

Learning and Memory

Short-Term and Long-Term Memory Involve Different Neural Systems

Short-Term Memory Maintains Transient Representations of Information Relevant to Immediate Goals

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Errors and Imperfections in Memory Shed Light on Normal Memory Processes

An Overall View

IN HIS MASTERFUL NOVEL *One Hundred Years of Solitude* Gabriel Garcia Marquez describes a strange plague that invades a tiny village and robs people of their memories. The villagers first lose personal

recollections, then the names and functions of common objects. To combat the plague, one man places written labels on every object in his home. But he soon realizes the futility of this strategy, because the plague eventually destroys even his knowledge of words and letters.

This fictional incident reminds us of how important learning and memory are in everyday life. Learning refers to a change in behavior that results from acquiring knowledge about the world, and memory is the process by which that knowledge is encoded, stored, and later retrieved. Marquez's story challenges us to imagine life without the ability to learn and remember. We would forget people and places we once knew, and no longer be able to use and understand language or execute motor skills we had once learned; we would not recall the happiest or saddest moments of our lives, and would even lose our sense of personal identity. Learning and memory are essential to the full functioning and independent survival of people and animals.

In 1861 Pierre Paul Broca discovered that damage to the posterior portion of the left frontal lobe (Broca's area) produces a specific deficit in language. Soon thereafter it became clear that other mental functions, such as perception and voluntary movement, are also mediated by discrete parts of the brain (see Chapter 1). This naturally led to the question: Are there discrete neural systems concerned with memory? If so, is there a "memory center" or is memory processing widely distributed throughout the brain?

Contrary to the prevalent view that cognitive functions are localized in the brain, many students of learning doubted that memory is localized. In fact,

until the middle of the 20th century many psychologists doubted that memory is a discrete function, independent of perception, language, or movement. One reason for the persistent doubt is that memory storage involves many different parts of the brain. We now appreciate, however, that these regions are not all equally important. There are several fundamentally different types of memory, and certain regions of the brain are much more important for some types of storage than for others.

During the past several decades researchers have made significant progress in the analysis and understanding of learning and memory. In this chapter we focus on three insights. First, there are several forms of learning and memory, each with its distinctive cognitive properties and mediated by specific brain systems. Second, memory can be deconstructed into discrete encoding, storage consolidation, and retrieval processes. Finally, imperfections and errors in remembering can provide clues about the nature and function of learning and memory.

Memory can be classified along two dimensions: (1) the time course of storage and (2) the nature of the information stored. We shall first consider the time course.

Short-Term and Long-Term Memory Involve Different Neural Systems

Short-Term Memory Maintains Transient Representations of Information Relevant to Immediate Goals

When we reflect on the nature of memory we usually think of the long-term memory that William James referred to as “memory proper” or “secondary memory.” That is, we think of memory as “the knowledge of a former state of mind after it has already once dropped from consciousness.” This knowledge depends on the formation of a memory trace that is durable, in which the representation persists even when its content has been out of conscious awareness for a long period.

Not all forms of memory, however, constitute “former states of mind.” In fact, the ability to store information depends on short-term memory, called working memory, which maintains current, albeit transient, representations of goal-relevant knowledge. In humans working memory consists of at least two subsystems—one for verbal information and another for visuospatial information. The functioning of these two subsystems is coordinated by a third system called the *executive control processes*. Executive control

processes are thought to allocate attentional resources to the verbal and visuospatial subsystems, and to monitor, manipulate, and update stored representations.

We use the verbal subsystem when we attempt to keep speech-based (phonological) information in conscious awareness, as when we mentally rehearse a phone number just obtained from an operator. The verbal subsystem consists of two interactive components: a store that represents phonological knowledge and a rehearsal mechanism that keeps these representations active while we need them. Neuropsychological and neuroimaging data indicate that phonological storage depends on posterior parietal cortices, and rehearsal partially depends on articulatory processes in Broca’s area.

The visuospatial subsystem of working memory retains mental images of visual objects and of the location of objects in space. The rehearsal of spatial and object information is thought to involve modulation of such representations in the parietal, inferior temporal, and extrastriate occipital cortices by the frontal and premotor cortices. Current research is concerned with whether visuospatial working memory might best be viewed as two subsystems, one for object knowledge and one for spatial knowledge.

Single-cell recordings in nonhuman primates indicate that some prefrontal neurons maintain spatial representations, others maintain object representations, and still others represent the integration of spatial and object knowledge. Although neurons concerned with working memory of objects tend to fall in the ventrolateral prefrontal cortex and those concerned with spatial knowledge tend to fall in the dorsolateral prefrontal cortex, all three classes of neurons are present in both prefrontal subregions (Figure 65–1).

Short-Term Memory Is Selectively Transferred to Long-Term Memory

In the mid-1950s startling new evidence about the neural basis of long-term memory emerged from the study of patients who had undergone bilateral removal of the hippocampus and neighboring regions in the medial temporal lobe as treatment for epilepsy. The first and best-studied case was a patient called H.M. studied by the psychologist Brenda Milner and the surgeon William Scoville. After H.M. died on December 2, 2008, his full name, Henry Molaison, was revealed to the world.

H.M., a 27-year-old man, had suffered for more than 10 years from untreatable temporal lobe epilepsy caused by brain damage sustained at age 7 years in a bicycle accident. As an adult his seizures rendered him unable to work or lead a normal life. At surgery Scoville removed the hippocampal formation, the

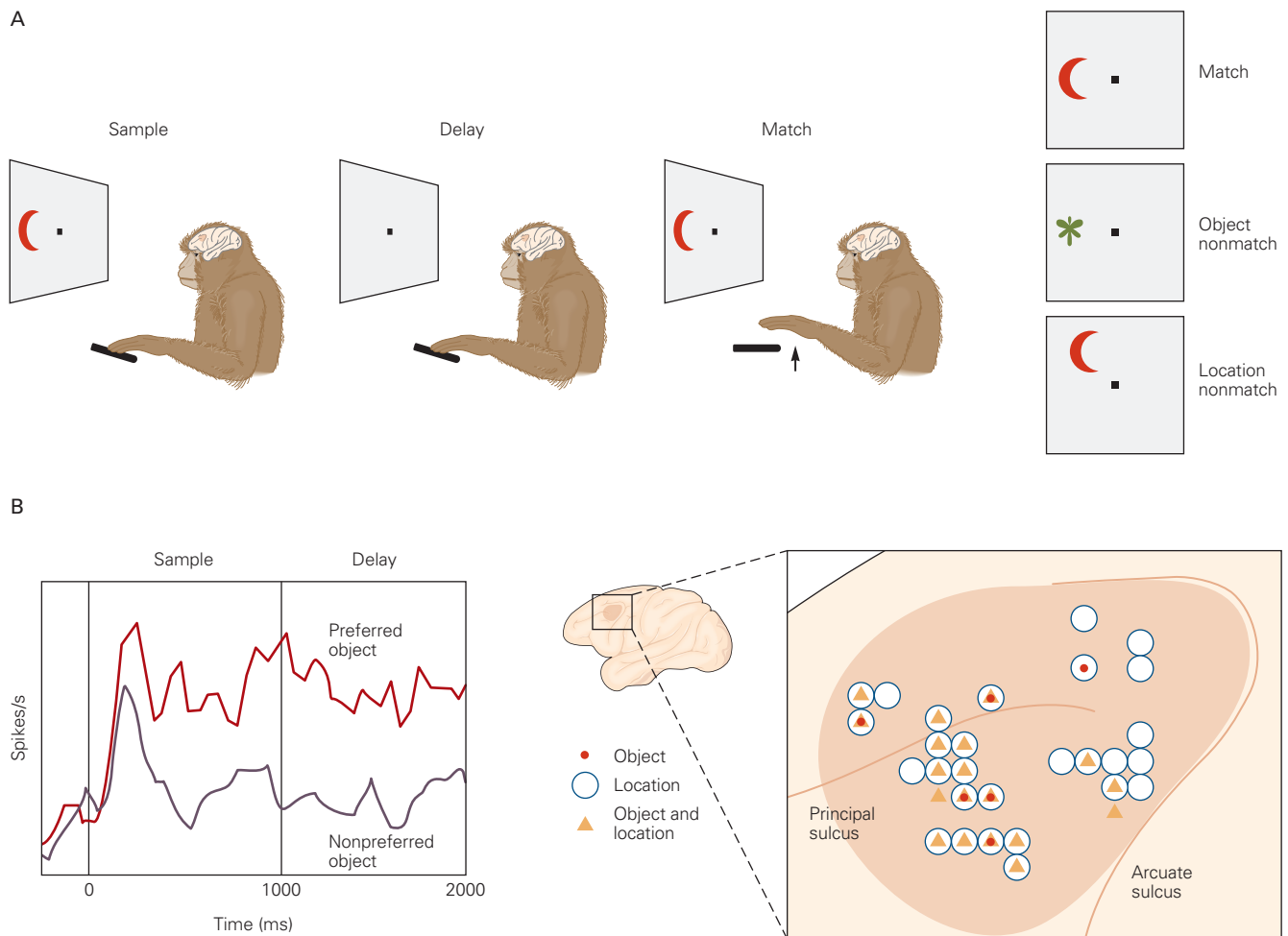


Figure 65–1 The prefrontal cortex maintains a working memory. (Adapted, with permission, from Rainer, Asaad, and Miller 1998.)

