

The Nature of Learning and Memory

Memory Defines Our Individuality

Genes Set the Range of Our Capacities but Do Not Determine Who We Are
Our Individual Personalities and Intellect Result from a Lifetime of Learning and Memory

Memory Plays a Pervasive Role in Daily Life

Memory Is Involved at Multiple Levels during Everyday Behavior

Amazing Cases of Amnesia

A "Prisoner of Consciousness" Repeatedly Awakens
A "Lost Mariner" Has a Vivid Past but Lives Only in the Present

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An Example Battle between Behaviorists and Cognitivists

Theme 2: Major Insights about Learning and Memory Have Come from Studies of the Brain

Theme 3: The Concept of Multiple Memory Systems Unifies the Study of Learning and Memory

Theme 4: The Underlying Bases of Learning and Memory Are the Same in Humans and Animals

One day I walked into the elevator in a large office building and pressed the button for the upper floor where I would meet a colleague. On the way up, the elevator stopped and several people crowded in, pushing me to the back of the car. I found myself squeezed behind a young woman. At first there was nothing remarkable about this event. Then I smelled perfume—a scent that was at once pleasant, familiar, and out of place. What was that smell? Why was it so meaningful yet remote? I was transported mentally 35 years back in time . . . to high school! I felt like a student again, standing in the crowded hallway, wondering what class I was headed for. Then I remembered particular people, especially a girlfriend who wore that perfume. Her name came back to me, and the mystery was solved: She wore that perfume. I mulled it over, enjoying this olfactory journey into my past and recalling several nearly forgotten high school friends. Later I remembered that the perfume was Shalimar, a popular scent at that time.

This unexpected rush of memories happened in seconds. How did I learn and retain so much information? How did the faint cue of a perfume I last sensed so long ago evoke such a powerful memory? And why did the recollection unfold as it did, beginning with a sense of familiarity and importance, then a feeling of being in a particular place and time, and then the rush of images of specific places and people, and finally names and circumstantial details?

WE TAKE LEARNING and memory for granted. We use them all the time and in virtually everything we do. Do you ever think about what memory is and how it works? Memories are processed and stored by the brain, but brain science alone will not provide a complete understanding of memory. Memories can be relived like videos of our personal experiences, and memory has been described as a storehouse of accumulated knowledge about the world. But it is more than a large col-

lection of video clips and a library. Beneath our conscious awareness, memory contributes to a multitude of acts of perception, coordination, and emotion. For example, we learned to distinguish cars from other objects, to drive a car, and to be afraid at the sight of a car careening at us. How does memory help us accomplish these things?

This chapter has two purposes: to convince you that learning and memory play a central role in our mental lives, and to introduce you to the major themes of the science of learning and memory, which are also the main themes of this book.

Fundamental Questions

1. What are the contributions of genes and experience to our individuality?
 2. How big are the roles that learning and memory play in our everyday lives?
 3. What do early conceptions of learning and memory have to do with the modern science of learning and memory?
 4. What are the central principles of organization for understanding how learning and memory work?
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Memory Defines Our Individuality

How much of who we are is determined by our genetic makeup? How much is determined by learning from and remembering experiences? This, of course, is the *nature-nurture debate*: the long-standing and continuing controversy over human nature. This issue frequently comes up in cases of unusual individuals. When we hear about mass murderers, terrorists, and the like, we wonder whether a propensity or genetic determination might incline someone to violence, or whether violent tendencies are learned from abusive parents or a harmful social context. The more positive exceptions are our heroes, star athletes, political leaders, or famous scientists and thinkers. Did they inherit their intelligence, skills, and drive or learn these from others? Two overall points will help explain what makes each of us unique. First, genes operate in a general, statistical way to set the boundaries of our behavioral capacities. Second, the memories we accrue by learning from experiences shape our individual characteristics within the boundaries determined by our genes.

Genes Set the Range of Our Capacities but Do Not Determine Who We Are

Half a century of DNA research has highlighted the importance of genes. Of course genes play a major role in determining our externally apparent characteristics—

from our facial features to our particular tastes in music and food. Decades of research indicate that genes set the general range of our intellectual capabilities and determine the scope of our perceptual abilities and emotional sensitivities. And genes contribute to our predispositions for particular personality types, preferences, aversions, and abilities. Thus there are many well-characterized examples of relationships between genetic constitution (called the *genotype*) and observable mental and physical qualities and abilities (the *phenotype*). Consider the research showing that the male genotype is better at spatial memory than the female genotype. Thus, for example, males generally outperform females in navigating within a large building to find their way back to a starting position (Postma et al., 2004). Conversely, females are better at memory for some nonspatial details of specific experiences; these differences may be due to differences in sex hormones and their effects on brain development. Such studies show that genes in some way contribute strongly to certain cognitive capacities.

However, the relationship between genotype and phenotype is general and statistical. The genotype characterizes the range and distribution of a particular phenotype over a population (see Figure 1.1). In other words, genotype-phenotype correlations tell us more about populations than individuals. Thus, continuing with the example of sex differences in spatial and nonspatial memory, the full range of male spatial and nonspatial memory abilities overlaps considerably with that of females. So although the population of males generally performs better than the population of females in spatial memory tasks, some females surpass some males in this area, and vice versa for nonspatial memory. Individuals' qualities can fall anywhere in the broad range described by these correlations.

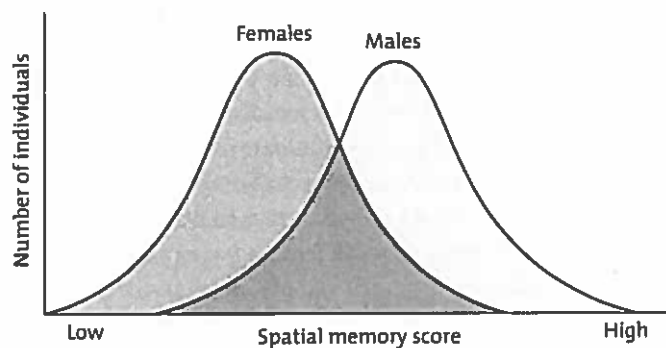


FIGURE 1.1 Overlapping distributions of scores on an ideal test of spatial memory.

Our Individual Personalities and Intellect Result from a Lifetime of Learning and Memory

Genetic predispositions characterize the *range* of our capacities, not the specific ways in which we use those capacities. Consider once more the finding that males tend to excel at some aspects of spatial learning and memory. That superior general capacity does not give any individual man the memory of any particular building. Likewise, some people have a strong predisposition for expertise in music or art. But if they are untrained in these skills, the phenotype may not be observed. Even among those who can learn to play instruments readily, the ability to play a violin (or any particular instrument) is not innate. Thus, in a general and statistical way, genes influence how we think and even the general topics we think about (food, sex, power, and so on). But that is where genetic influence stops. Genes do not influence the particulars of what we think about (fast food or particular dates or bosses, respectively).

We are programmed to babble, but we *learn* to speak a particular language. We *learn* to speak a particular language fluently and accumulate many facts and concepts to speak about. And we *learn* our personal memories from childhood accidents to first dates to first jobs. These memories of a lifetime of first-person events constitute a unique personal history.

We are genetically programmed to crawl, then to walk, then to run. But the refinement of motor coordination, even for these basic skills, relies on substantial experience and learning. Moreover, the development of specific skills depends critically on our ability to learn through extensive practice. Most of us learned to ride a bike. Now you do this easily. But do you remember how difficult and scary it was as you began to learn? Some of us learn to dance, swing a baseball bat or tennis racket, or play the piano. And we learn to do each of these with a personal style. These are examples of a broad variety of unique, specialized learned skills we pursue and use every day, effortlessly.

