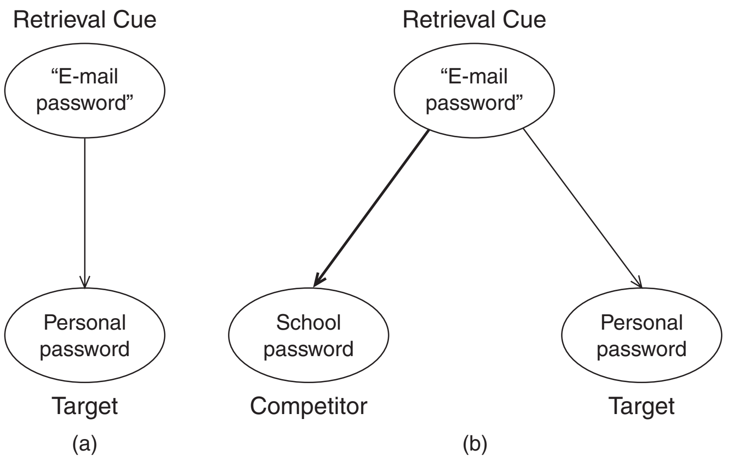


FIGURE 5–16 Cue overload and blocking

(a) The retrieval cue ("e-mail password") is associated with a single item ("personal password").
(b) The later learning and use of your new "school password" results in its also being associated with the cue "e-mail password," and thus begins to overload the cue. Because of its more recent use, the association between "school password" and the cue may be stronger (depicted by a thicker line) than the association between your earlier "personal password" and the cue. This stronger association may block retrieval of your earlier password.

words, does the competitive nature of memory actually cause some memories to weaken? (Is memory for your earlier password suppressed by repeated retrieval of your school password?) The answer appears to be yes, as shown by a phenomenon called **retrieval-induced forgetting**, forgetting that occurs when a memory is suppressed during the retrieval of another memory (Anderson & Spellman, 1995). **Suppression**, the active weakening of a memory, occurs because the act of retrieval is competitive: to retrieve a desired memory (your school password) you must not only strengthen its representation, you also must suppress the representations of competing associates (your earlier password).

Note the important difference between suppression and blocking: if memory for a competitor has been *suppressed,* one has difficulty retrieving it even when using a cue that has not been overloaded, which is not the case in *blocking,* which depends on multiple associations—that is, cue overload. In the password example, let's say your earlier password was "Batman Begins," the name of a movie. To the extent that the representation of this earlier password was suppressed during retrieval of your school password, then you should have increased difficulty retrieving it even when using an alternative cue ("movie names") rather than the trained cue ("e-mail password") (Figure 5–17). Anderson and Spellman demonstrated that retrieval of one representation associated with a cue results in the active weakening or suppression of other representations associated with that cue, as revealed by increased difficulty remembering the item when probed with an alternative cue.

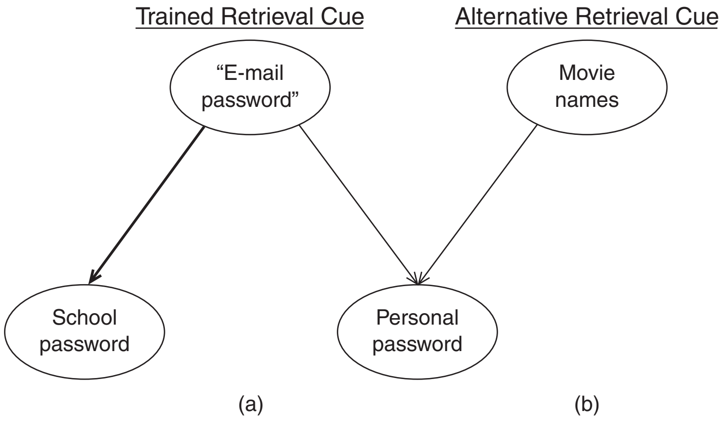


FIGURE 5–17 Two mechanisms that can explain interference

(a) *Blocking* posits that learning and using (that is, retrieving) your new school password with the cue "e-mail password" serves to hinder access to your earlier and less-used personal password (note the relative thickness of the lines). The *suppression* hypothesis states that retrieval of your new password serves actively to suppress (that is, weaken) the representation of your earlier password. (b) Testing memory with an alternative cue—one that is not overloaded, as is "e-mail password," which can apply to both passwords—provides evidence of forgetting that is not a result of blocking.