A. The role of prefrontal cortex in maintaining information in working memory is often assessed in monkeys using electrophysiological methods in conjunction with the delayed-match-to-sample (DMS) task. In this type of task each trial begins when the monkey grabs a response lever and fixates a small target at the center of a computer screen. An initial stimulus (the “sample”) is briefly presented and must be held in working memory until the next stimulus (the “match”) appears. In the task illustrated here the monkey was required to remember the sample (“what”) and its location (“where”) and release the lever only in response to stimuli that “matched” on both dimensions.

B. Neural firing rates in the primate lateral prefrontal cortex during the delay period in the task are often above baseline and represent responses to the type of stimulus (what), the location (where), and the integration of the two (what and where). At left is the activity of a prefrontal neuron to preferred objects (to which the neuron responds robustly) and to nonpreferred objects (to which the neuron responds minimally) during the task. Activity is robust when the monkey encounters the preferred object (sample) and during the delay. In the sketch at right the symbols represent recording sites where neurons that maintained each type of information (what, where, and what and where) were found. Typically, several types of neurons were found at one site; hence many symbols overlap and some symbols indicate more than one neuron.

amygdala, and parts of the multimodal association area of the temporal cortex bilaterally (Figure 65–2). After the surgery H.M.’s seizures were better controlled, but he was left with a devastating memory deficit (or amnesia). What was so remarkable about H.M.’s deficit was its specificity.

He still had normal working memory, for seconds or minutes, indicating that the medial temporal lobe is not necessary for transient memory. He also had long-term memory for events that had occurred before the operation. He remembered his name, the job he had held, and childhood events, although his memory of

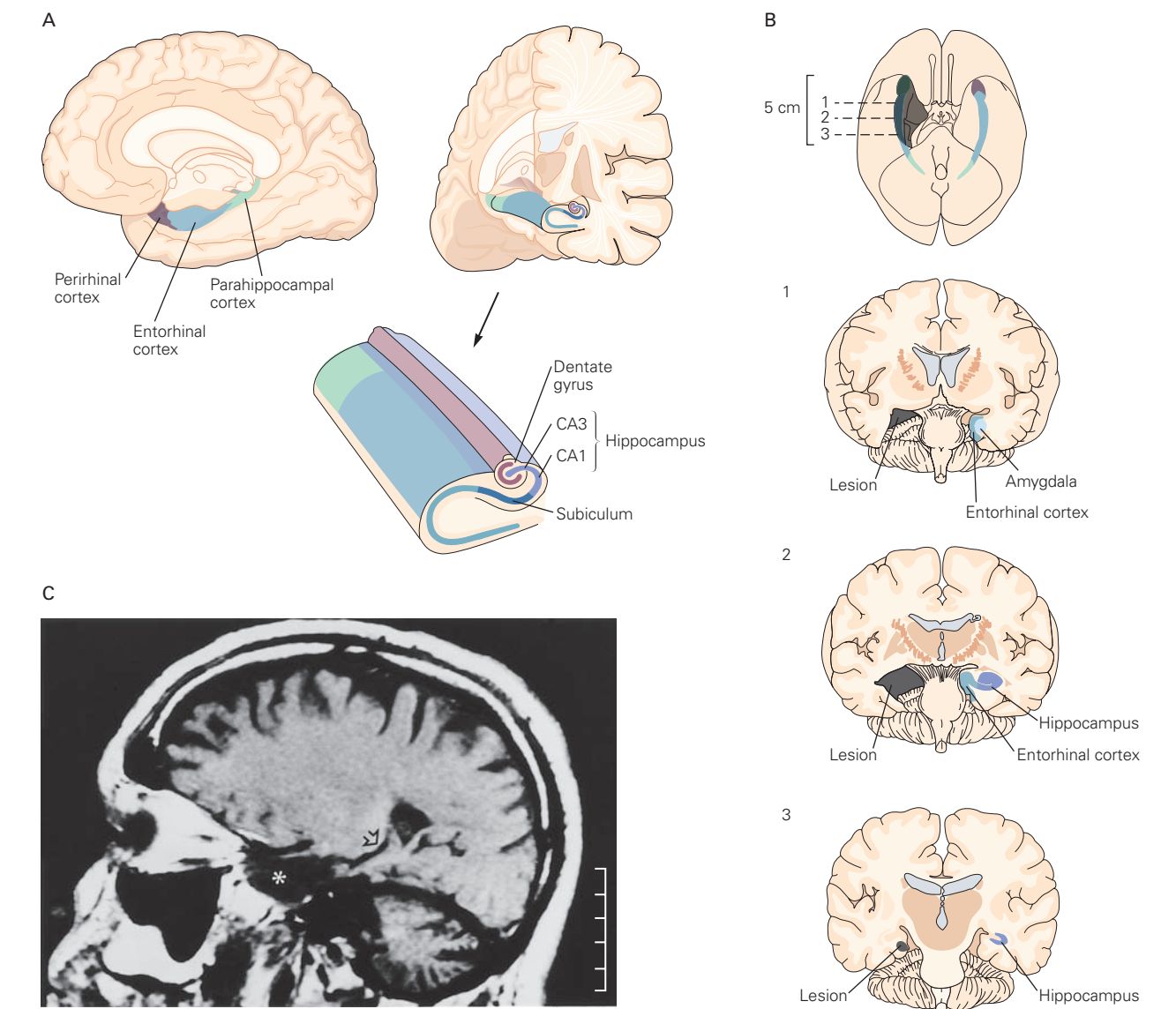


Figure 65-2 The medial temporal lobe and memory storage.

A. The key components of the medial temporal lobe important for memory storage.

B. The areas of temporal lobe resected (gray shading) in the patient known as H.M., viewed from the ventral surface of the brain (left hemisphere is on the right side of the image). Surgery was a bilateral, single-stage procedure, but to illustrate the structures that were removed the right side of the image is shown here intact. The longitudinal extent of the lesion is shown in a ventral view of the brain (top). Cross sections 1 through 3 show the estimated extent of areas of the brain

removed from H.M. (Adapted, with permission, from Corkin et al. 1997.)

C. Magnetic resonance image (MRI) scan of a parasagittal section from the left side of H.M.'s brain. The calibration bar at the right of the panel has 1-cm increments. The **asterisk** indicates the resected portion of the anterior temporal lobes. The **arrow-head** points to the remaining portion of the intraventricular portion of the hippocampal formation. Approximately 2 cm of preserved hippocampal formation is visible bilaterally. Note also the substantial degeneration in the enlarged folial spaces of the cerebellum. (Adapted, with permission, from Corkin et al. 1997.)

information acquired in the years just before surgery was not robust. In addition, he retained a command of language, including his vocabulary, indicating that semantic memory was preserved. His IQ remained unchanged in the range of bright-normal.

What H.M. now lacked, and lacked dramatically, was the ability to transfer new information from working memory into long-term memory. He was unable to retain for lengthy periods information about people, places, or objects that he had just encountered. Asked to remember a new telephone number, H.M. could repeat it immediately for seconds to minutes because of his intact working memory. But when distracted, even briefly, he forgot the number. H.M. could not recognize people he met after surgery, even when he met them again and again. For several years he saw Milner every month, yet each time she entered the room he reacted as though he had never seen her before. H.M. is not unique. All patients with extensive bilateral lesions of the limbic association areas of the medial temporal lobe from either surgery or disease show similar long-term memory deficits.

H.M. is a historic case because his deficit provided the first clear link between memory and the medial temporal lobe, including the hippocampus. Given the large size of the hippocampus proper, the question next arose: How extensive does a bilateral lesion have to be to produce a memory deficit? Clinical evidence from several patients as well as data from experimental animals suggests that a lesion restricted to any of the major components of the system can have a significant effect on long-term memory. For example Larry Squire, David Amaral, and their colleagues found that the patient R.B. had only one detectable lesion after a cardiac arrest—destruction of the pyramidal cells in the CA1 region of the hippocampus. Nevertheless, R.B.'s memory deficits were qualitatively similar to those of H.M., although quantitatively much milder.

The different subregions of the medial temporal lobe, which together comprise the medial temporal lobe memory system, may not have equivalent roles, however. For example, some areas in the medial temporal lobe circuit may be particularly important for object recognition. Damage to the perirhinal cortex that spares the underlying hippocampus produces a greater deficit in object recognition than do selective lesions of the hippocampus that spare the overlying cortex.

In contrast, some theorists have argued that the hippocampus may be relatively more important for spatial representation than for object recognition. In mice and rats lesions of the hippocampus interfere with memory for space and context, and single neurons in the hippocampus encode specific spatial

information (see Chapter 67). Functional imaging of the brain in healthy humans shows that activity increases in the right hippocampus when spatial information is recalled, and in the left hippocampus when words, objects, or people are recalled. These physiological findings are consistent with the clinical observation that lesions of the right hippocampus give rise to problems with spatial orientation whereas lesions of the left hippocampus cause defects in verbal memory.

Long-Term Memory Can Be Classified As Explicit or Implicit

Another crucial finding about H.M. was that not all types of long-term memory were impaired. Even though H.M. and other patients with damage to the medial temporal lobe had profound memory deficits, they were able to form and retain certain types of durable memories as well as healthy subjects.

