undergoing brain surgery for medical reasons, such as severe epilepsy, when electrode implantation is used to localize the site of seizure generation. In one study, intracranial electroencephalography (iEEG) signals were measured using subdural electrodes placed in the medial temporal lobe and other areas of cortex. A subject first learned associations between pairs of words and then had to retrieve memories of those associations. The retrieval of memories was associated with neural activity in the hippocampus, coupled with neural activity in temporal association cortex, a region involved in language and multisensory integration. This coupled neural activity was associated with a reactivation of cortical patterns that were initially observed when participants first memorized word pairs. This finding provides a link between the neural activity observed in the hippocampus during initial encoding of a memory and the later coupled activity in the temporal association cortex during retrieval. Related observations of reactivation of encoding patterns during retrieval have been reported in numerous human functional imaging studies, documenting the ubiquity of such effects. As with encoding of episodic memory, retrieval involves a complex interaction between the medial temporal lobe and distributed cortical regions, including frontoparietal networks and other high-level association areas.

Episodic Memory Contributes to Imagination and Goal-Directed Behavior

Memory enables us to use our past experience to predict future events, thus promoting adaptive behavior. Like retrieval of memories, imagination of future events involves construction of details from memory. The first report of a possible connection between memory and imagination came from the case study of patient K.C., as reported by Endel Tulving in 1985. Patient K.C. displayed typical and devastating amnesia as a result of damage to his hippocampus and medial temporal lobe. Similar to patient H.M., he had a complete lack of episodic memory while language and nonepisodic functions were unimpaired. Tulving's studies revealed further that such brain damage was associated with the loss of the ability to imagine events in the future. When asked what he would be doing the next day, K.C. was unable to provide details.

The importance of the hippocampus in imagining future events is also seen with fMRI studies. Such studies examined brain activity of healthy individuals, comparing activity when subjects were asked to remember an event from the past (eg, think of your birthday last year) with activity when they imagined events in the future (eg, imagine a beach vacation next summer). The subjects were asked to report any vivid details of the event that came to mind. The MRI scans showed a striking overlap in the network of brain regions that were active during memory retrieval and imagination of future events. This network included the hippocampus, prefrontal cortex, posterior cingulate cortex, retrosplenial cortex, and lateral parietal and temporal areas (Figure 52–7).

Further evidence supporting the view that episodic memory and hippocampal function are necessary for planning future behavior comes from a study on human performance of a spatial navigation task using virtual reality simulations. High-resolution fMRI and multivoxel pattern analysis (Chapter 6) showed that activity in the hippocampus was related to simulation of navigation goals. Moreover, hippocampal activity during planning covaried with goal-related activity in prefrontal, medial temporal, and medial parietal cortex (Figure 52–8).

Episodic memory encoding and storage are also influenced by the adaptive value of events. Alison Adcock and colleagues showed that the anticipation of a potential reward can enhance memory by eliciting coordinated activity between the medial temporal lobe and midbrain regions that are rich in dopamine neurons. Reward can also retroactively enhance memories. When human participants navigate a maze for a reward, they have better memory for neutral events that happened right before the reward. The ability to retroactively shape episodic memory based on outcomes is important because the relevance of a specific episode may only become known after the fact. Together with the role of episodic memory in constructing the retrieval of past events and in imagining and simulating future events, the findings on reward support the view that a major function of episodic memory is to guide adaptive behaviors.