(Adapted from Anderson, M. C., and Green, C. (2001). Suppressing unwanted memories by executive control. *Nature* 410: 366–369. Reprinted with permission.)

Comprehension Check: ✓

1. What factors lead to forgetting?
2. How do blocking and suppression account for forgetting?

5. NONDECLARATIVE MEMORY SYSTEMS

The cognitive and neurobiological mechanisms that support declarative memory—and lead to forgetting—were best explored through our discussion of episodic memory, one form of declarative memory. We experience other forms of long-term memory quite differently. These other forms are known collectively as *nondeclarative (or implicit) memory.*

In discussing nondeclarative memory systems, concepts such as "recollection" do not apply. Nondeclarative memory operates outside of awareness: we typically are unaware of the influences of nondeclarative memory on our behavior, and we cannot describe the contents of retrieved nondeclarative memories. Rather, their retrieval and influence are expressed implicitly, by changes in behavior. As we noted earlier, nondeclarative memory supports forms of learning (habits, for instance) and remembering (the ability to ride a bike) that are qualitatively distinct and functionally independent of declarative memory.

There are a number of nondeclarative memory systems, each with unique qualities and dependent on specific brain circuits (see Figure 5–1). The medial temporal lobes are not involved, and therefore amnesic patients such as H.M., who suffer devastating declarative memory losses, can still form and retrieve nondeclarative memories, such as learning and expressing new motor skills (see Figure 5–4).

5.1. Priming

The phenomenon of priming illustrates some of the central characteristics of nondeclarative memory systems. Through priming, we can be unconsciously influenced by our experiences in such a way that previously encountered stimuli and concepts become more readily available. Specifically, as observed in memory, *priming* follows an encounter with a stimulus—a word or a face or other object—and constitutes unconscious alterations in our subsequent response to that stimulus or a related one. These behavioral changes can include increasing the speed of response, increasing the accuracy of the response, or biasing the nature of the response.

Changing vocabulary can be an interesting example of priming. Are you using a particular expression or bit of slang more often than you used to? Perhaps you picked it up from a friend. You may have begun using this phrase unintentionally, without considering its source or the original influence. Your mimicking of your friend occurs unconsciously in conversation, because your memory of that expression has been primed by your friend's use of it, increasing the likelihood that you will use it spontaneously.

Although there are a number of forms of priming, most instances fall into one of two broad categories: perceptual and conceptual (Roediger & McDermott, 1993). **Perceptual priming** results in an enhanced ability to identify a stimulus; **conceptual priming** results in facilitated processing of the meaning of a stimulus or enhanced access to a concept.