Some people are nervous and easily provoked, whereas others are mellow and imperturbable. These are examples of genetic predispositions for a comfortable level of stimulation. But we *learn* to appreciate forms of music and art that make us feel at ease or get us excited. A few specific fears may be genetically programmed (such as fear of snakes). But mostly we learn to fear particular people, dark alleys, or perhaps the music that precedes a shark attack in a summer action movie. Our individual personalities are defined as we learn a broad range of attractions, aversions, comforts, and neuroses.

In sum, the study of memory can reveal how we came to be who we are. Our genes set broad limits on the characteristics we develop. Our experiences and the ways in which we integrate them compose the details of our individuality. Understanding how memory works has led us to a greater general appreciation of the

complex interactions between the mind and brain, and especially of how memory influences cognition, emotion, and consciousness.

Memory Plays a Pervasive Role in Daily Life

We usually speak of the capacity for learning and memory as an isolated ability, like the ability for athletics or music. But learning and memory can also be viewed as features of all our abilities. In this view, **learning** is the feature by which we can alter our skills, change our dispositions, add to our knowledge, and generally benefit or suffer from experience. And **memory** is the expression of that learning, revealed in alterations of our performance across a broad range of daily activities. Learning and memory influence many aspects of everyday activities simultaneously—from the simplest perceptions and movements to the most complex thought processes.

Memory Is Involved at Multiple Levels during Everyday Behavior

Think about the different levels in which your memory comes into play as you read this textbook. You remembered that Chapter 1 was your assignment and that this book was the text for the course. You instantly recognize the text as English, even if you know other languages; and you know how to find the first page of the assigned chapter and read down the page from left to right. Your knowledge of the structure of English-language books has already served you well.

You begin to read this chapter, and the letters are elements you remember. This may sound trivial; but compare how readily you read the current text with the next sentence printed in an unusual font. *Is this sentence as easy to read as the text of the previous sentence?* It probably requires just a little more time to read that last sentence, at least at first; but if you read it a couple of times, it becomes easy. So your memory is at work—first in recognizing letters and words in a familiar typeface, then in learning a new typeface.

Next consider your memory's role in recognizing words. Read the following text aloud: "Is-thay ext-tay is in ig-pay atin-Lay." Was this difficult? If you remember pig Latin from childhood, you can soon read it quickly and can translate the sentence into "This text is in pig Latin." Now let's put that recovered language to use: "Is-thay entence-say ould-shay e-bay ick-quay oo-tay ead-ray." You probably read and understood that sentence more readily than the first, demonstrating that you have reacquired a general facility with pig Latin. So even the simple act of reading requires memory at several levels: from recognizing letters in a particular font, to recognizing combinations of letters that compose words, to recognizing

and using language rules to learn a new language, to translating text into speech. Memory is critical to the simple act of reading at an amazing number of levels.

Now consider any thoughts you had when you encountered the pig Latin examples. Did that experience spark memories of learning to speak pig Latin and perhaps of the friends with whom you shared that language? Did you remember any particular people or events or just a feeling of what childhood was like?

Interim Summary

Memory, accumulated over a lifetime of learning, constitutes the individuality of every human being. Genes set the range and limits of our mental and physical capacities. But the specifics of each person's intellect, personality, and talents result from learning and the expression of memory throughout life. Along with the myriad acquired physical and mental skills we take for granted, we learn to fear dangerous situations, and we learn to appreciate particular styles of music and art. These broad learned aversions and enjoyments are elements of our personalities. We learn to speak and understand our particular languages. We learn world history, our family trees, and our own autobiographies. The vast contents and complex organization of our memories make each of us unique.

Amazing Cases of Amnesia

Another way to appreciate the central and pervasive role of learning and memory is to consider what life would be like without them. A loss of learning and memory capacity is called **amnesia**. Symptoms of amnesia have many possible causes, including major depression, head trauma, strokes, brief anoxia (loss of oxygen), normal aging, Alzheimer's disease, and many other ailments.

In many cases, amnesia causes partial memory loss, noticed as merely an increased forgetfulness of everyday events or an increase in the amount of study required to learn new information. But some cases involve a severe learning and memory impairment that may contrast with otherwise intact perceptual and cognitive capacities. Next we will consider case studies that illustrate the devastating effect of losing learning and memory capacity. A *complete* loss of learning and memory, including both the storehouse of memories you have accumulated to date and the ability to form new ones, would render you frightened and confused. However, even a limited impairment can be devastating. Many individuals lose certain components of memory while retaining other perceptual or intellectual abilities. These cases have helped researchers understand how memory works and recognize its broad importance.

A "Prisoner of Consciousness" Repeatedly Awakens

Consider Clive Wearing, a man described by Dr. Jonathan Miller in a television program titled *Prisoner of Consciousness*. Wearing (Figure 1.2) is a British musician who suffered an infection by the herpes simplex virus. This virus sometimes causes encephalitis, or brain inflammation, that leads to permanent brain damage. In Wearing's case the damage was diffuse and widespread, but the effects on intellectual capacity were specific and dramatic. He lost the capacity to form new lasting memories, a phenomenon called **anterograde amnesia**. In addition, Wearing lost some of his memories formed prior to the damage, a phenomenon called **retrograde amnesia**. Wearing's memories lost from retrograde amnesia date back for only a variable period of years prior to the onset of amnesia. A combination of anterograde and partial retrograde amnesia is a common pattern in memory loss following brain damage.

Wearing's disorder is particularly striking because his amnesia is severe and tragic in its emotional consequences. Wearing lives in a constant state of feeling that he has just awoken from a long sleep; he feels this sense of awakening each time there is a mere shift in focus during an otherwise continuity of wakefulness. He keeps a diary detailing the dates and times when he "regains consciousness." Wearing is obsessively committed to the notion that he has suddenly recovered his conscious state and is now well, and he becomes upset when this view is challenged. Thus he lives without a sense of the past or future, remembering experiences for only a few minutes while they are within his attention. Whenever the topic of activity or conversation turns, the emotional event wherein he "regains consciousness" begins again.



FIGURE 1.2 Clive Wearing with his wife, Deborah.

Notably, substantial components of Wearing's memory are intact. He can remember and use information long enough to carry a conversation. He knows his name and can generally describe his life before the memory loss, including highlights such as singing for the Pope and directing Handel's *Messiah* in London. His musical skills are remarkably spared. Thus he can still sight-read music and can sing a complex piece while accompanying himself on the harpsichord. On the other hand, much of his specific knowledge of facts and personal events in his musical career are lost. In one striking example, he wrote a book before suffering the memory loss, but he knows nothing about this topical material now.

A "Lost Mariner" Has a Vivid Past but Lives Only in the Present

Another remarkable case is Jimmie G., an amnesic man described by Dr. Oliver Sacks (1985) in his book *The Man Who Mistook His Wife for a Hat*. Jimmie G. suffered from Korsakov's syndrome—the destruction of neurons in the prefrontal cortex, temporal lobe, and mammillary bodies resulting from a combination of chronic alcoholism and associated poor diet. Jimmie grew up normally with a special interest in math and science. In 1943 he was drafted into the navy. Jimmie was a natural for radio and electronics and became a submarine radio operator. He pursued a long career in the navy and retired in 1965. Subsequently Jimmie ceased working, led an aimless life, and began to drink heavily. In 1970 he suffered a period of unconsciousness and delirium typical of Korsakov's syndrome. Over the following weeks, the confusional aspects of the disorder dissipated, leaving partial memory impairment.