For example, H.M. learned to draw the outlines of a star while looking at the star and his hand in a mirror (Figure 65-3). Like healthy subjects learning to remap hand-eye coordination, H.M. initially made many mistakes, but after several days of training his performance was error-free and comparable to that of healthy subjects. Nevertheless, he did not consciously remember having performed the task.

Later work by Squire and others made it clear that the long-term memory capabilities of H.M. and other amnesic patients are not limited to motor skills. These patients retain simple reflexive learning, including habituation, sensitization, classical conditioning, and operant conditioning (to be discussed later in this chapter). Furthermore, they are able to improve their performance on certain perceptual and conceptual tasks. For example, they do well with a form of memory called priming, in which perception of a word or object is improved by prior exposure. Thus, when shown only the first few letters of previously studied words, a subject with amnesia is able to generate the same number of words as normal subjects, even though the amnesic patient has no conscious memory of having recently studied the words (Figure 65-4).

Is this distinction between forms of long-term memory in amnesic patients a fundamental difference in normal memory function? To address this question the cognitive psychologists Peter Graf and Daniel Schacter examined healthy subjects and found two types of long-term memory that differed in whether conscious awareness was required for the recall.

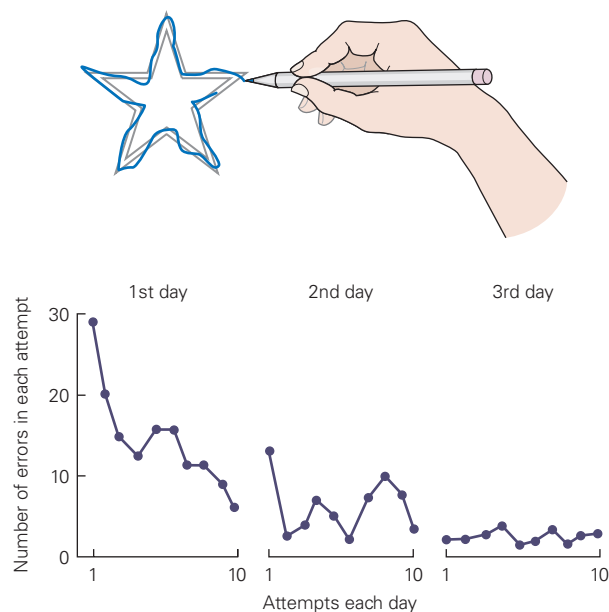


Figure 65-3 The amnesic patient H.M. could learn skilled movements. He was taught to trace between two outlines of a star while viewing his hand in a mirror. The graph plots the number of times, during each attempt, that he strayed outside the outlines as he drew the star. As with healthy subjects, H.M. improved considerably with repeated attempts despite the fact that he had no recollection of having performed the task before. (Reproduced, with permission, from Blakemore 1977.)

One type is an unconscious form of memory that is evident in the performance of a task and is known as *implicit memory* (also referred to as nondeclarative or procedural memory). Implicit memory is typically manifested in an automatic manner, with little conscious processing on the part of the subject. Different forms give rise to priming, skill learning, habit memory, and conditioning (Figure 65-5).

The other type is the deliberate or conscious retrieval of previous experiences as well as conscious recall of factual knowledge about people, places, and things. This type is known as *explicit memory* (or declarative memory). Explicit memory is highly flexible; multiple pieces of information can be associated under different circumstances. Implicit memory, however, is tightly connected to the original conditions under which the learning occurred.

Explicit Memory Has Episodic and Semantic Forms

The Canadian psychologist Endel Tulving first developed the idea that explicit memory can be further

classified into episodic memory (the memory of personal experiences or autobiographical memory) and semantic memory (memory for facts). *Episodic memory* is used to recall that we saw the first flowers of spring yesterday or that we heard Beethoven’s “Moonlight Sonata” several months ago. *Semantic memory* is used to learn the meanings of new words or concepts. The medial temporal lobe plays a critical role in both episodic and semantic memory, as is evident in patients like H.M., who have difficulties in forming and retaining new conscious memories of their personal experiences or the meanings of new concepts.

We have learned two additional important things about explicit memory. First, the brain does not have a single long-term store of explicit memories. Instead the storage of any item of knowledge is widely distributed among many brain regions and can be accessed independently (by visual, verbal, or other sensory clues).

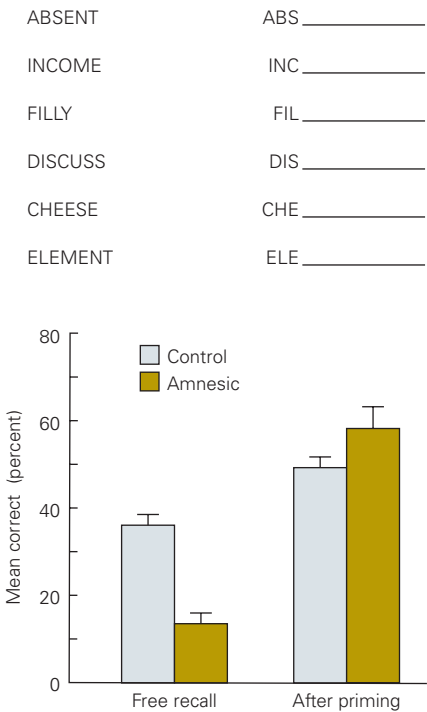
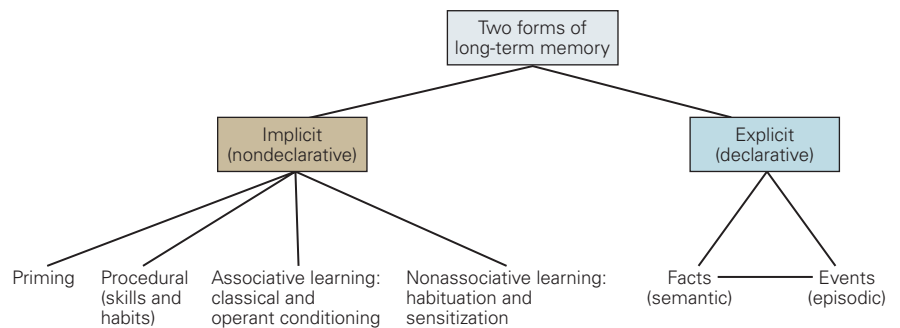


Figure 65-4 Amnesic and normal control subjects were tested on recall of words under two conditions. First they were presented with common words and then asked to recall the words (free recall). Amnesic patients did not do well on this test. However, when subjects were given the first three letters of a word and instructed simply to form the first word that came to mind (completion), the amnesic subjects performed as well as normal subjects. The baseline guessing rate in the word completion condition was 9%. (Reproduced, with permission, from Squire 1987.)

Figure 65–5 Long-term memory is either explicit (conscious) or implicit (subconscious).



Second, explicit memory is mediated by at least four related but distinct types of processing: encoding, storage, consolidation, and retrieval.

Explicit Memory Processing Involves at Least Four Distinct Operations

Encoding is the process by which new information is attended and linked to existing information in memory. The extent of this process is critically important for determining how well the learned material will be remembered. For a memory to persist and be well remembered, the incoming information must be encoded thoroughly, what the psychologists Fergus Craik and Robert Lockhart called “deep” encoding. This is accomplished by attending to the information and associating it with knowledge that is already well established in memory. Memory encoding also is stronger when one is well motivated to remember.

Storage refers to the neural mechanisms and sites by which memory is retained over time. One of the remarkable features about long-term storage is that it seems to have an almost unlimited capacity; there is no known limit to the amount of information in long-term storage. In contrast, working memory storage is very limited; psychologists believe that human working memory can hold only a few pieces of information at any one time.

Consolidation is the process that makes the temporarily stored and still labile information more stable. As we shall learn in the next two chapters, consolidation involves expression of genes and protein synthesis that give rise to structural changes at synapses.

Finally, *retrieval* is the process by which stored information is recalled. It involves bringing back to mind different kinds of information that are stored in different sites. Retrieval of memory is much like perception; it is a constructive process and therefore subject to distortion much as perception is subject to illusions (Box 65–1).

Retrieval of information is most effective when a retrieval cue reminds individuals of how they initially encoded an experience. For example, in a classic behavioral experiment Craig Barclay and colleagues asked some subjects to encode sentences such as “The man lifted the piano.” On a later test, “something heavy” was a more effective cue for recalling piano than “something with a nice sound.” Other subjects, however, encoded the sentence “The man tuned the piano.” For them, “something with a nice sound” was a more effective retrieval cue for piano than “something heavy.” Retrieval, particularly of explicit memories, also is partially dependent on working memory.

Episodic Knowledge Depends on Interaction Between the Medial Temporal Lobe and Association Cortices

Although studies of amnesic patients during the past few decades have refined our understanding of various types of memory, medial temporal lobe damage affects all four operations of memory—encoding, storage, consolidation, and retrieval—and thus it is often difficult to discern how the medial temporal lobe contributes to each. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) allow us to scan the healthy brain in the process of building new memories or retrieving existing memories, and thus to identify specific regions that are active during different processes.

Functional MRI scans show that activity in the medial temporal lobe is greater when subjects engage in deep encoding (eg, attending to the meaning of information by judging whether a word is concrete or abstract) than when they engage in shallow encoding (eg, judging whether a word is presented in upper or lower case letters). Activity in parts of the left prefrontal cortex is also enhanced during deep encoding,

Box 65–1 The Transformation of Explicit Memories

How accurate is explicit memory? This question was explored by the psychologist Frederic Bartlett in a series of studies in the 1930s in which the subjects were asked to read stories and then retell them. The recalled stories were shorter and more coherent than the original stories, reflecting reconstruction and condensation of the original.