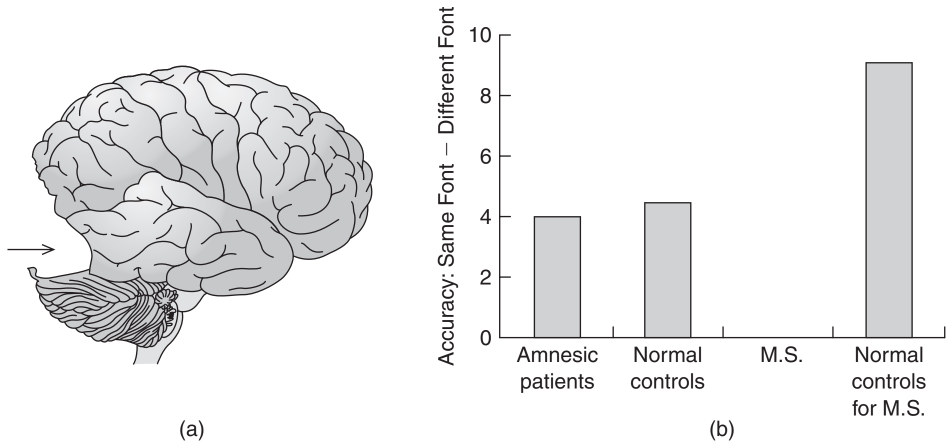
5.1.1. Perceptual Priming

In what is known as the *perceptual identification task,* test words are presented on a computer screen for as short a time as 34 milliseconds, and the task is to identify each flashed word. Because the perceptual input is limited in such a brief presentation, participants typically can identify only a small proportion of the test words. However, when a test word is visually presented in a study list before the performance of the task, the probability of identifying that word increases, even though participants are unaware that they have been influenced by the study list. This difference in accuracy for studied and unstudied stimuli—the measure of priming—occurs even though participants often report that they are simply guessing the flashed test words, thus indicating that declarative memory is not guiding performance.

Perceptual priming reflects the consequences of perceptual learning, and thus is highly dependent on the degree of perceptual overlap between the initial encounter with the stimulus and repeated ones. The degree of overlap is greatest, of course, when both initial and subsequent encounters are in the same modality; seeing a word primes seeing it again, but does little or nothing for hearing it (Jacoby & Dallas, 1981). Perceptual priming has been observed in all modalities tested (vision, audition, and touch), suggesting that it reflects a general form of learning in perceptual representation systems (Tulving & Schacter, 1990).

Because patients whose amnesia results from injury to the medial temporal lobes show intact perceptual priming, this form of memory cannot depend on the mechanisms that support declarative memory. Rather, perceptual priming is thought to emerge from learning within sensory cortices. The experience of a patient known as M.S. is illustrative (Gabrieli et al., 1995).

Like H.M., M.S. suffered from epileptic seizures that could not be controlled with medication, although in M.S.'s case the epilepsy was due to abnormalities in the occipital cortex, not the medial temporal lobes. Surgery to remove most of M.S.'s right occipital lobe controlled his seizures, but also resulted in a remarkably subtle memory deficit of which he was unaware: although M.S.'s declarative memory is intact, he fails to show perceptual priming in the visual domain. For example, his ability to identify briefly presented visual stimuli is not improved by prior viewing of the stimuli (Figure 5–18). This memory pattern has two important implications. First, M.S.'s priming deficit allows us to rule out the possibility that intact priming



(a)

(b)

FIGURE 5–18 Priming, memory, and brain damage

M.S. has intact declarative memory, but does not benefit by visual perceptual priming; amnesic patients do. (a) A three-dimensional MRI rendering of the right hemisphere of M.S.'s brain, showing the extent (*arrow*) of the removal of the right occipital cortex.

(Wagner, A. D., and Koutstaal, W. Priming. In *Encyclopedia of the Human Brain,* Vol. 4. Elsevier Science, 2002, pp. 27–46, Fig. 1. Reprinted with permission from Elsevier.)

(b) The magnitude of visual priming in amnesic patients and their age-matched normal controls, and in M.S. and his age-matched normal controls. In all groups, except M.S. himself, word-stem completion priming was greater when the font of the word stem matched the font of the studied word.

(Data from Vaidya, C. J., Gabrieli, J. D., Verfaellie, M., Fleischman, D., and Askari, N. 1998. Font-specific priming following global amnesia and occipital lobe damage. *Neuropsychology 2:* 183–192. © 1998 American Psychological Association. Reprinted with permission.)

in amnesic patients simply reflects residual declarative memory function. To the contrary, because M.S. has impaired perceptual priming and intact declarative memory, which is the reverse pattern of that seen in amnesic patients, it seems clear that perceptual priming and declarative memory reflect different forms of memory that depend on distinct brain structures. Second, M.S.'s memory deficit provides compelling evidence that sensory-specific cortical processing is necessary for perceptual priming.