As in Clive Wearing's case, Jimmie G.'s amnesia is selective to particular aspects of memory. Jimmie's retrograde amnesia can be dated to approximately 1945. Memories of his childhood and wartime experiences are vivid. His knowledge about the ships, radios, and science he used in the military is intact. But Jimmie is "stuck" in 1945. For example, Jimmie was shown a picture of the warship *Nimitz*, which was commissioned in 1975 and named for deceased Fleet Admiral Chester W. Nimitz, who had commanded the Pacific fleet in World War II. Jimmie was amazed at the ship's ultramodern design and could not understand how a new ship could have the name of a living admiral. When shown a picture of the Earth taken from the Moon, he wondered how that photograph could have been created. Jimmie panicked when he saw a current picture of himself, much older and grayer than his 19-year-old self of 1945. He wondered if the event was a nightmare or if he was crazy. Yet moments later, when Jimmie was distracted, he forgot the event and politely introduced himself to the doctor with whom he had just carried out such an upsetting conversation.

Other than his memory, Jimmie G.'s intellectual capacities are normal. However, his memory impairment affects everything he does. For example, Jimmie is

good at arithmetic calculations, but only those that can be solved quickly. If a problem has many time-consuming steps that involve remembering earlier parts, he becomes lost. As another example, Jimmie can reproduce the periodic table of chemical elements from memory acquired before his brain damage; but he leaves out elements discovered after 1945.

Sacks characterized Jimmie as “isolated in a single moment of being, with a moat or lacuna of forgetting all around him. . . . He is a man without a past (or future), stuck in a constantly changing, meaningless moment.” The nature of a sense of self without the contributions of memory is worth emphasizing. When Sacks asked Jimmie how he felt about his state, he responded, “I cannot say I feel ill. But I cannot say I feel well. I cannot say I feel anything at all.” Jimmie could not say that he was miserable, nor could he say he enjoyed life. When he was engaged in a game or puzzle, Jimmie would become keenly involved. But this, he felt, was meaningless play. The hospital staff once employed Jimmie’s intact typing skill, giving him a job typing forms from handwritten notes. Jimmie worked proficiently and with some satisfaction in his efforts. Yet this satisfaction was superficial because he could not hold thoughts about what he was typing. It was no more than a mechanical transformation of words to keystrokes, lacking content to contemplate for interest. Jimmie does derive meaning and enjoyment from attending church services, where he becomes absorbed in the feeling of the moment and in the context of memories of his religious upbringing. Jimmie also enjoys gardening and, interestingly, has somehow learned his way around the hospital garden, even though each day he is reintroduced to it. We will study how amnesic individuals exhibit the acquisition of unconscious habits in Chapter 6.

Interim Summary

Amnesia reveals what it is like to lose the ability for learning and memory. Amnesia following trauma or brain damage usually preserves what was learned early in life—basic knowledge such as language and identity as well as memory for common objects (such as houses and faces) and specific examples (your parents’ house, your mother), along with childhood experiences. Anterograde amnesia is loss of the ability to form new memories, and retrograde amnesia is loss of memories acquired shortly before the event that caused the amnesia. During a conversation, amnesic individuals can usually hold relevant information in mind. In contrast, their ongoing lives are locked into the present: They cannot learn from new experiences or remember earlier events. Note that these qualities of amnesia are similar in the cases of Clive Wearing and Jimmie G. Keep in mind these features of the impaired and spared cognitive capacities that are hallmarks of amnesia.

The Study of Learning and Memory Has a Long History

For thousands of years, philosophers have pondered the qualities of memory, and writers have analyzed its pleasures and agonies. For over a hundred years, psychologists have examined the nature of learning and its consequences in memory. Neuroscientists have explored the basis of learning and memory in the structure of the nervous system. Given such a broad and deep interest, it should not be surprising that several perspectives on the nature of learning and memory have generated distinct bodies of knowledge. This section outlines some prescient ideas of the early philosophers, then introduces some early psychologists who pioneered research on human memory and animal learning.

Ancient Philosophers Proposed Ideas Central to Today's Views of Learning and Memory

Modern ideas about learning and memory originated with introspection and logical analysis of how learning and memory might work. The ideas derived from this approach foreshadowed current conceptions of learning and memory that have come from technologically driven scientific investigations. For most of the 20th century learning and memory researchers failed to acknowledge these early philosophical contributions. But as the saying goes, "Those who forget history are condemned to repeat it." And repeat it modern scientists did. Modern "discoveries" about learning and memory have been hailed as breakthroughs; and in the modern era, they indeed have broken new ground integrating neuroscience and psychology. However, the fundamental insights of the current era can also be viewed as resurrecting many basic theories of the ancients. The major thinkers considered here had profound insights that remain key to our modern understanding of learning and memory.

Aristotle Distinguished Familiarity from Recollection

Aristotle (c. 350 B.C.) distinguished two forms of remembering: one he called *memory* and the other *reminiscence*. In making this distinction, Aristotle (Figure 1.3) conceived memory as a replication of a sensory perception, whereas reminiscence involved replaying an entire experience. Thus Aristotle proposed that memory is an extension of the senses that incorporates the passage of time since the actual sensory experience. He envisioned a memory as a replicate of a perceived object on some sort of recording device, perhaps comparable to an instant photograph or audiotape. Remembering, then, is a passive "reperception" of the recorded object, independent of its original context.

Aristotle contrasted this form of sense-based memory with reminiscence, which, he asserted, involved the active replay of an entire experience, triggered by an ini-



FIGURE 1.3 Aristotle.

tial memory of one event in that experience. This first memory would lead to a recovered sense of the situation and flow of events that compose the experience. Thus Aristotle viewed reminiscence as a process of recovering single items in succession. The difference Aristotle conceived between memory and reminiscence is recognized today in the distinction we make between familiarity and recollection. **Familiarity** is a passive sense of knowing a previously experienced stimulus, like an object or a discrete event; **recollection**, on the other hand, involves actively reconstructing the flow of events in a complete experience. In Chapter 9 we will consider modern psychological and biological distinctions between familiarity and recollection.

Notably, Aristotle also took a stand on differences between humans and animals with regard to these different kinds of remembering. He asserted that “other animals (as well as man) have memory, but, of all that we are acquainted, none . . . except man, shares in the faculty of recollection.” You may judge this claim for yourself when you read the evidence concerning recollection in animals in Chapter 9.

Maine de Biran Distinguished Conscious Memory from Habits and Emotional Memory

Two thousand years after Aristotle, a less familiar philosopher using the pen name Maine de Biran (1804/1929) offered a prescient view of different forms of memory. Maine de Biran began with the assumption that there is a simple, automatic mechanism for associating events, which he called “habit.” He proposed that the

habit mechanism underlies three different forms of memory. Maine de Biran called the most complex form *representative memory*, and he argued that this involves the ability to consciously relive and think about a prior experience. He viewed this kind of memory as unique in its access to consciousness and in the flexibility with which we can think about and use memories to solve novel problems in daily life.