The subjects were unaware that they were editing the original stories and often felt more certain about the edited parts than about the unedited parts of the retold stories. They were not confabulating; they were merely interpreting the original material so that it made sense on recall.

Observations such as these lead us to believe that explicit memory, at least episodic (autobiographical) memory, is a constructive process like sensory perception. In fact, explicit memory is a product of the perceptual process. Sensory perception is not a passive recording of the external world but a process in which

sensory signals produce information that is shaped by the way in which afferent pathways process those signals.

It is also constructive in the sense that individuals perceive the environment from the standpoint of a specific point in space as well as a specific point in their own history. As described in Chapter 27, optical illusions nicely illustrate the active role of perceptual processes in arriving at our personal knowledge of our surroundings.

Likewise, once information is stored, recall is not an exact copy of the information stored. Past experiences are used in the present as cues that help the brain reconstruct a past event. During recall we use a variety of cognitive strategies, including comparison, inference, shrewd guessing, and supposition, to generate a memory that not only seems coherent to us but is also consistent with other memories and with our “memory of the memory.”

suggesting that frontal lobe and medial temporal lobe processing contribute to encoding episodic memory.

Anthony Wagner and his colleagues tested the relation between frontal and medial temporal lobe activity during encoding of an experience and the later remembering of the experience. Subjects were scanned using event-related fMRI while they learned a long series of words (event-related fMRI allows researchers to examine brain activity based on participants’ responses to specific items or events). Their memory of the words was then tested outside the scanner to compare their recall with the activity recorded while learning the series of words. At the time of encoding, activity in several regions of the left prefrontal cortex was enhanced when subjects were studying words that they were later able to recall (Figure 65–6). Using similar methods to examine the encoding of memories of pictures, James Brewer and John Gabrieli and their colleagues found greater activity in the right prefrontal cortex during encoding of pictures that were later recalled compared to pictures that could not be recalled.

Both studies also revealed greater activity in the medial temporal lobe during encoding of stimuli that were subsequently remembered compared to those that were forgotten. This is further evidence that

episodic learning depends on interaction between cognitive control processes in the prefrontal cortex and associative binding mechanisms in the medial temporal lobe.

Interaction between the medial temporal lobe and distributed cortical regions is also central in current thinking about memory consolidation. Recall that patient H.M., whose medial temporal lobe was surgically removed, could still recall childhood memories. In fact, early observations suggested that H.M. could recall many of the experiences of his life up until several years before his operation. These observations of H.M. and other amnesic patients with damage to the medial temporal lobe suggest that old memories are not stored in the medial temporal lobe itself; if they were, H.M. would not be able to recall his early experiences. Rather, they are stored in various other cortical regions.

According to Larry Squire and others, the medial temporal region may play a temporary role in the consolidation of memories, but after a sufficiently long period is no longer needed as memories can be retrieved directly from cortical regions. This finding is consistent with the fact that amnesic patients are better able to recall remote memories than memories from the period just before they became amnesic.

As with studies of encoding, studies of retrieval of episodic knowledge have implicated the prefrontal cortex and medial temporal lobe. In one study, monkeys were trained to associate a specific visual object with a preceding visual cue. During training the monkeys learn that they will receive a reward if they press a lever when a specific object is shown, but only when that object is preceded by the learned visual cue. Electrophysiological recordings reveal that, after training, the visual cue activates neurons in the monkey's inferior temporal cortex during the recall of the stored visual memory.

Importantly, even after the monkey has undergone brain surgery to prevent the afferent flow of visual information from primary visual cortex to inferior temporal cortex, the visual cue is able to elicit the correct behavioral response and to elicit firing in the inferior temporal cortex neurons. This implies that information about the visual cue must reach neurons in the inferior temporal cortex through a "top-down" pathway in which signals from the primary visual cortex activate neurons in prefrontal cortex that in turn activate neurons in the inferior temporal cortex. When this "top-down" pathway is also surgically interrupted, the monkeys fail to respond to the visual cue, which can no longer trigger activity in the inferior temporal cortex neurons (Figure 65–7). PET and fMRI scans of human subjects asked to recall or recognize

previously studied words or pictures show activity in the anterior and lateral prefrontal cortex.

The retrieval of contextual or event details associated with episodic memory also involves activity in the medial temporal lobe, particularly in the hippocampus. Medial temporal lobe activity is thought to facilitate the activation of neocortical representations that were present during encoding. Consistent with this perspective, Yasushi Miyashita and colleagues have demonstrated that signals from the medial temporal lobe precede the recruitment of episodic knowledge in the neocortex. Mark Wheeler and colleagues and Lars Nyberg and colleagues observed similar patterns of activation in visual and auditory association areas during both the encoding and retrieval of pictures and sounds. As with encoding of episodic memory, retrieval involves a complex interaction between the medial temporal lobe and distributed cortical regions, including the prefrontal cortex and other high-level association areas.

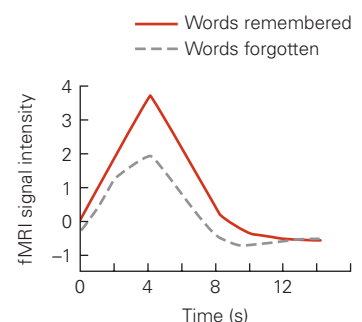
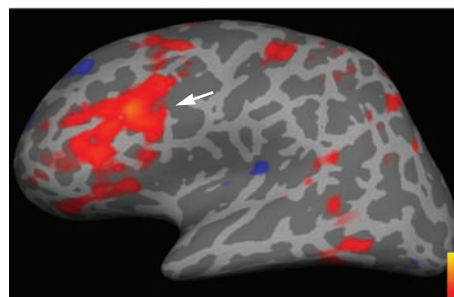
Semantic Knowledge Is Stored in Distinct Association Cortices and Retrieval Depends on the Prefrontal Cortex

Semantic knowledge is our general knowledge about the world, encompassing facts, concepts, and information

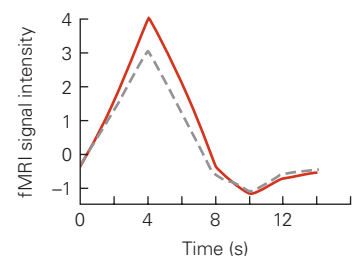
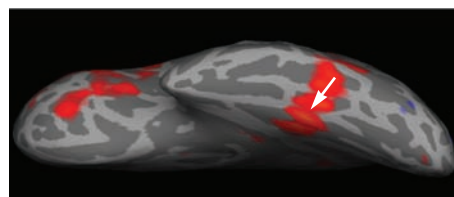
Figure 65–6 Activity in the prefrontal cortex and medial temporal lobe during an experience is essential to remembering the experience.

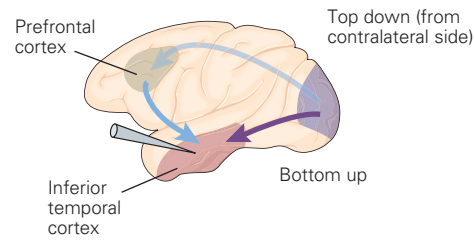
Neural activity during encoding of visual events (presentation of words) was measured using functional magnetic resonance imaging (fMRI). Subsequently, recall of the studied words was tested and each word was classified as either remembered or forgotten. The scans taken during encoding were then sorted into two groups: those made during encoding of words that were later remembered and those made during encoding of words that were later forgotten. This subsequent memory analysis reveals greater activation in regions of the left prefrontal cortex and medial temporal lobe during the encoding of words later remembered than those later forgotten (locations denoted by **white arrows**). At right are the observed fMRI responses in these regions for words later remembered (**red line**) and those later forgotten (**dashed line**). (Adapted from, with permission, from Wagner et al. 1998.)

Left inferior prefrontal cortex

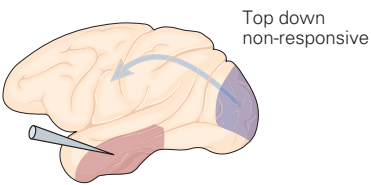


Left medial temporal lobe

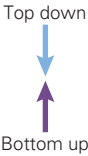
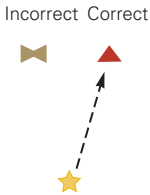




Corpus callosum partially split



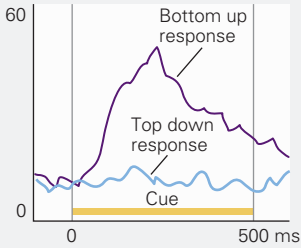
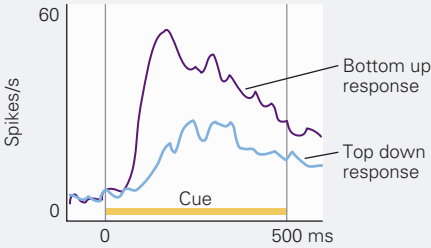
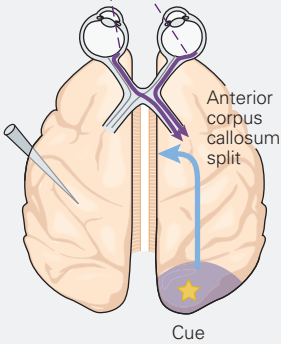
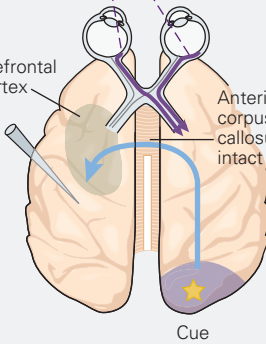
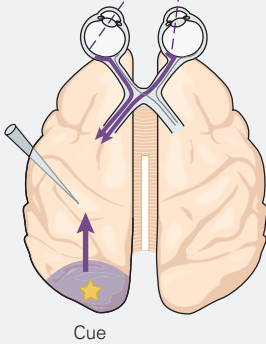
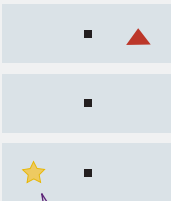
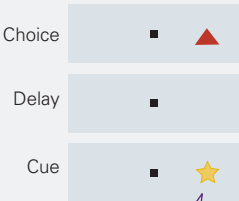
Corpus callosum fully split



A₁ Bottom-up retrieval

A₂ Top-down retrieval

B Top-down non-responsive



about objects, as well as words and their meanings. Semantic knowledge is distinguished from episodic knowledge in that it is typically not associated with the context in which the information was acquired. It is stored in a distributed manner in the neocortex, including the lateral and ventral temporal lobes.