During the past decade, researchers have used neuroimaging to examine the neural correlates of perceptual priming in the intact human brain (Schacter et al., 2004). In the typical experiment, the activation level during the initial processing of visual stimuli is compared to that during the repeated (that is, primed) processing of the same stimuli. Such experiments have revealed that visual priming is accompanied by *decreased* activation in the regions of visual cortex that were engaged during the initial processing of stimuli (Figure 5–19 see Color Insert H). This finding has been seen across a variety of tasks and stimuli types, including words and objects, suggesting that it reflects a fundamental operating principle shared by sensory processing regions. Localization of visual priming to visual cortex is further evidence that modality-specific sensory cortices are central to perceptual priming.

Neuroimaging observations of priming in human sensory cortex bear a striking resemblance to the phenomenon of **repetition suppression** observed in studies of nonhuman primates and rats; that is, a reduced firing rate of neurons in visual regions with repeated exposure to a stimulus (Desimone, 1996). Perceptual priming in the human and repetition suppression in the nonhuman might reflect the operation of a single underlying learning mechanism that changes the response properties of sensory neurons that process perceptual features of a stimulus and, accordingly, affects behavior. One hypothesis is that this change consists of dampening down the responses of neurons that, though initially responsive to stimulus presentation, are not essential for stimulus identification. This process results in a sparser and more selective neural representation—fewer neurons fire in response to the stimulus, leading to reductions in the fMRI signal and neural firing rate—and enhanced stimulus identification (Wiggs & Martin, 1998; see Figure 5–19).

5.1.2. Conceptual Priming

Modifications of speech, such as incorporating a new expression into your everyday vocabulary, often occur outside conscious awareness, and do not reflect changes in perceptual representation systems. Rather, the form of priming that gives rise to an increased accessibility to concepts, such as slang terms, is thought to emerge as a result of learning in semantic representation systems. Conceptual priming, which results in facilitated processing of the meaning of a word, is demonstrated by the *category exemplar generation task*. Participants are presented a category cue, such as "fruit," and are asked to name the first few fruits that come to mind. Typically, the probability of spontaneously generating a given exemplar, such as "cherry," is higher if that word had appeared on an earlier (unrelated) study list. This increase does not reflect declarative memory, because amnesic patients show intact levels of conceptual priming even though they have impaired episodic memory for the study list as such. In other words, if asked to recall the words on a study list, they can't; nonetheless, they show improvement in the category generation task when they've seen the words before.

Neuroimaging studies of the healthy human brain during conceptual priming have revealed changes in frontal and temporal lobe activation. The typical study compares activation in response to initial and repeated conceptual decisions about words or objects (for example, deciding whether a word is "abstract" or "concrete"). In contrast to perceptual priming, which is associated with decreased activation in modality-specific perceptual cortices, neuroimaging studies of conceptual priming reveal that the left inferior frontal lobe and left lateral temporal cortex are less active during repeated conceptual processing of a stimulus. The left frontal lobe is thought to contribute to semantic retrieval when the sought information does not immediately come to mind upon cue presentation (Wagner et al., 2001). The increased accessibility of sought semantic information as a result of priming serves to decrease demands on this retrieval process. In this way priming decreases the cognitive effort required to retrieve relevant information.

5.2. Beyond Priming: Other Forms of Nondeclarative Memory

Although priming is arguably the best understood form of nondeclarative memory, there are other memory systems that operate independently of the medial temporal lobes to acquire and store knowledge that can be unconsciously or implicitly expressed. These other nondeclarative systems support skilled behavior, the acquisition of stimulus–response habits, and the formation and expression of conditioned associations. Learning within these systems is typically gradual and incremental.

5.2.1. Skill Learning

Humans are capable of acquiring remarkably skilled behavior. Skill learning supports our ability to become experts, to a greater or lesser degree, at things like snowboarding and typing. With practice, skilled behavior becomes more accurate and responses are made more quickly.