The Hippocampus Supports Episodic Memory by Building Relational Associations

In addition to the broad role of the hippocampus in episodic memory, future thinking, and goal-directed behavior, studies of rodents first pointed to a role for the hippocampus in spatial navigation (Chapter 54), findings that were later supported by studies of nonhuman primates and humans. In rodents, single neurons in the hippocampus encode specific spatial information, and lesions of the hippocampus interfere with the animal's memory for spatial location. 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,
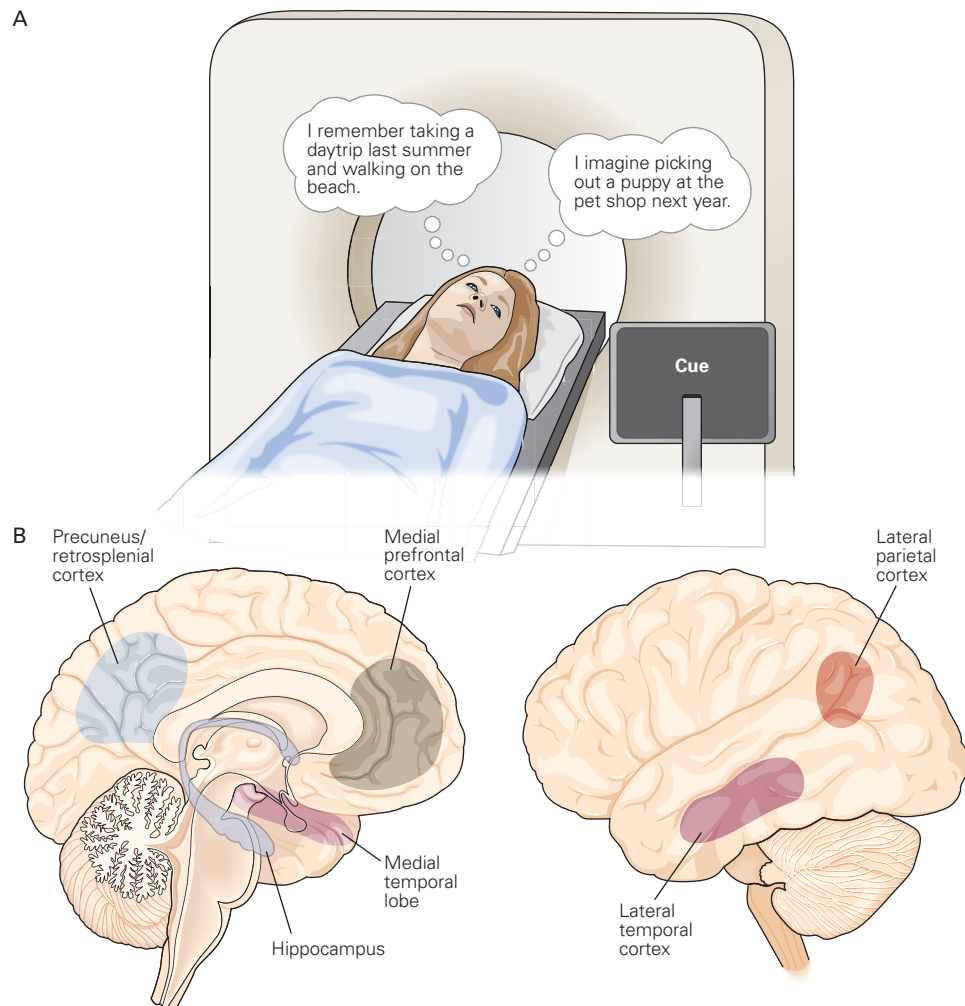
Figure 52–7 Brain regions supporting retrieval of memories for past events and imagination of future events. (Adapted, with permission, from Schacter, Addis, and Buckner 2007.)

A. Subjects were instructed to either remember a personally experienced event in their past or imagine a plausible event in their future while lying inside a functional magnetic resonance imaging scanner. Events are elicited by a cue word (eg, "beach" or "birthday"). Subjective ratings of event phenomenology (eg, vividness and emotionality of the episode) and detailed event descriptions are often obtained in an interview following the scanning in order to confirm that an episodic event was successfully generated.

B. The core brain system that mediates past and future thinking is consistently activated while remembering the past, when envisioning the future, and during related forms of mental simulation. Prominent components of this network include medial prefrontal regions, posterior regions in the medial and lateral parietal cortex (extending into the precuneus and retrosplenial cortex), the lateral temporal cortex, and the medial temporal lobe. Moreover, regions within this core brain system are functionally correlated with each other and with the hippocampus. This core brain system is thought to function adaptively to integrate information about relationships and associations from past experiences to construct mental simulations about possible future events.

objects, or people are recalled. These physiological findings are consistent with the clinical observation that lesions of the right hippocampus differentially give rise to problems with spatial orientation, whereas lesions of the left hippocampus differentially cause deficits in verbal memory.