The other two forms of memory Maine de Biran identified, *mechanical memory* and *sensitive memory*, differed from representative memory in two important ways. First, neither of these forms of memory could access consciousness. Second, both of these “unconscious” forms of memory had rigid limits on their expression. That is, they could be expressed only under circumstances closely resembling the learning experience, and they could not be used to solve new problems. Specifically, Maine de Biran believed that *mechanical memory* involves learning a movement through repetition. In his view, mechanical memory uses the habit mechanism to improve the speed or coordination of an action through practice. Thus as we practice coordinated movements, such as parking a car or serving a tennis ball, we get better at them, and we exhibit this improvement within the execution of the movement without any effortful recollection of how these movements are performed. Indeed, Maine de Biran distinguished mechanical memory as a form of habit learning that—unlike representative memory—does not generate a recalled idea.

Maine de Biran called the other form of unconscious and inflexible memory *sensitive memory*, which he argued occurs during emotional experiences. Maine de Biran proposed that during such an experience, sensitive memory works when the habit mechanism retrieves a feeling without recalling the circumstances in which the feeling became associated with that type of emotional situation. For example, many people have learned that flashing lights in a hallway are associated with danger in the building. When the lights begin to flash, we may feel our hearts race and a sense of concern and arousal, even without recalling the times this has happened before. We reexperience the acquired emotion without an effortful recall of similar experiences or their emotional consequences.

Both forms of unconscious memory express simple associations. Mechanical memory associates stimuli with movements, and sensitive memory associates stimuli with their emotional significance. Each of these works without conscious recall. Maine de Biran added that although these forms of memory are unconscious, they can cause inflexible and obstinate behavior, as anyone with an irrepresible habit or uncontrollable fear knows.

Maine de Biran was remarkably ahead of his time in realizing the distinction between conscious and unconscious forms of learning and memory and in distinguishing between three types of memory. Later in this book we will examine modern studies that separate acquisition of unconscious habits, similar to Maine de Biran’s mechanical memory; learning of emotional reactions, similar to Maine de

Biran's sensitive memory; and the complexities of conscious memory, identical to Maine de Biran's representative memory.

William James Distinguished between Habits and Memories and Envisioned Memory as a Network of Associations

At the threshold of experimental psychology, William James (1890/1918) distinguished between memory as a complex cognitive phenomenon and habits founded in a simple automatic mechanism. James was guided by observations from biology that identified reflex pathways in the nervous system through which a stimulus (such as a pinch) automatically generates a specific motor response (withdrawal). Influenced by the descriptions of these *reflex arcs*, James suggested that nerve impulses in reflex paths more readily traverse paths previously taken. Thus, he wrote, habits form when reflex paths become well worn. Like Maine de Biran, James attributed great importance to habits as the building blocks of more complicated behaviors. James said that practiced behaviors and skills are mediated by sequentially linked discharges that "awaken each other in succession" through connected reflex paths. He held that this kind of chain reaction mediated the production of learned movement sequences.

James distinguished active memory from the acquisition of skills and from a sense of familiarity. James emphasized the warmth and intimacy of recollection from the cold repetition of practiced movements and from the passive feeling of familiarity for a reexperienced stimulus or event. In addition, James characterized memory in terms of its structure as an elaborate network of associations, vastly richer and more complicated than a connected series of habits or a general sense of familiarity. Thus the underlying foundation of recall involves a complex set of systematic associations between particular memories.

James's interest in the biological basis of memory led him to assert that memory depends on two aspects of the physiology of habit mechanisms. First, he suggested that the persistence of a memory depends on our innate capacity for strengthening its reflex pathway. Second, he proposed that access to a memory depends on the number of pathways through which we associate an item. James emphasized that associational links are more malleable than reflex pathways, and he argued that the key to remembering is building many diverse associations with our experiences, weaving memories into a network of systematic relationships. The capacity to search through our network of associations, he wrote, is the basis of conscious recollection and can lead to creative use of memory to address new problems. James admonished his students not to simply rehearse learned material because repetition would not help form diverse associations that support creative use of memories to address new questions. James also distinguished two forms of

conscious memory. He differentiated *primary memory*, the ability to hold and manipulate information in mind for a short period, from the permanent memory store he called *secondary memory*.

These fundamental distinctions between unconscious impressions and conscious memories were initially lost in experimental psychologists' efforts to characterize memory as a single system. However, the distinctions were rediscovered and confirmed by modern cognitive and neuroscience research, as we will see later in this chapter. James's distinction between primary and secondary memory was also confirmed much later by cognitive science and neuroscience (see Chapter 12).

Herman Ebbinghaus Developed the Systematic Study of Human Memory

The era of experimental analysis of memory began with the German psychologist Herman Ebbinghaus (1885/1913), who performed the first rigorous studies of human memory capacities. Ebbinghaus rejected the use of introspection and abhorred the complexity of early elaborate explanations of how memory worked. Instead he developed several techniques to control the nature of the material to be learned and generate quantitative and objective assessments of memory. In essence, he tried to reach a scientific understanding of memory.

How did Ebbinghaus do this? First he needed an experiment that would allow rigorous control of the learning process. To accomplish this, he needed learning materials that were uniformly simple so he could test the reliability of memory across new learning experiences and compare memory across changes in the amount of material to be learned, the duration of retention, and other variations of the learning task. Ebbinghaus's solution was to invent the *nonsense syllable*: a meaningless consonant-vowel-consonant letter string (such as *ket*, *poc*, and *baf*). With this device he avoided the influences of what he called "interest," "beauty," and other features that might affect the memorability of real words. In addition, nonsense syllables simultaneously equalized the length and meaning of the items by minimizing the former and eliminating the latter. To quantify memory, Ebbinghaus invented the measure of *savings*—a method of scoring that measured retention of memories by the reduction in the number of trials or amount of time required to relearn material. In addition, he was the first to employ mathematical and statistical analyses to describe and test the reliability of his findings.

Ebbinghaus's work, performed entirely with himself as the experimental subject, provided a wealth of information about learning and forgetting, the amount of information that can be learned, and the effects of practice on retention and subsequent savings. He also provided the first evidence showing that humans remember the order of items in which they are learned, and he demonstrated that the linkage between items in a learned sequence weakens with the number of intervening items in the list. In these studies Ebbinghaus quantified in the labora-

tory something we observe in remembering everyday experiences: The more extended and complicated your day, the more difficult it becomes to remember what happened when. The importance of the order of items for our ability to recall experiences will be explored in detail in Chapter 9.

A Separate Line of Research Developed Theories about the Elements of Animal Learning

At the turn of the 20th century, while Ebbinghaus began studying human memory, other pioneers in psychology began to investigate animal learning and develop theories about its basic elements and rules. One early landmark was Ivan Pavlov's discovery of **classical conditioning**, a behavioral protocol in which an initially neutral stimulus is consistently paired with a stimulus that automatically produces a reflexive response. Pavlov (Figure 1.4) was a Russian physiologist who began his career examining how the nervous system controls digestion. He found that when food excites the taste sensors in the mouth and gullet, nerve signals travel through the brain stem to the stomach, where they stimulate the release of gastric fluids.