It has been proposed that skill acquisition entails three stages (Fitts & Posner, 1967). Learning begins with a *cognitive stage,* in which knowledge is declaratively represented, often in a verbal code, and attentional demands are high. When you begin learning to snowboard, you have to remember consciously a set of instructions on, for example, how to turn; and inattention is often followed by a spill. With practice, you gradually move to an *associative stage.* Behavior begins to be tuned and error rates and "verbal mediation"—that is, talking to yourself as you learn—decline as the visual information about the mountain's terrain and your motor responses that allow you to navigate the terrain come together, and the associations in memory required for snowboarding are formed and strengthened. Finally, you may reach an *autonomous stage,* in which behavior is highly accurate, rapidly executed, and relatively automatic, requiring little attention. If you've reached this stage, you may find it hard to explain to a novice exactly how you do what it is you do, because your knowledge now is typically expressed without awareness of the underlying memories that make it possible.

Skill learning is distinguished from priming on the basis of specificity of the memory change. Priming reflects a change in the perceptual or conceptual representation of a specific item; skill learning generalizes to new instances or exemplars that were not encountered during learning. You don't lose your ability to type when you're using someone else's computer keyboard.

Skill learning also is distinguished from priming, and from declarative memory, with respect to the brain regions that are ultimately necessary to acquire and express skills. In general, the acquisition of skills partially depends on the basal ganglia, a set of subcortical structures long known to be important for motor execution and more recently linked to memory and various cognitive processes. Particular skills also place additional demands on the cerebellum and on cortical regions. The importance of the basal ganglia for skill learning has been revealed in studies of patients with Parkinson's and Huntington's disease, both disorders of basal ganglia function. Basal ganglia dysfunction spares priming, but it differentially impairs skill learning relative to declarative memory. Consistent with these findings, neuroimaging of neurologically healthy people has revealed changes in the activation of the caudate and putamen, portions of the basal ganglia, as a skill is acquired (Grafton et al., 1995; Poldrack et al., 1999).

5.2.2. Habit Memory

Nondeclarative memory also encompasses the acquisition of **stimulus–response habits**, habits that emerge through the slow accumulation of knowledge about the predictive relation between a stimulus and a response. The acquisition and expression of habit memories has been assessed using the *probabilistic classification task,* in which participants learn to predict one of two possible outcomes from a set of cues, each cue bearing a probabilistic relation to the outcome. For example, participants may be asked to predict rain or sunshine from a set of cue cards. Because the cue–outcome associations are probabilistic—that is, a given card never perfectly predicts rain or sunshine—retrieving episodic memory for specific study trials is an ineffective learning strategy. Rather, through repeated presentation of cards and resulting outcomes, participants gradually accumulate implicit knowledge about the stimulus–response associations.

In contrast to patients with medial temporal lobe damage, patients with basal ganglia dysfunction are severely impaired in this task (Knowlton et al., 1994, 1996). Neuroimaging of neurologically healthy people has shown increasing basal ganglia activation and decreasing medial temporal lobe activation over the course of habit learning (Poldrack et al., 2001). Thus, the basal ganglia become increasingly involved across the course of habit learning, whereas the declarative memory system appears to shut down.

5.2.3. Conditioned Associations

Nondeclarative memory mechanisms support the learning and expression of conditioned associations such as those described by the Russian psychologist Ivan Pavlov early in the twentieth century. The simplest form of conditioning, referred to as **classical conditioning**, entails learning a predictive relationship between two successive stimuli such that a response that is triggered by an initial stimulus (the *unconditioned* *stimulus*) prior to learning comes to be triggered by a second stimulus (the *conditioned stimulus*) that predicts onset of the unconditioned stimulus. The formation of a conditioned association depends on the degree to which the presence of one stimulus predicts the occurrence of the other. Accordingly, effective learning occurs when one stimulus reliably and predictably signals the occurrence of the second stimulus. (Classical conditioning will be discussed further in Chapter 8.)

As with other forms of nondeclarative memory, the medial temporal lobes are not necessary for conditioning. Thus, H.M. and other amnesic patients can form a conditioned eye-blink response with the repeated pairing of a tone and a following puff of air to the eye. (H.M., like you, will soon start to blink when the tone is sounded.) This knowledge is nondeclarative: the patients cannot state the temporal relation between the tone and the air puff. The cerebellum is thought to be the site at which perceptual inputs (such as the sound of the tone and the sensation of the puff of air) are associated; it has been demonstrated that cerebellar lesions disrupt the acquisition of conditioned eyeblink responses (Solomon et al., 1989).