The organization and flexibility of semantic knowledge is remarkable. Consider the concept “elephant.” When first learned through a picture it appears to be quite simple. With further learning, however, many images of elephants become associated with a name, at first spoken and then written. Later other pieces of information are associated: elephants are living things, they live in a particular environment and have unique patterns of behavior, they emit distinctive sounds and are often gray in color, and they perform in circuses. Given this associative structure—which would collectively correspond to the concept “elephant”—any one feature, such as the word *elephant*, can serve as a cue that leads to recovery of other associated features.

There is no single storage site for all of the semantic knowledge that we have acquired over our lifetime. Rather, the semantic components of a concept are distributed among many brain regions. Specific brain regions are dedicated to representing specific features (eg, form, color, or motion), such that a lesion in one

region can impair a specific type of knowledge associated with a particular concept while sparing others.

Rosaleen McCarthy and Elizabeth Warrington described patients whose knowledge about living things was impaired while their knowledge about inanimate objects was intact. For example, one patient correctly defined towel as “material used to dry people,” but incorrectly defined wasp as a “bird that flies.” Other patients demonstrate the reverse deficit. The brain appears to organize semantic knowledge according to conceptual primitives, eg, form and function. Because some categories are particularly dependent on information about form (eg, living things) whereas others depend on knowledge of function (eg, inanimate things), focal brain damage can result in the loss of memory for particular semantic categories while sparing knowledge of others.

Neuroimaging studies using PET and fMRI provide more evidence about how different categories of knowledge are represented in the intact human brain. When people name pictures of animals there is greater activity in left inferior temporal regions, which represent information about the form of objects, than when they name pictures of tools. In contrast, tool naming is associated with activity in left premotor regions, which represent information about the patterns of motor

Figure 65-7 (Opposite) The prefrontal cortex contributes to recall of associated knowledge. (Reproduced, with permission, from Tomita et al. 1999.)

A. The experimental design includes “bottom-up” and “top-down” retrieval conditions. A monkey was trained to associate a specific object with a prior visual cue. During testing the monkey was shown a visual cue on a screen. After a delay the monkey was then shown one of several objects (choice). The monkey had to choose whether the object is the one that is associated with the visual cue (by releasing a lever). The posterior corpus callosum of the monkeys in the study was partially split so that the bottom-up sensory signal from visual cortex could not directly reach visual areas in the opposite hemisphere. **1.** In the bottom-up retrieval condition the retrieval cue and choice object are presented in the right visual hemifield contralateral to the recording site (electrode) in the left inferior temporal cortex. Because the left hemisphere processes the right visual field, visual information enters the primary visual cortex in the same hemisphere as the recording electrode. The monkey was able to choose the correct object associated with the cue (data not shown) indicating that bottom-up sensory signals are sufficient for retrieval. The bottom-up signal in response to the visual cue also elicits a large increase in neural firing rate in the inferior temporal cortex neurons. **2.** In the top-down retrieval condition the cue is presented in the left visual hemifield ipsilateral to the recording site, whereas the choice object is presented contralaterally in the right visual hemifield.

Thus visual information about the cue enters the hemisphere opposite to the recording site. Because the posterior corpus callosum is cut, there is no direct bottom-up pathway from right visual cortex to left inferior temporal cortex. Nonetheless the visual cue is able to elicit a strong electrophysiological response in inferior temporal cortex neurons in the left hemisphere and the monkey is able to choose the correct object associated with the cue. In this condition visual information from the right hemisphere crosses over to the left hemisphere through the intact anterior portion of the corpus callosum. Top-down signals from prefrontal cortex, which carry information about the retrieval cue, elicit neuronal firing and retrieval of associated representations through feedback connections to the inferior temporal cortex.

B. When the corpus callosum is fully split, visual information from the contralateral hemisphere can no longer reach the ipsilateral prefrontal cortex. This prevents top-down retrieval signals from being transmitted to inferior temporal neurons. As a result, neurons in the left inferior temporal cortex are no longer activated by the presentation of the visual cue to the left hemifield. In addition, the monkeys no longer choose the correct object when the cue is presented to the contralateral visual hemifield. In contrast, left inferior temporal cortex neurons show a strong response when the cue is presented to the right visual hemifield because the bottom-up pathway from left visual cortex to left inferior temporal cortex is intact.

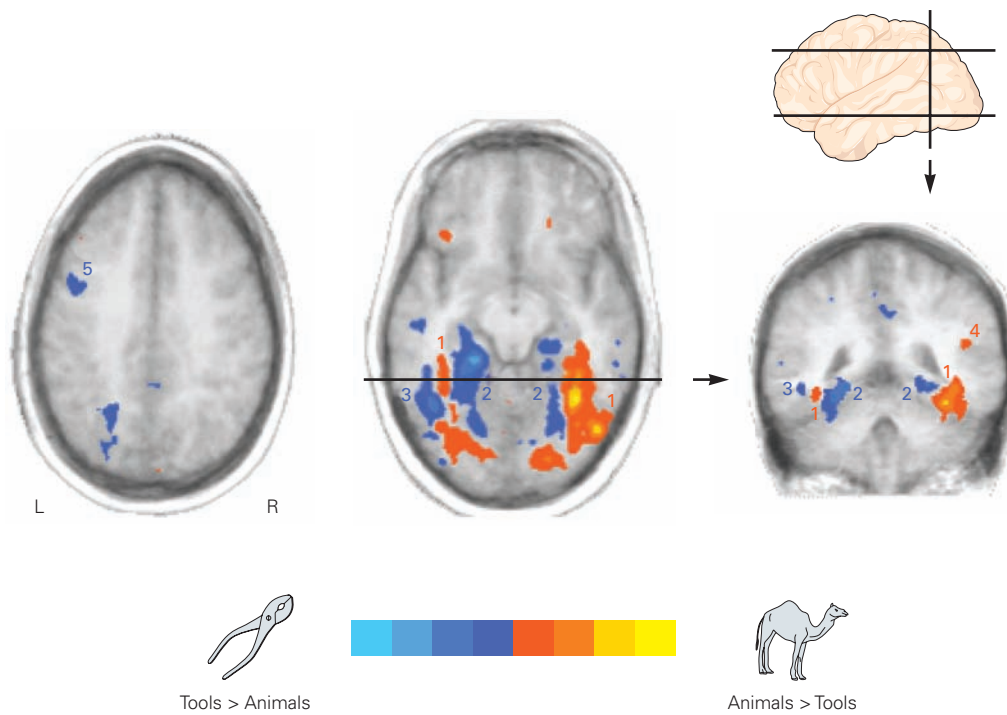


Figure 65–8 Neural correlates of category-specific knowledge. Functional magnetic resonance imaging (fMRI) data show neural activity associated with silent naming of animals and tools shown in pictures. Regions with greater activity when animals were named (shown in **yellow and red**) include the lateral fusiform gyrus (1) and right superior temporal sulcus (4).

Regions with greater activity when tools were named (**blue**) include the medial fusiform gyrus (2), left middle temporal gyrus/inferior temporal sulcus (3), and left ventral premotor cortex (5). (Reproduced, with permission, from Martin and Chao 2001.)

movements associated with the use of an object, and in left middle temporal regions, which represent information about how objects move in space (Figure 65–8).

Implicit Memory Supports Perceptual Priming

Implicit memory stores forms of knowledge that are typically acquired without conscious effort and which guide behavior unconsciously. Priming is a type of implicit memory that operates in amnesic patients as well as healthy subjects, suggesting that it does not depend on medial temporal lobe structures.

Two types of priming have been proposed. *Conceptual priming* provides easier access to task-relevant semantic knowledge because that knowledge has been used before. It is correlated with decreased activity in left prefrontal regions that subserve initial retrieval of semantic knowledge. In contrast, *perceptual priming* occurs within a specific sensory modality, and according to Tulving and Schacter it depends on cortical

modules that operate on sensory information about the form and structure of words and objects.