Pavlov's later studies showed that dogs produced salivary and gastric secretions at the mere sight of food, without having tasted anything—a phenomenon called *psychic secretion*. Pavlov also noticed that this phenomenon was unreliable: Salivation tended to decrease when the dogs were shown beef repeatedly. Conversely,

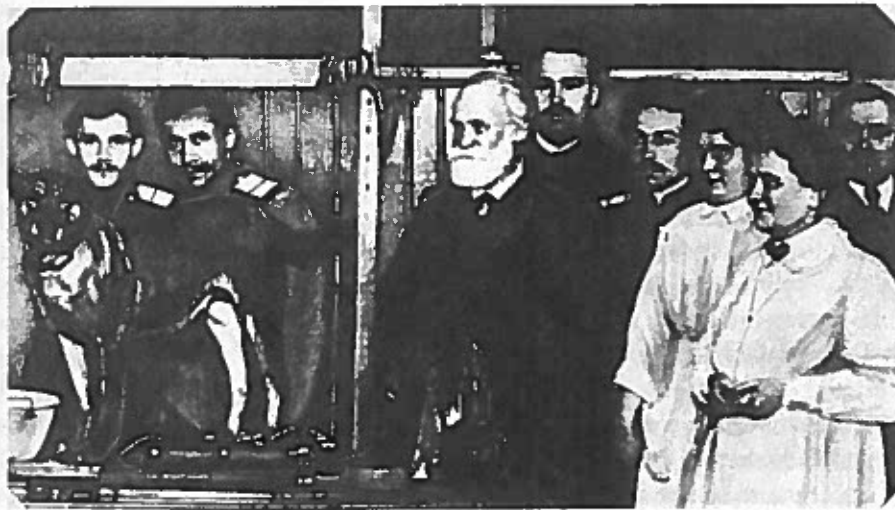


FIGURE 1.4 Pavlov and his staff.

They are shown here with his famous conditioning apparatus and a subject of his classical conditioning studies.

seemingly arbitrary events that preceded the sight of food could trigger salivation, such as when the person who regularly provided food entered the testing room. By studying psychic secretion, Pavlov formalized the perspective that learning is based in the *conditioning* of reflexes by reliable contiguity of an arbitrary stimulus (like the sight of a person) and a stimulus that automatically, and unconditionally, produces a particular behavioral response (such as food producing reflexive salivation). Pavlov's experiments with the conditioning of salivary reflexes became the model for later studies of how basic motor responses are learned—a subject that is the focus of Chapter 5.

Edward L. Thorndike and John B. Watson Studied How Animals Learn Responses for Rewards

Another turn-of-the-century landmark in animal learning theory was the research of psychologist Edward L. Thorndike, who investigated the basic mechanisms of learning using an approach called **instrumental conditioning**—a behavioral protocol in which rewards or punishments that follow particular behaviors tend to alter the probability of that behavior. Thorndike invented an apparatus called the *puzzle box*: a cage with a door that was locked by a latch on the outside that could be manipulated from the inside (Figure 1.5). Thorndike observed how cats placed in the puzzle box learned to flip its latch to open the door and obtain food just outside. The initial learning was by *trial and error*: The cat's behavior appeared random, but eventually the cat would open the latch. Over repeated training trials, the random behavior gradually diminished. Instead the animal appeared to intentionally manipulate the latch and could open the door readily. Thorndike concluded that the cat had formed an association between the latch as the stimulus (S) and the appropriate manual response (R), and that learning was based on the **stimulus-response (S-R) association**.

Following Thorndike, John B. Watson heralded the view that all learning could be reduced to a set of S-R associations. In one of his most famous experiments, Watson trained rats to run a maze and then sought to determine what kind of information the rats were using to guide their behavior by eliminating each of the rats' senses one after another. He found the rats could still run the maze using only the sensory feedback from the contractions of their muscles. The observation that animals could learn a maze based only on muscle sensations led Watson to conclude that learning can be reduced to a chain of acquired reflexes. By 1913 Watson was so convinced that he wrote a manifesto beginning a movement called **behaviorism**. This school of thought asserts that we can understand all learning in terms of simple stimulus and response associations, without considering less measurable concepts such as consciousness, insight, or intent.

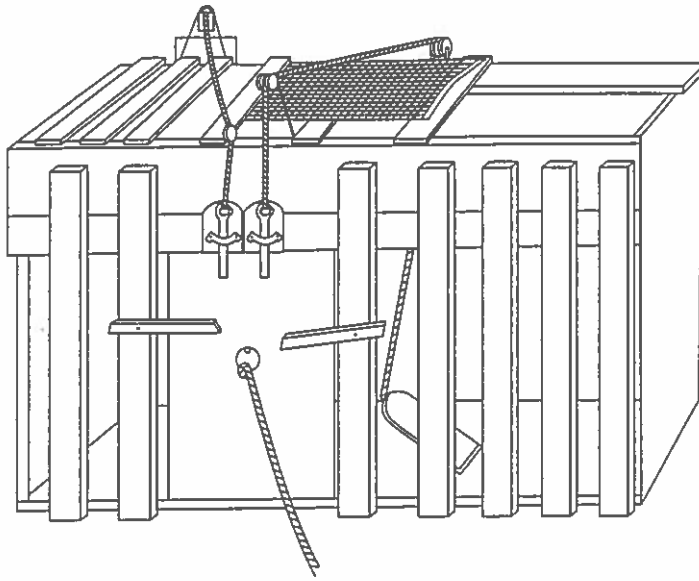


FIGURE 1.5 One of Thorndike's puzzle boxes.

To open the door, the animal had to step on the peddle inside the box, shown to the right of the door (after Thorndike, 1898).

Interim Summary

The idea that there are different forms of memory dates back to Aristotle, and many distinct forms of learning and memory proposed long ago prefigured aspects of learning and memory studied today. Two key distinctions include (1) the difference between familiarity of stimuli and recollection of experiential circumstances and (2) the differences among learned motor habits, emotional responses, and conscious memories. Early psychologists, including William James, elaborated on these ideas; but they receded into the background when researchers like Herman Ebbinghaus emphasized learning and memory as simple processes of association. Parallel studies of animals described two key forms of learning: classical conditioning, which consistently associates a neutral stimulus and another stimulus that elicits a reflexive behavioral response; and instrumental conditioning, which alters the probability of specific behaviors by reward and punishment. Thus, whereas early views espoused multiple forms of learning and memory, the first experimentalists considered learning and memory as a single faculty of the mind and sought to reduce its basis to simple associations. As we will see next, this approach had only limited success.

Modern Scientific Approaches to the Study of Learning and Memory

The pioneering work just described provided the basis of the modern scientific approaches used in studying learning and memory. These approaches highlight the development of hypotheses that can be tested empirically. For example, Watson's hypothesis that all learning can be reduced to stimulus-response associations contrasted with the hypothesis that animals have conscious memories of their prior experience in a maze. A critical feature of the hypothesis testing approach is that experimenters must provide an **operational definition** for each hypothetical construct—that is, they must have an observable measure of each proposed mental function. Experimental analyses of learning and memory involve constructing operational definitions and testing hypotheses based on those definitions. Thus, in the example of maze learning, experiments were designed to predict the specific choices animals would make if their performance were guided by stimulus-response associations or instead by conscious memory of previous experiences in the maze.

Correlational and Experimental Studies of Memory

Two general approaches are pursued in learning and memory research. One approach seeks correlations between psychological or biological variables. Correlational studies identify likely substrates or consequences of learning and memory; they can characterize changes in behavior and biology in great detail. However, the correlational approach does not tell us definitively whether any particular change is essential to learning or memory. Thus a study that shows a correlation between variable A and variable B does not tell us whether A causes B, B causes A, or both A and B are caused by some other unidentified variable. The other approach involves experimentally manipulating one variable and observing the effects of that manipulation on another variable. Such experiments require preselection of a variable or variables to be manipulated, and this preselection is often based on initial correlational studies that suggest a relationship. Then a subsequent experimental analysis can test whether changes in one variable have a causal role in affecting another variable.