The fact that the hippocampus supports spatial processing, semantic memory, and episodic memory raises questions about how the hippocampus contributes to such different behaviors. One compelling theory, proposed by Howard Eichenbaum and Neal Cohen, suggests that the hippocampus provides a general mechanism for forming and storing complex multimodal associations. According to this view, the hippocampus binds in memory the separate elements of experiences, encoding events as relational maps of

Figure 52–8 Neural circuits supporting memory-based goal-directed navigation. (Reproduced, with permission, from Brown et al. 2016.)

A. Human participants navigate to goals in a virtual reality environment while being scanned with functional magnetic resonance imaging. They first explore the space and learn where goals are located and then are tested on their ability to navigate to specific goals.

B. Navigational planning elicits goal-related activity in a core network including the hippocampus, medial temporal lobe, parahippocampal cortex (**PHC**), and orbitofrontal cortex (**OFC**).
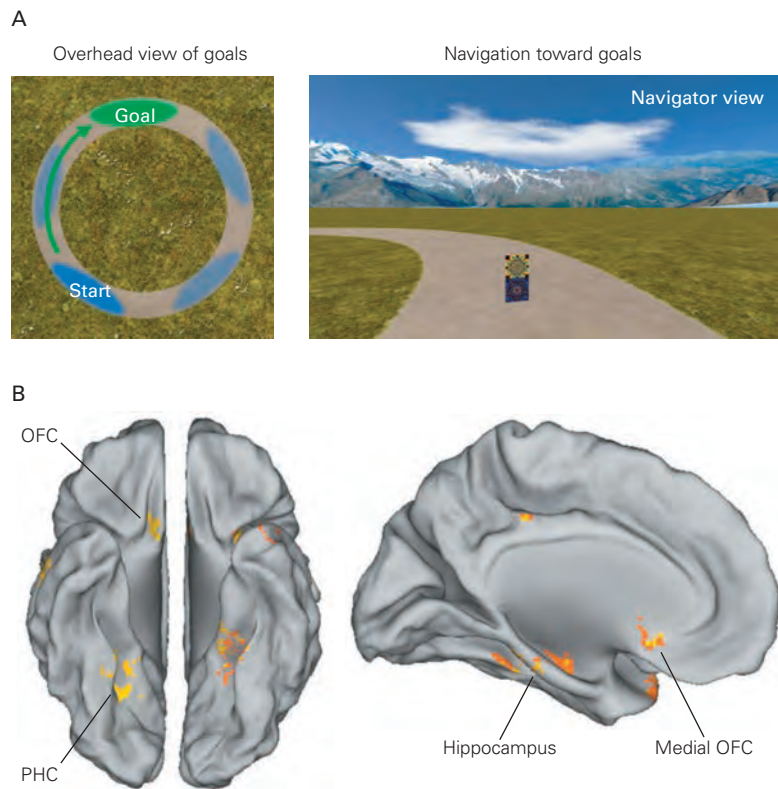
items within spatial and temporal contexts, thus composing a "memory space" that can distinguish distinct episodes, or sequences of events, even when the same (or similar) events occur in different episodes (Figure 52–9). As discussed later in this chapter, the view that the hippocampus encodes relations offers insights into the mechanism by which memories are built and explains why, in some cases, the hippocampus may contribute to memory processes that are not consciously accessible but do encode relations.
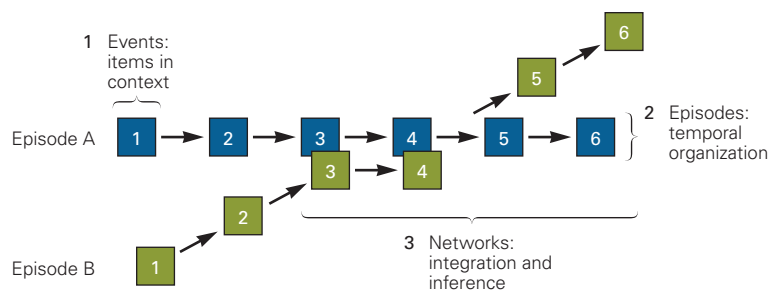