Damage to unimodal sensory regions of cortex impairs modality-specific perceptual priming. For example, one patient with an extensive lesion of the right occipital lobe failed to demonstrate visual priming for words but had normal explicit memory (Figure 65–9). This condition is the reverse of that found in amnesic patients such as H.M., and provides further evidence that the neural mechanisms of priming are distinct from those for explicit memory.

Visual priming is almost always correlated with decreased activity in higher-order visual (extrastriate) areas of cortex. Randy Buckner and his colleagues using fMRI found that activity in extrastriate cortex was greater during the initial exposure to an object than when the object was presented again later. These findings parallel the finding that activity in the left prefrontal cortex is reduced during conceptual priming. Most tasks include both perceptual and conceptual priming, and there probably are no sharp distinctions between the two.

Other forms of nondeclarative memory subserve the learning of habits, the learning of motor, perceptual, and cognitive skills, and the formation and expression of conditioned responses. In general, these forms of implicit memory are characterized by incremental learning, which proceeds gradually with repetition. The neural circuits that initiate habit, motor skill, and conditioned learning are independent of the medial temporal lobe system responsible for explicit memory.

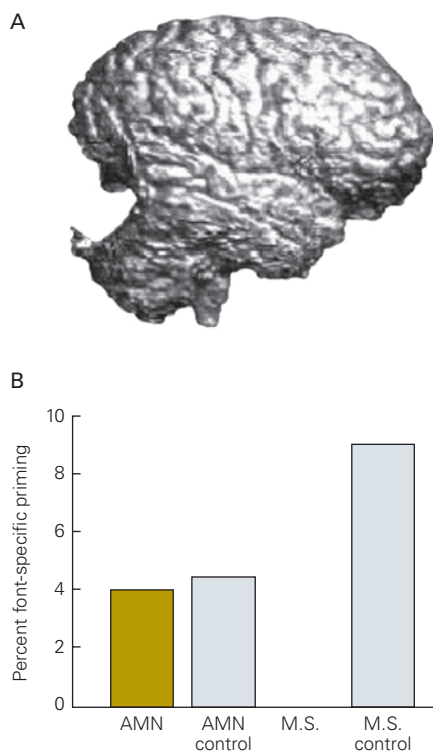


Figure 65-9 The right occipital cortex is required for visual priming for words. (Adapted with permission, from Vaidya et al. 1998.)

A. Structural magnetic resonance imaging (MRI) depicts the near complete removal of the right occipital cortex in a patient, M.S., who suffered pharmacologically intractable epilepsy with a right occipital cortical focus.

B. Font-specific priming is intact in amnesic patients (AMN) and their controls as well as in the controls for patient M.S., but not in M.S. himself. Font-specific priming is a form of visual priming in which the individual is better able to identify a briefly flashed word when the type font is identical to an earlier presentation, compared to identification when the font is different (priming equals performance when the font is the same minus performance when the font is different). The patient M.S. has normal explicit memory, even for visual cues (data not shown), but lacks implicit memory for specific properties of visually presented words.

For example, H.M. is able to acquire new visuomotor skills, like the mirror-tracing task (see Figure 65-3).

New perceptual, motor, or cognitive abilities are also learned through repetition. With practice, performance becomes more accurate and faster, and these improvements generalize to learning novel information. Skill learning moves from a cognitive stage, where knowledge is represented explicitly and the learner must pay a great deal of attention to performance, to an autonomous stage, where the skill can be executed without much conscious attention. As an example, driving a car initially requires that one pay attention to each component of the skill, but after practice one no longer attends to the individual components.

The learning of sensorimotor skills depends in part on the basal ganglia, cerebellum, and neocortex. Dysfunction of the basal ganglia in patients with Parkinson and Huntington disease impairs learning of motor skills. Patients with cerebellar lesions also have difficulties acquiring some motor skills, and functional imaging of healthy individuals during sensorimotor learning shows changes in the activity of the basal ganglia and cerebellum. Finally, skilled behavior can depend on structural changes in motor neocortex, as seen by the expansion of the cortical representation of the fingers in musicians (see Chapter 67).

Perceptual learning improves the ability to make sense of novel sensory inputs, as in learning to read mirror-reversed text or recognizing novel objects by reference to familiar categories. Amnesic patients with damage to the medial temporal lobe can learn to read mirror-reversed text but this learning is mildly impaired in Huntington disease and variably impaired in Parkinson disease. Patients with cerebellar lesions have no difficulty with perceptual learning, even though the learning of motor skills is impaired.

A neuroimaging study by Russell Poldrack and his colleagues suggests that extensive practice with mirror reading produces a shift in the parts of the brain involved in the task. In this study performance of the mirror-reading task before practice was correlated with activity in ventral visual processing regions as well as extensive activity in the parietal cortex. After practice, activity decreased in the parietal cortex but increased in the left inferior temporal cortex, a region associated with representing visual form (Figure 65-10). These results reflect a transition from having to mentally rotate the mirror-reversed words to the ability to read directly the reversed letters. Different neural processes are involved once skilled performance moves from the cognitive to the autonomous stage. Similar neural changes have been observed in imaging studies of motor and visual-motor skill learning.

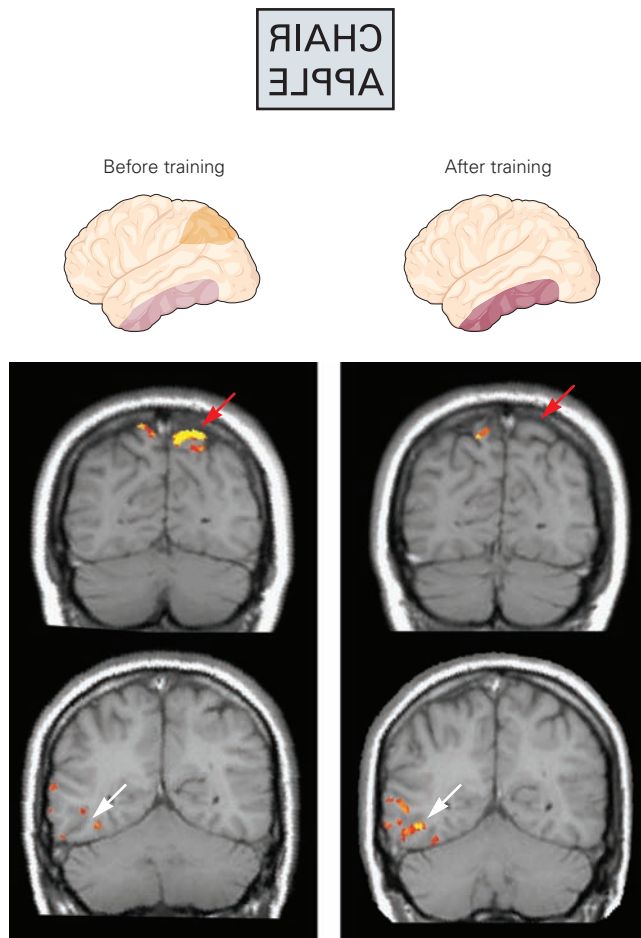


Figure 65–10 Perceptual learning involves a shift from cognitive to autonomous stages that use different neural pathways. Subjects are asked to read mirror-reversed text, something most people rarely encounter. Prior to training individuals rely on the parietal cortex (red arrow) and to a lesser extent the inferior temporal cortex (white arrow). After extensive training the processing pathways involved in the task appear to be different. Individuals rely less on the parietal cortex and more on the inferior temporal cortex. (Reproduced, with permission, from Poldrack et al. 1998.)

Implicit memory also underlies habit learning or Pavlovian associative conditioning, the gradual learning about the predictive relationship between a stimulus and a response (discussed later). Habit learning in humans has been studied using the probabilistic classification task, where subjects attempt to predict accurately one of two possible outcomes based on the presentation of a set of cues, with each cue having a probabilistic relation to each outcome. For example, subjects may be asked to predict the weather (rain or sunshine) based on a set of cue cards (Figure 65–11).

Because the associations between the cues and outcomes are probabilistic, thus requiring numerous trials to learn, explicit (conscious) memory of specific trials is not as useful for successful performance as the gradual accumulation of knowledge about the stimulus-outcome associations. Barbara Knowlton and colleagues have shown that, in contrast to patients with medial temporal lobe lesions, patients with basal ganglia disorders are severely impaired in this task.

Implicit Memory Can Be Associative or Nonassociative

Our consideration of implicit memory has so far focused on humans. But some forms of implicit memory can also be studied in nonhuman animals, and animal studies have distinguished two types of implicit memory: nonassociative and associative. With nonassociative learning an animal learns about the properties of a single stimulus. With associative learning the animal learns about the relationship between two stimuli or between a stimulus and a behavior.

Nonassociative learning results when a subject is exposed once or repeatedly to a single type of stimulus. Two forms of nonassociative learning are common in everyday life: habituation and sensitization. Habituation, a decrease in a response, occurs when a benign stimulus is presented repeatedly. For example, most people in the United States are startled when they first hear the sound of a firecracker on Independence Day, but as the day progresses they become accustomed to the noise and do not respond. Sensitization (or pseudo-conditioning) is an enhanced response to a wide variety of stimuli after the presentation of an intense or noxious stimulus. For example, an animal will respond more vigorously to a mild tactile stimulus after receiving a painful pinch. Moreover, a sensitizing stimulus can override the effects of habituation, a process called dishabituation. For example, after the startle response to a noise has been reduced by habituation, one can restore the intensity of response to the noise by delivering a strong pinch.