CORRELATIONAL STUDIES In correlational studies, we observe changes in some behavioral, anatomical, or physiological parameter as human or animal subjects learn or express memory. Some changes may be observed at only the behavioral level—such as the tendency to emit a particular verbal response or choice in humans or a particular action or choice in animals. For example, memory of emotionally charged events is generally more detailed than memory of neutral events.

Do we think longer and deeper about emotional events, and is this why we remember them better? Or do hormones released during emotional arousal directly influence how well memories are stored? The correlation between emotional content and detail in memory does not answer these questions, but it has inspired experiments.

In many biologically oriented studies, experimenters track changes in the anatomy, biochemistry, or activity of brain cells or circuits during or following learning. For example, neurophysiological studies that monitor the activity of single brain cells (neurons) have found that patterns of neural activity in the visual cortex are modified during learning about important visual stimuli. Does this mean visual memories are stored in the visual cortex? Or could the changes in activity patterns of visual neurons be driven by memories stored in other brain areas that connect with the visual cortex? Again, the correlational study does not tell us the location of the memories' storage, but this kind of correlation demonstrates the nature of neural activity patterns associated with memory and inspires experimental studies that can trace the sites of memory storage.

EXPERIMENTAL STUDIES The other general approach involves directly or indirectly manipulating some behavioral or biological variable and determining the consequences of these manipulations on learning or memory. In experimental studies, it is important to distinguish the **independent variable** (the variable the experimenter determines independent of the subject's control) and the **dependent variable** (the variable generated by the subject that the experimenter measures). For example, in studying the role of emotional content in memory, the experimenter could manipulate the level of arousal by giving the subject a drug that elevates or depresses emotional arousal as the independent variable, and then measure the detail of memories as the dependent variable.

An appropriate **control group** is a critical part of any experimental analysis. In principle, a control group is a set of subjects who are treated exactly like the group that receives a manipulation of the independent variable (called the **experimental group**); but the independent variable is not manipulated in the control group. In the example of the study of emotional arousal and memory, the experimental group might receive an injection of a drug that creates arousal, whereas the control group might receive an injection of saline fluid that has no biological effects. Thus the control group would be treated exactly like the experimental group, right down to the detail of receiving an injection; but the drug that influences arousal would be left out.

Sometimes it is difficult to produce perfect control that leaves out only one influence. For example, an experimenter wanted to determine whether contiguity of a neutral stimulus and a painful stimulus was essential to learning an association between the stimuli. To examine this, an experimental group of rats was

trained to press a lever to receive regular food rewards. Then occasionally a light stimulus was presented for a few seconds, followed by a brief shock. This experimental group rats learned to cease pressing the lever when the light stimulus came on, showing that they had learned the association. The control group received the same light stimulus and shock, but these were always separated in time. The experimenter thought this procedure exquisitely controlled for the contiguity of the two stimuli while giving the control group both kinds of stimuli. However, the control group rats actually pressed the lever more when the light came on, suggesting the light had become a "safety signal" predicting that the shock would not occur. The control group had received a *negative contiguity*—the two stimuli never occurred together. To address this problem, the experimenter created a different control group for which the light and shock stimuli were independently presented, so they occurred occasionally together and at other times far apart. This group's rats did not alter their rate of lever pressing when the light came on—but they did get ulcers, which are a consequence of the unpredictability of painful events. The lesson of this study is that there is no perfect control for learning. Rather, animals and people learn any contingency or lack of it between salient variables.

Investigators alter training or testing protocols or manipulate brain function in various ways. In some cases the variable involves direct manipulation, such as in the drug study previously described. But sometimes there are natural variations of a variable. In learning and memory research, important examples of this can be found in studies of unusual individuals, such as people with exceptional memory ability or particular types of brain damage. In general, researchers can make the strongest conclusions with a sufficiently large number of subjects in each experimental and control condition to allow statistical analyses of the reliability of any observed differences in the dependent variable. But often observations gleaned from individual case studies are compelling.

A final consideration in the design of experimental studies is the possibility of a **confounding variable**: an unintended independent variable occurring along with the intended independent variable that could change the dependent variable. For example, imagine an experiment showing that damage to brain area A affects learning task 1 but has no effect on learning task 2. We might want to conclude that brain area A is critical to task 1 and not task 2. However, perhaps task 1 is easier, and damage to brain area A affects difficult tasks more than easy tasks. Or maybe task 1 is just more sensitive to any kind of brain damage. Here task difficulty and sensitivity are potential confounding variables with the kind of learning that task 1 represents. One way to remove this confounding effect is to identify another brain area B that, if damaged, affects learning task 2 but not learning task 1—the opposite findings of the effects of damage to brain area A. The full pattern of results cannot be explained by differences in difficulty or sensitivity of the two tasks

because performance of each task is affected by damage to one brain area and not the other. This pattern of findings is called a **double dissociation** because the effects of each of two types of brain damage are dissociated or distinguished from the effects of the other.

In general, both correlational and experimental approaches are valuable. Correlational approaches can provide considerable detail about associated variables and generate new ideas about variables to manipulate in subsequent experiments. And experiments can be designed with appropriate controls and elimination of confounds to test the causal roles of variables in learning and memory processes.

Themes of This Book

Four closely related themes guide the current science of learning and memory and are also the main theses of this book:

1. Learning and memory are closely intertwined stages of information processing. Learning is the process that generates memories; memories reflect successful learning.
2. Major insights into learning and memory have come from studying the brain. Neurobiological studies provide insights into how memories are represented in the brain, and they provide data that allow us to test psychological theories.
3. Together, psychological and biological studies have revealed multiple forms of learning and memory, each with its own domain of information, rules of organization, and brain pathways.
4. Humans and other mammals share much in the nature of their learning and memory systems and the brain structures that support them. In addition, virtually all animal species share cellular and molecular mechanisms that underlie memory. The neurobiological approach has bridged the distinct lines of study of human memory and animal learning. Merging evidence from humans and animals allows us to understand learning and memory across many levels of analysis, from simple neural circuits to human cognition.

Theme 1: Learning and Memory Are Closely Intertwined Stages of Information Processing

Learning and memory do not reflect separate phenomena but instead are the opposite ends of a continuum of information processing: from acquiring information during learning, to organizing and storing memories, and finally to retrieving and expressing memories. Although studies of human memory and animal learning have run separate courses and dealt with different issues, both lines of study have

encountered the same controversies. Researchers in both camps want to understand whether learning and memory can be reduced to simple associations or require more complex ways of representing information. Over this point of controversy, the fields of human memory and animal learning have converged.

In the early part of the 20th century, when the behaviorist approach was at the peak of its influence, most human memory research was guided by the rigorous methods introduced by Ebbinghaus and the notion that human memory could be reduced to a predictable set of events governed by simple laws. But some researchers in the separate fields of human memory and animal learning remained skeptical about the explanatory power of behaviorism. They believed that learning and memory are more complicated than simple stimulus-response associations.

In the field of human memory research, British psychologist Frederic Bartlett's work (1932) contrasted with the reductionist view that human memory can be reduced to simple associations. Bartlett had people read a brief mythical tale about a war between a South American Indian tribe and ghosts. The story contained both ordinary events and surreal events that were described in only fragmentary detail. When, after a delay, Bartlett asked his subjects to repeat the tale, he found that people did not remember all aspects of the story equally well. Rather, they were more likely to forget the surreal events or distort them to fit their understanding of cause and effect. Bartlett's insights about the structure and richness of memory have proven critical for modern views of conscious recollection. Bartlett showed that memory cannot be explained based only on association and repetition. Rather, new memories are woven into an organization of prior knowledge that strongly influences what is remembered.