Figure 52–9 The hippocampus supports relational processing underlying episodic memory. A conceptual illustration of a memory space designating three key types of relational processing: events, episodes, and networks. The schematic illustrates processing of two distinct episodes (Episode A and Episode B), which have both distinct and overlapping elements. For example, the episodes might be two distinct visits to an Italian restaurant on separate evenings with the same friend. The evenings are experienced as distinct (different days, different weather, different moods), yet they share some overlap (the company of the same friend at the same restaurant). *Events* (**1**) are defined as items (objects, behaviors) that are associated with the context in which they occurred (denoted here as events 1 to 6 in each episode, such as the specific table you sat at, the food you ordered, etc.). *Episodes* (**2**) are defined in this view as the temporal organization of these events. While most of the items in each episode are unique, some of them overlap (here, items 3 and 4; in the example, your friend and the restaurant). Relational *networks* (**3**) are formed via associations between events and episodes by way of the overlapping events, supporting the capacity for links between indirectly related events. (Reproduced, with permission, from Eichenbaum and Cohen 2014. Copyright © 2014 Elsevier Inc.)

Implicit Memory Supports a Range of Behaviors in Humans and Animals

Just as there are many ways in which explicit memory guides behavior, there are also many ways in which nonexplicit forms of memory, those without conscious awareness, can influence behavior. Implicit memory refers to forms of knowledge that guide behavior without conscious awareness. Priming, for example, is the automatic influence of exposure to one cue on processing of a later cue.

Priming can be classified as conceptual or perceptual. *Conceptual priming* provides enhanced 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 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 surgical lesion of the right occipital lobe failed to demonstrate visual priming for words but had normal explicit memory (Figure 52–10). This condition is the reverse of that found in amnesic patients such as H.M., suggesting that the neural mechanisms of priming are distinct from those for explicit memory. The fact that perceptual priming can be intact in patients with amnesia due to medial temporal damage further suggests that it is distinct from explicit memory.

Different Forms of Implicit Memory Involve Different Neural Circuits

Other forms of implicit memory subserve the learning of habits and 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 and, in some cases, is driven by reinforcement.

The learning of habits, motor skills, and conditioned responses can take place independently of the medial temporal lobe system. For example, H.M. was able to acquire new visuomotor skills, like the mirror-tracing task (see Figure 52–3). Therefore, early theories posited that these forms of memory generally do not depend on the medial temporal lobe but, rather, depend on the basal ganglia and cerebellum (see Chapters 37 and 38). However, subsequent work
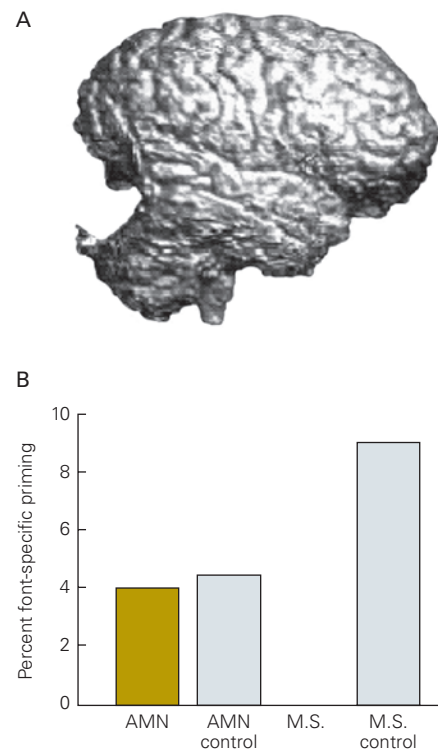
Figure 52–10 The right occipital cortex is required for visual priming for words. (Adapted from Vaidya et al. 1998.)

A. Structural magnetic resonance imaging 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 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 is measured as performance when the font is the same minus performance when the font is different. 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. 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.

suggested that this is not a general rule and that the medial temporal lobe is required for forms of implicit learning that store relational associations, even when such associations are learned through repetition and appear to take place without conscious awareness.