With sensitization and dishabituation the timing of stimuli is not important because no association between stimuli must be learned. In contrast, with two forms of associative learning the timing of the stimuli to be associated is critical. Classical conditioning involves learning a relationship between two stimuli, whereas operant conditioning involves learning a relationship between the organism's behavior and the consequences of that behavior.

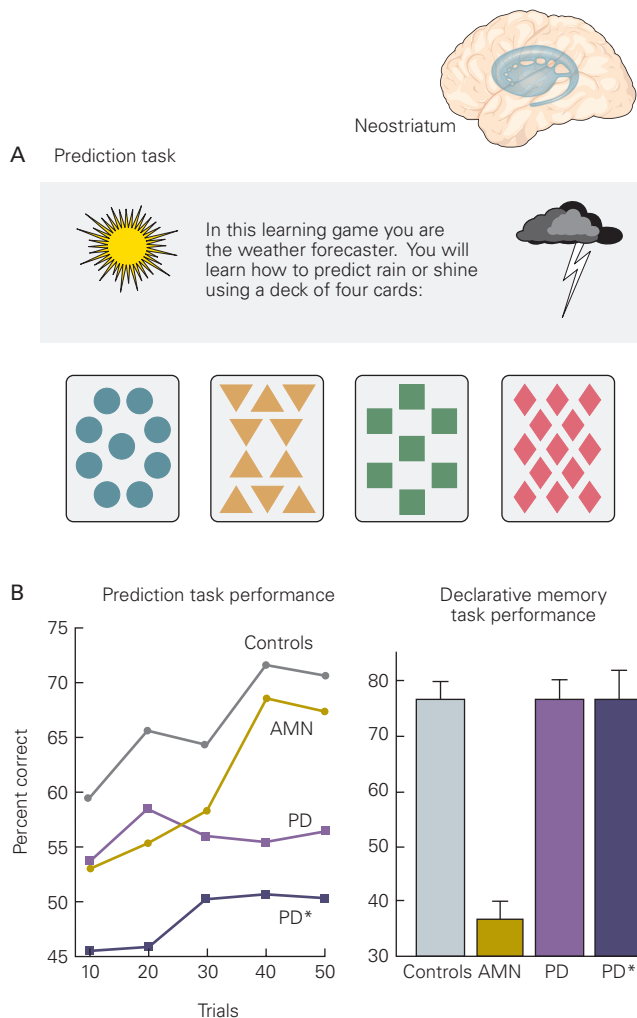


Figure 65-11 Learning predictive relationships involves the neostriatum.

A. Subjects are instructed to predict whether the weather will be rain or sunshine based on a set of cue cards. Each cue card has a probabilistic relation to each weather outcome (eg, predicting sunshine either 75, 57, 43, or 25% of the time). Subjects attempt to learn these relations during training and they are told after each trial whether their prediction is correct or incorrect.

B. Performance on the prediction task across the first 50 training trials is plotted on the left; performance results on a declarative memory test are shown on the right. Amnesic patients (**AMN**) initially learn the prediction task at the same rate as healthy control subjects, although their performance on the declarative memory task is impaired. By contrast, patients with Parkinson disease (**PD**), who suffer impairments in basal ganglia function, perform poorly on the prediction task but perform as well as controls on the declarative memory task. **PD*** identifies a subgroup of the Parkinsonian patients with the most severe symptoms. (Reproduced, with permission, from Knowlton, Mangels, and Squire 1996.)

Classical Conditioning Involves Associating Two Stimuli

Classical conditioning was first described at the turn of the century by the Russian physiologist Ivan Pavlov. The essence of classical conditioning is the pairing of two stimuli. The conditioned stimulus (CS), such as a light, a tone, or a touch, is chosen because it produces either no overt response or a weak response usually unrelated to the response that eventually will be learned. The reinforcement, or unconditioned stimulus (US), such as food or a shock, is chosen because it normally produces a strong and consistent response (the unconditioned response), such as salivation or withdrawal of the leg. Unconditioned responses are innate; they are produced without learning. Repeated presentation of a CS followed by a US gradually elicits a new or different response called the conditioned response.

One way of explaining conditioning is that repeated pairing of the CS and US causes the CS to become an anticipatory signal for the US. With sufficient experience an animal will respond to the CS as if it were anticipating the US. For example, if a light is followed repeatedly by the presentation of meat, eventually the sight of the light itself will make the animal salivate. Thus classical conditioning is the way an animal learns to predict events.

The probability of occurrence of a conditioned response decreases if the CS is repeatedly presented without the US. This process is known as extinction. If a light that has been paired with food is later repeatedly presented in the absence of food, it will gradually cease to evoke salivation. Extinction is an important adaptive mechanism; it would be maladaptive for an animal to continue to respond to cues that are no longer meaningful to it. The available evidence indicates that extinction is not the same as forgetting, but that something new is learned—the CS now signals that the US will not occur.

For many years psychologists thought that classical conditioning resulted as long as the CS preceded the US by a critical time interval. According to this view, each time a CS is followed by a US (reinforcing stimulus) a connection is strengthened between the internal representations of the stimulus and response or between the representations of one stimulus and another. The strength of the connection was thought to depend on the number of pairings of CS and US.

A substantial body of evidence now indicates that classical conditioning cannot be adequately explained simply by the fact that two events or stimuli occur one after the other (Figure 65-12). Indeed, it would not be

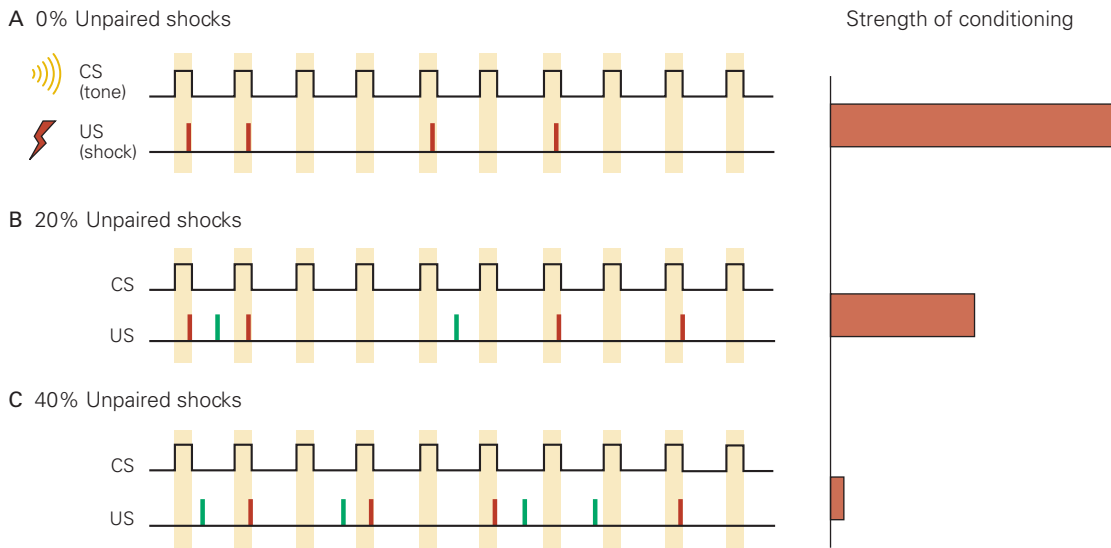


Figure 65-12 Classical conditioning depends on the degree to which two stimuli are correlated. In this experiment on rats a tone (the conditioned stimulus or CS) was paired with an electric shock (the unconditioned stimulus or US) in four out of 10 of the trials (red ticks). In some trial blocks the shock was presented without the tone (green ticks). The degree of conditioning was evaluated by determining how effective the tone alone was in suppressing lever-pressing to obtain food. Suppression of lever-pressing is a sign of a conditioned

defensive response, freezing. (Adapted, with permission, from Rescorla 1968.)

A. Maximal conditioning occurred when the US was presented only with the CS.

B–C. Little or no conditioning was evident when the shock occurred without the tone as often as with it (40%). Some conditioning occurred when the shock occurred 20% of the time without the tone.

adaptive to depend solely on sequence. Rather, all animals capable of associative conditioning, from snails to humans, remember actual relationships rather than simply sequential events. Thus classical conditioning, and perhaps all forms of associative learning, enables animals to distinguish events that reliably occur together from those that are only randomly associated.

Lesions in several regions of the brain affect classical conditioning. A well-studied example is conditioning of the protective eyeblink reflex in rabbits, a form of motor learning. A puff of air to the eye naturally causes an eyeblink. A conditioned eyeblink can be established by pairing the puff with a tone that precedes the puff. The conditioned response (an eyeblink in response to a tone) is abolished by a lesion at either of two sites. Damage to the vermis of the cerebellum abolishes the conditioned response but does not affect the unconditioned response (eyeblink in response to a puff of air). Interestingly, neurons in the same area of the cerebellum show learning-dependent increases in activity that closely parallel the development of the conditioned behavior. A lesion in the interpositus nucleus, a deep cerebellar nucleus, also abolishes the conditioned eyeblink. Thus both the vermis and the deep nuclei of

the cerebellum play an important role in conditioning the eyeblink and perhaps other simple forms of classical conditioning involving skeletal muscle movement.