At the same time, Edward Tolman's research (1932/1951) in animal learning challenged the behaviorist view that learning can be reduced to stimulus-response mechanisms. Tolman used the same species (rats) and maze learning tasks as the prominent S-R theorists so his ideas could be tested against those of the behaviorists using the same experimental variables. Though the behaviorists discounted mental processes that could not be directly demonstrated and measured, Tolman aimed to identify the underlying cognitive mechanisms, purposes, expectations, and insights that guided behavior; his studies revealed certain capacities rats use to solve maze problems that cannot be explained in terms of simple S-R mechanisms. For example, Tolman and his students observed that rats could take novel routes through a maze when trained routes were blocked (Figure 1.6). Tolman theorized that these rats could not have acquired the novel responses through previously rewarded behaviors and must have instead used general knowledge of the maze as a guide. Bartlett and Tolman were among the first memory researchers to endorse **cognitivism**—the belief that learning cannot be explained by simple S-R associations but requires a more elaborate network of knowledge and expectancies.

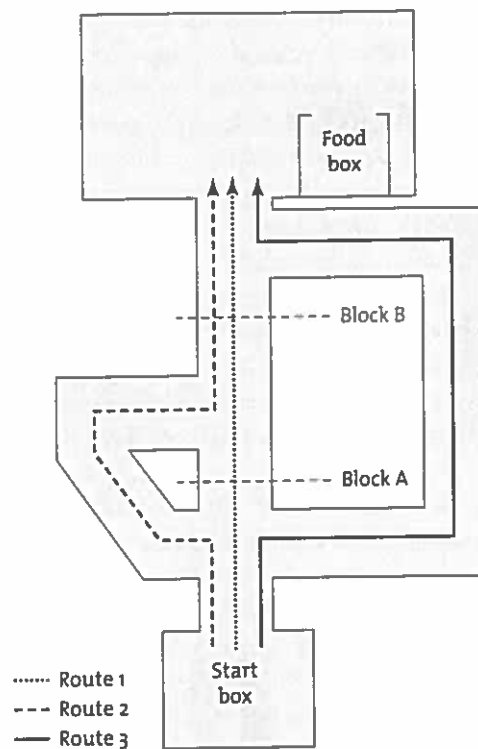


FIGURE 1.6 One of Tolman's mazes.

The rats first learned the three possible routes through the maze. When no blocks were inserted, rats preferred route 1. When block A was added, rats would immediately take route 2. When block B was added, rats seemed to realize that route 2 could not be followed to completion, and they took route 3.

AN EXAMPLE BATTLE BETWEEN BEHAVIORISTS AND COGNITIVISTS The battle between behaviorism and cognitivism was not resolved by Barlett's and Tolman's groundbreaking studies; rather, it continued into the middle of the 20th century. A compelling example of many battles about this issue is a set of experimental studies that pitted the behaviorist view against the cognitivist view in predicting strategies animals use to solve a simple maze problem. The experiments used a T-shaped maze in which the rat began each trial at the base of the T and was rewarded at the end of only one of the upper arms of the T—for example, the one reached by a left turn as the rat reached the top (Figure 1.7A). The maze was open to views of various stimuli in the room, so the animal could see spatial cues outside and within the maze.

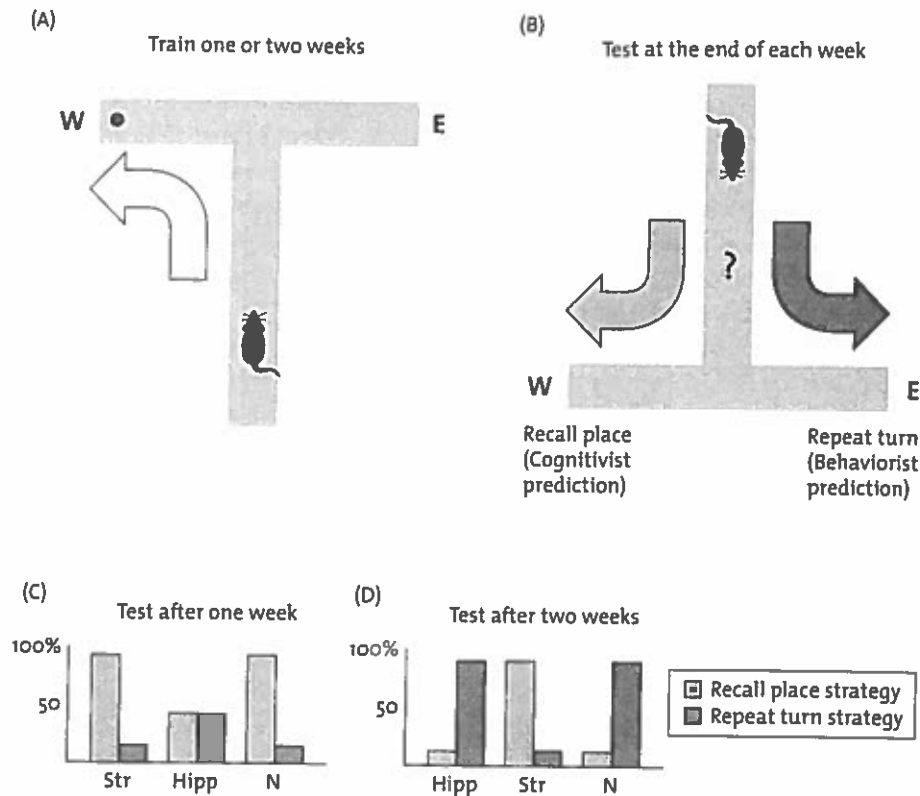


FIGURE 1.7 The T-maze task.

A. Training to take a left turn to reach the west side of the maze. B. Test of strategy. C. Effects of inactivation of the striatum (Str), hippocampus (Hipp), or no treatment (N) on performance measured as the percentage of animals that chose the recall place strategy (light gray bars) or repeat turn strategy (dark gray bars) when tested after one week of training. D. Effects of inactivation of the same brain areas when the animals were tested after two weeks of training.

Behaviorists and cognitivists offered different accounts of what the rats learned in this situation. According to behaviorist theory, learning involves the association between stimuli in and around the maze (S) and the rewarded left turn response (R) as a conditioned S–R. According to this view, animals acquired the association between seeing the choice point in the maze and turning left, and this association was reinforced by food rewards. Behaviorists call this strategy *response learning*: Rewards increase the likelihood of a particular (left turn) behavioral response to a stimulus (the choice point) without reference to the animal “thinking” about what happened last time it took a left turn at the choice point.

In contrast, according to the cognitive account, the rat's learning involved acquiring general knowledge about the layout of the environment using the visible spatial cues around the room and the memory of previously finding food at a particular location in the room defined by the spatial cues outside the maze. According to this view, when rats repeated the task, they used their cognitive capacities to explicitly remember where the food was (on the west side of the room) and then utilized any responses required to reach the place where the reward should be. This strategy, called *place learning*, differs from response learning in two ways. Place learning involves knowledge about the whole environment and memory of each experience in it, whereas response learning involves specific, limited stimulus-response associations. Also, place learning can be expressed in a variety of ways other than previously rewarded behaviors, and it can even support novel responses such as taking different turns through the maze if those are necessary to reach the reward.