It is now thought that several kinds of incremental implicit learning involve the medial temporal lobes. For example, Turk-Browne and colleagues investigated implicit learning of regularities between visual cues, called statistical learning. In a typical statistical learning task, human subjects are presented with a

stream of sounds or images that follow a structured sequence or "grammar" of repetitions. Learning of the sequence is typically measured by a faster reaction time to repeated compared to nonrepeated sequences. At first glance, it would appear that statistical learning should not involve the medial temporal lobe: The learning is nonverbal, it does not require conscious thought and is therefore implicit, and it is assumed to reflect the accumulated computation of probabilistic relationships across multiple episodes, rather than the specific memory of one episode. Yet fMRI studies show that the hippocampus is active during statistical learning, and damage to the medial temporal lobe has been found to impair performance on this implicit task.

Statistical learning is an example of how learning takes place through repetition. 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 be consciously aware of each component of the skill, but after practice, one no longer attends to the individual components.

The learning of sensorimotor skills depends on numerous brain regions that vary with the specific associations being learned. As we learned in Chapter 38, these include 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. Functional imaging of healthy individuals during sensorimotor learning shows changes in the activity of the basal ganglia and cerebellum and their connectivity with cortical regions. Danielle Bassett and colleagues have used network-analysis algorithms applied to whole-brain fMRI data to characterize dynamic changes in network functional connectivity that take place during motor skill learning. 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 (Chapter 53).

Habits emerge from the repeated association of cues or actions with rewarding outcomes. Habit learning in humans is studied with tasks that involve incremental learning of stimulus–reward associations. In a typical task, subjects perform a series of trials in which they are asked to choose among visual cues and receive trial-by-trial feedback on their choice. The relationship between the cues and the feedback varies probabilistically over the course of the task so that participants must keep updating their responses based on the feedback. Because learning takes place over numerous trials, explicit memory of any one specific trial may not be as useful for successful performance as the gradual accumulation of feedback-driven learning of stimulus–outcome associations.

fMRI studies demonstrate that incremental learning of stimulus–reward associations depends on the striatum, the area of the basal ganglia that receives input from neocortex, and its modulatory dopaminergic inputs. Patients with a loss of striatal dopamine, as occurs in Parkinson disease, are less effective at learning based on trial-by-trial reinforcement. These findings are consistent with other studies that indicate dopamine has an important role in modulating cortico-striatal circuitry for reinforcement learning (see Chapter 38).

At first glance, stimulus-reward learning appears to be precisely the sort of learning that does not depend on the medial temporal lobe: It is implicit rather than explicit, and it occurs gradually rather than through an explicit memory for a single event. Indeed, early theories posited that learning probabilistic stimulus–reward associations does not depend on the medial temporal lobe. However, subsequent work has revealed that the hippocampus does contribute to stimulus–reward learning under some circumstances, such as when the task demands learning of more complex stimulus–stimulus associations (Figure 52–11). The contribution of the hippocampus to implicit learning takes place via interactions with other cortical and subcortical circuits. fMRI studies show functional connectivity between the hippocampus and the striatum in support of learning across a variety of tasks. Interactions between the hippocampus and the striatum are sometimes competitive and sometimes cooperative, depending on the demands of the task.