Operant Conditioning Involves Associating a Specific Behavior with a Reinforcing Event

A second major paradigm of associative learning, discovered by Edgar Thorndike and systematically studied by B. F. Skinner and others, is operant conditioning (also called trial-and-error learning). In a typical laboratory example of operant conditioning a hungry rat or pigeon is placed in a test chamber in which the animal is rewarded for a specific action. For example, the chamber may have a lever protruding from one wall.

Because of previous learning, or through play and random activity, the animal will occasionally press the lever. If the animal promptly receives a positive reinforcer (eg, food) after pressing the lever, it will begin to press the lever more often than the spontaneous rate. The animal can be described as having learned that among its many behaviors (for example, grooming, rearing, and walking) one behavior is followed by food. With this information the animal is likely to press whenever it is hungry.

If we think of classical conditioning as the formation of a predictive relationship between two stimuli (the CS and the US), operant conditioning can be considered as the formation of a predictive relationship between an action and an outcome. Unlike classical conditioning, which tests the responsiveness of a reflex to a stimulus, operant conditioning tests behavior that occurs either spontaneously or without an identifiable stimulus. Operant behaviors are said to be emitted rather than elicited. In general, actions that are rewarded tend to be repeated, whereas actions followed by aversive, although not necessarily painful, consequences tend not to be repeated. Many experimental psychologists feel that this simple idea, called the law of effect, governs much voluntary behavior.

Because operant and classical conditioning involve different kinds of association—an association between an action and a reward or between two stimuli, respectively—one might suppose the two forms of learning are mediated by different neural mechanisms. However, because the laws of operant and classical conditioning are quite similar, the two forms of learning may use the same neural mechanisms. For example, timing is critical in both. In operant conditioning the reinforcer usually must closely follow the operant action. If the reinforcer is delayed too long, only weak conditioning occurs. Similarly, classical conditioning is generally poor if the interval between the conditioned and unconditioned stimuli is too long or if the unconditioned stimulus precedes the conditioned stimulus.

Associative Learning Is Constrained by the Biology of the Organism

Animals generally learn to associate stimuli that are relevant to their survival. For example, animals readily learn to avoid certain foods that have been followed by a negative reinforcement (eg, nausea produced by a poison), a phenomenon termed *taste aversion*.

Unlike most other forms of conditioning, taste aversion develops even when the unconditioned response (poison-induced nausea) occurs after a long delay, up to hours after the CS (specific taste). This makes biological sense, because the ill effects of infected foods and naturally occurring toxins usually follow ingestion only after some delay. For most species, including humans, taste-aversion conditioning occurs only when certain tastes are associated with illness. Taste aversion develops poorly if a taste is followed by a painful stimulus that does not produce nausea. Animals do not develop an aversion to a visual or auditory stimulus that has been paired with nausea.

Errors and Imperfections in Memory Shed Light on Normal Memory Processes

Memory allows us to revisit our personal past, provides access to a vast network of facts, associations, and concepts, and supports learning. But memory is not perfect. We often forget events rapidly or gradually, sometimes distort the past, and occasionally remember events that we would prefer to forget. In the 1930s the British psychologist Frederic Bartlett reported experiments in which people read and tried to remember complex stories. He showed that people often misremember many features of the stories, often distorting information based on their expectations about what should have happened (Box 65–1). Forgetting and distortion can provide important insights into the workings of memory.

Daniel Schacter classified memory's imperfections into seven basic categories, called "the seven sins of memory": transience, absent-mindedness, blocking, misattribution, suggestibility, bias, and persistence. Here we focus on six of these.

Absent-mindedness results from the lack of attention to immediate experience. Absent-mindedness during encoding is a likely source of common memory failures such as forgetting where one recently placed an object. Absent-mindedness also occurs when we forget to carry out a particular task such as picking up groceries on the way home from the office, even though we initially encoded the relevant information. Little is known about the neural bases of absent-mindedness.

Blocking refers to temporary inaccessibility of information stored in memory. People often have partial awareness of a sought-after word or image but are nonetheless unable to recall it accurately or completely. People sometimes feel that a blocked word is on "the tip of the tongue"—we are aware of the initial letter of the word, the number of syllables in it, or a like-sounding word. Determining which information is correct and which is incorrect requires a great deal of conscious effort.

In an fMRI study Anat Maril and her colleagues scanned people while they tried to recall the names of people or places in response to cues. When they entered a tip-of-the-tongue state, brain regions that have been implicated in cognitive tasks—the anterior cingulate and the right dorsolateral prefrontal cortex—showed intense activity. This activity likely reflects a subject's attempts to sort out correct from incorrect information and to resolve the memory block.

Absent-mindedness and blocking are sins of omission: At a moment when we need to remember information, it is inaccessible. However, memory is also

characterized by sins of commission, situations in which some form of memory is present but wrong.

Misattribution refers to the association of a memory with an incorrect time, place, or person. False recognition, a type of misattribution, occurs when individuals report that they “remember” items or events that never happened. Such false memories have been documented in controlled experiments where people claim to have seen or heard words or objects that had not been presented previously but are similar in meaning or appearance to what was actually presented. Studies using PET and fMRI have shown that the hippocampus has similar levels of activity during both true and false recognition, which may be one reason why false memories sometimes feel like real ones.

Suggestibility refers to the tendency to incorporate external information into memory, usually as a result of leading questions or suggestions. Research using hypnotic suggestion indicates that various kinds of false memories can be implanted in highly suggestible individuals, such as remembering hearing loud noises at night. Studies with young adults have also shown that repeated suggestions to imagine a childhood experience can produce memories of episodes that never occurred. These findings are important theoretically because they highlight that memory is not simply a “playback” of past experiences. Despite these important theoretical and practical implications, next to nothing is known about the neural bases of suggestibility.

Bias refers to distortions and unconscious influences on memory that reflect one’s general knowledge and beliefs. People often misremember the past to make it consistent with what they presently believe, know, or feel. As with suggestibility, however, almost nothing is known about the brain mechanisms of bias.

Persistence refers to obsessive memory, constant remembering of information or events that we might want to forget. Neuroimaging studies have illuminated some neurobiological factors that contribute to persistent emotional memories. For example, Larry Cahill and collaborators performed PET scans of subjects viewing a sequence of slides depicting an emotional story. The key results concerned activity in the amygdala, the almond-shaped structure located near the hippocampus and long known to be involved in emotional processing (see Chapter 48). The level of recall of the emotional components of the story was highly correlated with the level of activity in the amygdala during presentation of the story. This and related studies implicate the amygdala in the encoding and retrieval of emotionally charged experiences that can repeatedly intrude into consciousness.

Although persistence can be disabling, it also has adaptive value. The persistence of memories of disturbing experiences increases the likelihood that we will recall information about arousing or traumatic events at times when it may be crucial for survival.

Indeed, many memory imperfections may have adaptive value. For example, although the various forms of forgetting (transience, absent-mindedness, and blocking) can be annoying, a memory system that automatically retains every detail of every experience could result in an overwhelming clutter of useless trivia. This is exactly what happened in the fascinating case of Shereshevski, a mnemonist studied by the Russian neuropsychologist Alexander Luria. Shereshevski was filled with highly detailed memories of his past experiences and was unable to generalize or to think at an abstract level. A healthy memory system does not encode, store, and retrieve the details of every experience. Thus transience, absent-mindedness, or blocking allows us to avoid the unfortunate fate of Shereshevski.

An Overall View

We began this chapter by noting three key principles: (1) several different forms of learning and memory can be distinguished behaviorally, (2) memory can be analyzed in terms of discrete operations (encoding, storage, consolidation, and retrieval), and (3) imperfections and errors in remembering can provide telltale clues about learning and memory.

Considerable evidence supports the first principle, that there are different forms of memory, and we are learning that each involves different regions or combinations of regions in the brain. Thus working memory, which maintains goal-relevant information for short periods, has several neural components. Explicit memory involves the encoding and retrieval of two classes of knowledge: episodic memory, which represents personal experiences, and semantic memory, which represents general knowledge and facts. Explicit memory is typically retrieved deliberately and with some awareness that one is engaged in an act of remembering.

Implicit memory includes forms of perceptual and conceptual priming, as well as the learning of motor and perceptual skills and habits. It tends to be inflexible and expressed in the performance of tasks without conscious awareness. Implicit memory flows automatically in the course of perceiving, thinking, and acting.

Considerable progress also has been made concerning our second principle, that memory involves discrete encoding, storage, consolidation, and retrieval

processes. Encoding of new memories depends critically on contributions from specific regions within the cortex and medial temporal lobe as shown most clearly in recent studies using fMRI.

The initiation of long-term storage of explicit memory requires the temporal lobe system, as highlighted by studies of amnesic patients such as H.M. Consolidation processes stabilize stored representations, rendering explicit memories no longer dependent on the medial temporal lobe. Retrieval of episodic memory involves the medial temporal lobe, as well as frontal and parietal cortices. Implicit memory, in contrast, involves a wide variety of brain regions, most often cortical areas that support the specific perceptual, conceptual, or motor systems recruited to process a stimulus or perform a task.

The third principle, that the past can be forgotten or distorted, is based on studies demonstrating that memory is not a faithful record of all details of every experience. Retrieved memories are the result of a complex interplay among various brain regions, and can be reshaped over time by multiple influences. Various forms of forgetting and distortion tell us much about the flexibility of memory that allows the brain to adapt to the physical and social environment.

Daniel L. Schacter
Anthony D. Wagner

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