Comprehension Check: ✓

1. How do perceptual and conceptual priming affect cognition?
2. What are the stages of skill learning?

Revisit and Reflect

1. *What are the characteristics of declarative and nondeclarative memory systems?*

   Declarative memory supports the encoding, consolidation, and retrieval of knowledge that can be consciously remembered and described, or "declared," to other people at the time of retrieval, such as memory for events (episodic memory) and for facts and concepts (semantic memory). When you recognize someone, you rely on episodic memory to remember details about your earlier encounter—perhaps her tastes in cuisine, her name, her politics—and you are aware of the contents of your memory and their relation to your past. To launch your new conversation you also rely on semantic memory to retrieve knowledge of relevant concepts—say, the views of her political party—and consciously use this knowledge to guide your discussion. Declarative memory depends on the medial temporal lobes.

   Nondeclarative memory supports forms of long-term knowledge that are implicitly expressed as a change in behavior rather than as conscious remembering. We are often unaware of the operations of nondeclarative memory and how such memories shape our thoughts and actions. Thus, your ability perceptually to process the face of someone you recognize is likely facilitated (that is, primed) by your having previously processed that face—and although you most likely do not notice the change, your second perceptual processing of a face is performed more quickly than was the first. Nondeclarative memory systems support skill learning, conditioning, habit memory, and priming, and all depend on brain structures outside the medial temporal lobes.

Think Critically

- Try to imagine what life would be like without the ability to form new declarative memories. What aspects of your life would change?
- Although we are typically not aware of when our behavior is being influenced by nondeclarative memory, can you think of three examples across the course of today where your actions were likely affected by one form of nondeclarative memory?

2. *How do we encode new declarative memories, what processes affect encoding efficacy, and what brain mechanisms build these memories?*

Declarative memories are encoded through medial temporal lobe processes that bind the various aspects of a stimulus or event into an integrated memory representation. Episodic encoding entails the binding of the elements of stimulus or event with its context. Thus, to remember a past encounter with someone, you must initially encode the elements of that encounter—binding together perceptual information (for example, her face), verbal information (for example, her name), spatial information (for example, where you met), and semantic information (for example, her taste in cuisine and her political views). Semantic memories are thought to emerge when the regularity of the co-occurrence of elements across multiple contexts is extracted; thus those elements are divorced from context but still capture the central tendencies of a stimulus or event. Thus, knowledge of Italian cuisine emerges by pooling across the various experiences one has had that included Italian food.

Episodic encoding is facilitated by a number of factors: attention, semantic processing and elaboration, generating information from memory, and the spacing of encoding trials. For example, failure to attend to a person's name when being introduced because of distraction (for example, thinking about an impending physics test) will result in poor encoding (and future embarrassment!). Attention, semantic processing and elaboration, and the generation of information all partially depend on frontal lobe brain mechanisms, and thus the frontal lobes are in a position to influence how we learn and what we learn. Although each of these encoding factors affects later memory performance, encoding is not deterministic—rather our ability later to remember critically depends on the overlap between the processing and cues present at encoding and those engaged and present at retrieval.

Think Critically

- How should you study to improve your learning of course material and the likelihood that you will be able to retrieve this material when necessary?
- Consider a recent instance in which you failed to remember a prior event. Can you trace this memory failure to ineffective encoding? How might you have changed this memory outcome?

3. *How are episodic memories retrieved, and why is it that sometimes what we retrieve is not an accurate reflection of our past?*

Remembering events past depends on episodic retrieval, the process by which stored memory representations are subsequently reactivated. According to dual-process theory, retrieval can take either of two forms: recollection of a past encounter with a stimulus or the subjective experience that a stimulus is familiar. Recollection is thought to depend on pattern completion processes in the hippocampus that recapitulate information in lateral cortex that was present during encoding of the event; a topic of current debate is whether familiarity particularly depends only on the medial temporal cortex or also on the hippocampus.