Implicit Memory Can Be Associative or Nonassociative

Some forms of implicit memory have also been studied in nonhuman animals, and these 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. We consider the cellular mechanisms of implicit memory in animals in the next chapter.
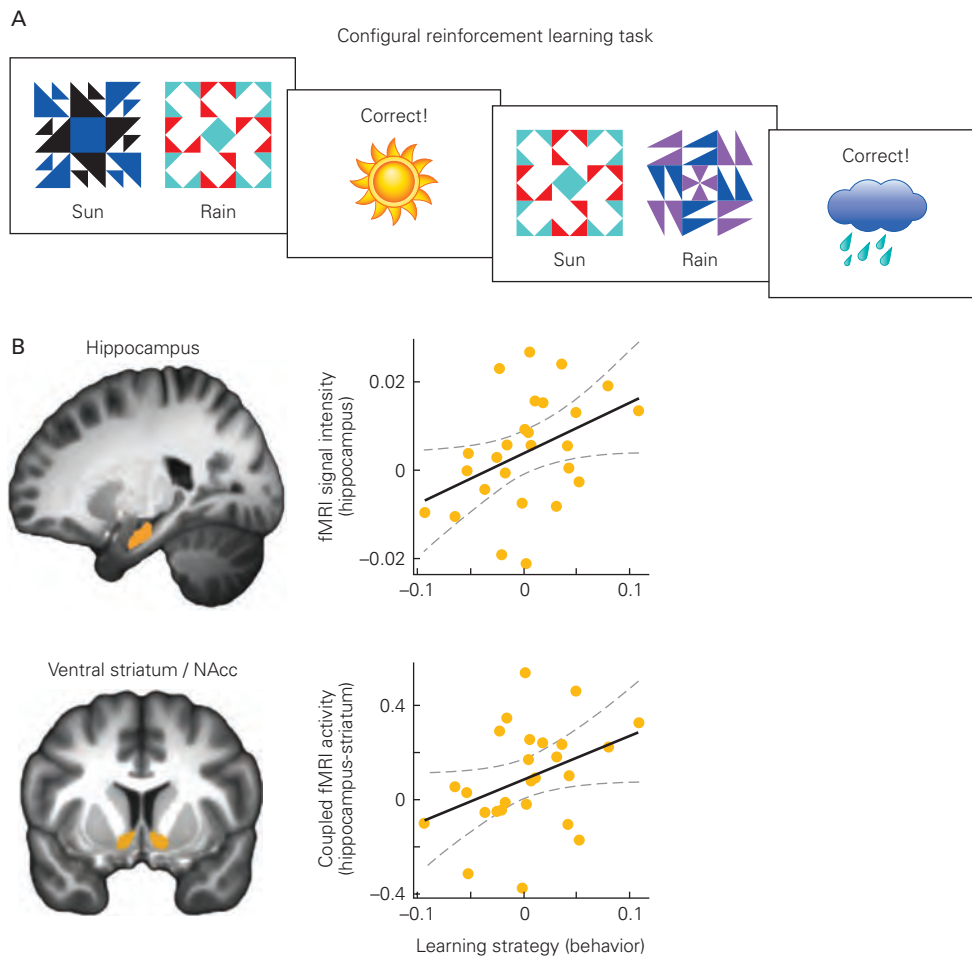
Figure 52–11 Learning stimulus–response associations involves both the striatum and the hippocampus. (Adapted, with permission, from Duncan et al. 2018.)

A. Participants use trial-by-trial reinforcement to learn to predict outcomes (rain or sun) based on cues (colorful shapes). The cues have a probabilistic relation to each weather outcome that the viewer learns by trial and error. The weather can be predicted based either on each individual cue or on the combined presentation of the two cues (their configuration). Reinforcement learning models can discern which strategy each subject uses.

B. The striatum is known to play a critical role in learning to update choices based on reinforcement. When subjects learn about the configuration, this same task also elicits activity in the hippocampus and increased coupling of activity in the hippocampus and the striatum. Scatter plots show that the extent to which subjects use a configural learning strategy correlates with blood oxygenation level–dependent activity in the hippocampus and with functional coupling between the hippocampus and the striatum. The images show activity in hippocampus and the nucleus accumbens (**NAcc**), a region in the ventral portion of the striatum that responds to rewarding stimuli. (Abbreviation: **fMRI**, functional magnetic resonance imaging.)

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 is a decrease in a response that 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.

Classical conditioning was first described in the early 1900s by the Russian physiologist Ivan Pavlov. The essence of classical conditioning is the pairing of two stimuli: a conditioned stimulus and an unconditioned stimulus. 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 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 a limb. 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 one way an animal learns to predict events.

The probability that an established conditioned response will occur 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. The available evidence indicates that extinction is not the same as forgetting; instead, 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 within 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 52–12). Indeed, it would not be adaptive to depend solely on sequence. Rather, all animals capable of associative conditioning, from snails to humans, remember the salient relationship between associated 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. One well-studied example is conditioning of the protective eyeblink reflex, 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. Studies in rabbits indicate that 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.

Another well-studied example is fear conditioning, which depends on the amygdala. In fear conditioning, a neutral cue, such as a tone, is paired with an aversive outcome, such as a shock. This pairing leads to a conditioned fear response in which the neutral tone alone elicits a behavioral reaction, such as freezing. Fear conditioning depends on plasticity in the inputs to and connections between the subnuclei of the amygdala, particularly the basolateral amygdala, as we will discuss in the next chapter.