Because pattern completion is triggered by retrieval cues, recollection critically depends on the cues used to probe memory and their overlap with the cues present at encoding—both external contextual cues and internal ones. Thus, you may fail to recognize someone you've previously met not because you have forgotten that person but because the contexts of the two encounters are different; many of the cues that may trigger pattern completion are not present when the context changes. The frontal lobes affect recollection partly because these brain regions serve to represent and elaborate on retrieval cues and to resolve interference between competing memories.

Memory is prone to distortion and error—what we retrieve is not always an accurate reflection of what we encountered. Biases at encoding can distort what is stored in memory—and even when memories are relatively accurately encoded, biases at retrieval can distort what is "remembered" as we reconstruct the past. Another common memory error is the misattribution of something remembered to the wrong source. Thus, you might become confused as to whether you actually performed an action that you'd simply thought about performing (did I lock the door?). We sometimes also mistakenly claim to have encountered stimuli that, though novel, are perceptually or conceptually similar to stimuli that we have previously encountered. Finally, memory can be led astray through suggestions by others: sometimes suggestion leads to error because it induces a misattribution, and at other times errors occur because we accept misleading information as true because we can't remember otherwise.

Think Critically

- In deciding whether or not a particular event happened just the way it was described to you by the sole eyewitness, what factors would you consider?
- What is the relation between binding in the medial temporal lobes and pattern completion? Is anterograde amnesia likely a failure of binding or of pattern completion? What about retrograde amnesia?

4. *Why do we sometimes forget?*

We forget for many reasons. Sometimes it is because we failed to encode the information effectively that we now are trying to remember. At other times it is because the cues that we are using to try to trigger remembering are ineffective; a change to other cues or elaboration on the cues we are using could help. Some theorists have hypothesized that forgetting can also occur because memories spontaneously decay over time; this hypothesis has been challenged, although it is difficult completely to discount decay as a possible forgetting mechanism. That said, there is strong agreement and extensive evidence that forgetting often is due to interference—memories compete (or interfere) with one another during retrieval, thus resulting in failure to recover the desired memory. Proactive and retroactive interference arise partly because having multiple associates to a cue serves to overload the cue, making it less effective for triggering remembering of any given associate. In addition, when one piece of information is more strongly associated with a cue than is another, our ability to retrieve the latter memory may be blocked by this competing stronger memory. Moreover, because memories compete during retrieval, the act of recovering one memory directly weakens or suppresses the representation of a related memory, resulting in retrieval-induced forgetting.

Think Critically

- Memory is critical for recording one's life narrative and thus for generating a sense of self. How should the knowledge that memory is fallible influence our confidence in what we know about our past and our sense of self?
- Often when we are having difficulties remembering something, a friend might try to lend a hand by suggesting possible answers. Although well intentioned, how might these efforts to be helpful result in the exact opposite outcome—decreasing the probability of remembering the desired information?

5. *What are the forms of nondeclarative memory, and how do they influence our behavior?*

The realization that the brain supports multiple memory systems makes a fundamental point: all regions of the brain change (or "learn") as they are engaged to perform some function or computation. What differs between declarative and nondeclarative memory systems are the particular kinds of processes or functions supported by different brain regions, and thus the particular kinds of memories that these regions can support. Whereas declarative memory depends on the unique ability of the medial temporal lobes to receive and bind inputs from elsewhere in the brain, nondeclarative memory typically depends on changes in local brain networks following previous engagement of these networks. Thus, priming reflects changes in perceptual and conceptual representation systems that follow prior perceptual or conceptual processing of stimuli; these changes are behaviorally expressed as facilitated performance. Skill learning, habit memory, and conditioning are other forms of nondeclarative memory that are gradually acquired and that ultimately shape our behavior in ways that we need not be aware.

Think Critically

- What are the implications of nondeclarative memory for the perspective that humans have free will—that is, that we make conscious choices on how to think and act?
- If you had a brain injury that resulted in impaired conceptual priming, how do you think this might impact your everyday functioning?