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
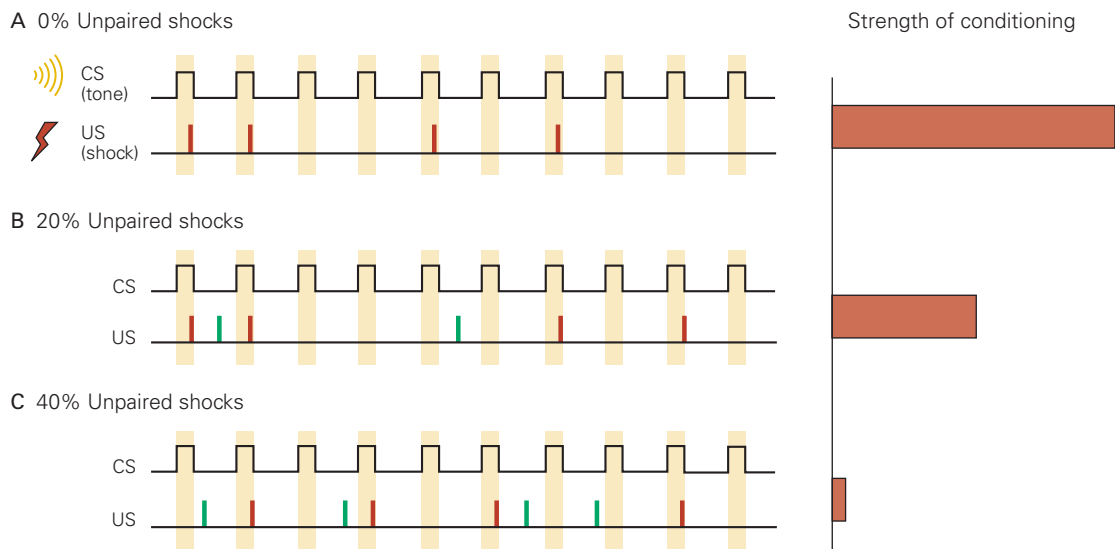
Figure 52–12 Classical conditioning depends on the degree of correlation of two stimuli. In this experiment with rats, a tone (the conditioned stimulus [**CS**]) was paired with an electric shock (the unconditioned stimulus [**US**]) in four out of 10 of the trials (**red ticks**). In some trial blocks, the shock was presented without the tone (**green ticks**). Suppression of lever-pressing to obtain food is a sign of freezing, a conditioned defensive response. The degree of conditioning was evaluated by determining how effective the tone alone was in suppressing lever-pressing to obtain food. (Adapted from Rescorla 1968.)

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

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

(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 (eg, grooming, rearing, and walking) one behavior is followed by food. With this information, the animal is likely to press the lever 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. Thus, 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 think that this simple idea, called the law of effect, governs much voluntary behavior.

Operant and classical conditioning involve different kinds of association—an association between an action and a reward or between two stimuli, respectively. However, the laws of operant and classical conditioning are quite similar. 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 CS and US is too long or if the US precedes the CS.

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. Also, 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 and adaptive behavior. 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 of what should have happened. Forgetting and distortion can provide important insights into the workings of memory.

Memory's imperfections have been classified into seven basic categories, dubbed 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 a 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.

Blocking refers to a temporary inability to access information stored in memory. People often have partial awareness of a sought-after word or image but are nonetheless unable to recall the entire word accurately or completely. Sometimes, it feels like 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.

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 positron emission tomography imaging and fMRI have shown that many brain regions show 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 new information into memory, usually as a result of leading questions or suggestions about what may have been experienced. 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 about a childhood experience can produce memories of events that never occurred. These findings are important theoretically because they highlight that memory is not simply a "playback" of past experiences (Box 52–1). 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. This idea is consistent with the idea of "predictive coding" supported by studies showing that even low-level neural mechanisms of perception and sensation are shaped by expectations. The specific brain mechanisms by which expectations influence memory are not well understood.

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. Some key results implicate the amygdala, the almond-shaped structure near the hippocampus long known to be involved in emotional