The crucial test that would reveal the rats' learning strategy involved rotating the T-maze 180 degrees so the choice arms still ended in the same two places in the room, even though the two arms had switched places, and the start point was at the opposite end of the room (Figure 1.7B). To envision this situation, imagine that during the initial training, the start point was in the south end of the room, so the arm of the maze with the reward would be on the west side of the room, whereas the arm with no reward would end on the east side. When the maze was rotated 180 degrees, the start point would move to the north, and the two arms would still end in the east and west. To determine which kind of learning supported maze behavior, researchers first trained animals with the T-maze in its initial orientation, then presented a single "probe" trial that tested which kind of learning was used by examining the rats' subsequent choices.

Behaviorists predicted that in the probe trial the rats would continue to execute the previously reinforced left turn response at the choice point, leading them to the east end of the room, where the rats had not found food during training. In contrast, the cognitive account predicted that the rats would seek the remembered location of food—the west end of the room—even though this required switching their response to a right turn at the choice point. Thus a single test with the rotated maze would examine the rats' underlying strategy.

Many experiments ensued, with mixed results. In general, place learning was favored, but under some conditions response learning was preferred. Place memory predominated when salient visual cues outside the maze differentiated one goal location from the other; but whenever external cues were minimized, response memory would predominate. Other studies reported that rats employed place memory early as they began to succeed in learning the task, and later they switched to response memory. Such a pattern of results did not, of course, declare a "winner" in the behaviorist versus cognitivist debate. Instead these results sug-

gested that both types of representation are available to rats, which might use either strategy depending on salient cues or response demands.

These studies showed that both behavioral and cognitive strategies exist, and either can be employed to solve maze problems. In addition, these studies demonstrated how strongly learning and memory are intertwined. For this seemingly simple maze problem, subtle differences in the available stimuli or the amount of learning altered the nature of the resulting memory. In perhaps the most striking demonstration of how learning and memory are intimately linked, it was found that early successful learning resulted in cognitive memory, whereas subsequent additional learning resulted in behavioral memory. Later in this book you will read about several additional situations in which learning can result in different forms of memory for the same experiences. These findings necessitate that we view learning and memory as intertwined: Learning is how memories are created. In other words, the important issue is not how learning and memory differ, but how they coordinate in producing different types of representations in the mind and brain.

Theme 2: Major Insights about Learning and Memory Have Come from Studies of the Brain

You have already read about some interesting contributions of brain science to studies of learning and memory. In particular, case studies of amnesia have revealed that learning and memory can function (or fail) separately from perception and other aspects of intellectual function, and that there are different stages of memory formation. Also, these studies have distinguished between different forms of memory based on the nature of the information stored and the ways memory can be expressed. You may recall, for example, that the amnesic man Jimmie G. was able to learn his way around the hospital's garden even while consistently experiencing it as a new and unfamiliar place. This surprising combination of intact brain function and impairment suggests a distinction or dissociation between the cognitive memory of previous visits to the garden and the behavioral memory that allowed Jimmie to navigate its paths with ease. That is, when one type of memory breaks down while another kind is preserved, this suggests that the two types of memory are dissociated, meaning they are supported by separate brain systems.

More recently, new brain imaging technologies monitoring humans performing memory tests have confirmed that distinct brain regions play different roles in memory processing. Also, animal studies have been crucial in identifying the distinct functions of brain areas that mediate memory. In some animal studies, distinct brain areas are selectively removed, and the effects of this surgery on memory can be studied in detail. Researchers have compared these changes to the firing patterns of neurons in the same brain areas of intact animals to determine the kind

of information represented in these brain areas. Experimental studies of humans and animals have revealed the circuitry of multiple memory systems in the brain. In addition, neurobiological studies of the cellular and molecular bases of memory have identified changes in connections of brain circuits that underlie memory. And these studies have revealed a cascade of molecular events that cause permanent changes in connections between elements of these circuits.

A key example of how neurobiology has contributed to our understanding of learning and memory relates to the theoretical battle between the cognitive and behavioral perspectives on maze learning in rats—a battle that neurobiological studies have sometimes helped to reconcile.

Recall that the psychological studies did not resolve the controversy; rather, they showed that both behavioral and cognitive strategies could be used to solve the T-maze problem. How can both models be solutions? What determines which strategy is used? These questions have been resolved through neuroscience, and the implications are important and broad, providing an example of different forms of learning and memory. In a landmark experiment, Mark Packard and James McGaugh (1996), taking advantage of previous findings showing that rats switch between place and response memories depending on their level of training, examined the roles of specific brain areas in supporting each kind of memory. They trained the rats for a week in the T-maze task, then assigned them the rotated maze probe trial. Subsequently these rats were trained for another week with the maze in its original orientation before a final additional probe trial. As in the earlier studies, rats initially used place memory, reflected in their strong preference during the first probe trial for the earlier location of food. However, after the additional week of overtraining, the rats' choice behavior changed, reflecting response memory on the final probe test. So under these training circumstances, rats acquired both types of memories successively. Their initial acquisition of place memory fit the cognitivist view, but subsequent overtraining developed response memory consistent with behaviorist theory.

But Packard and McGaugh's experiment went beyond merely showing anew that rats use both response and place learning. They also examined whether different brain systems support these types of learning and memory. Before training, Packard and McGaugh implanted the rats with needles that allowed them to inject specific parts of the brain with local anesthetic during the probe tests to silence certain brain cells for several minutes—either in the hippocampus or in the striatum. The rats were always trained without drugs; but during both probe tests, the rats received infusions of either the anesthetic or a placebo (saline solution) into one of those brain areas.

The striking effects of the anesthetic differed depending on when and where the drug was infused. In the first probe trial after one week of training, rats with anesthetic injected into the striatum behaved just like rats who received the

placebo in the same brain area. With or without anesthetic in the striatum, they were predominantly guided by place memory, showing that this kind of memory did not depend on the striatum (Figure 1.7C). In contrast, during the same initial probe trial, the rats with anesthetic injected in the hippocampus showed no preference for one end of the maze over the other: The behaviors they learned during the week of training seemed unavailable. This indicates that they relied on their hippocampus for the place memory, and that only this representation had been created at that stage of learning.

During the second probe test after two weeks of training, a different pattern emerged (Figure 1.7D). Whereas the placebo-infused rats now showed that they had acquired response memory (continuing the left turn response that led to food during training), animals given anesthetic in the striatum lost their response memory for the left turn and instead showed a striking opposite preference for turning right, toward the *place* where rewards had been obtained during training. Meanwhile, the rats with anesthetic injected into the hippocampus in the later probe trial maintained guidance by their response memory.

Combining these data shows clearly that multiple forms of memory develop at different times in training. Rats initially develop and use place memory, which depends on the hippocampus. We know this because when the hippocampus was anesthetized, the rats lost their ability to select the correct place. At this early point in training, the S-R representation had not yet developed: The rats could not resort to response memory when the hippocampus was inactivated. Instead, with no alternative form of memory, they randomly chose to turn either left or right.

After further training, the situation changed—the rats developed response memory. We know that this form of memory depends on the striatum because striatum inactivation affected their performance. Furthermore, it appears that after further training, response memory predominated over place memory, although the latter could be “uncovered” by inactivating the striatum where the response memory was stored. Note that these results, showing that hippocampal inactivation selectively eliminates place memory whereas striatum inactivation selectively eliminates response memory, constitute a double dissociation—the strongest form of evidence for distinct functions of these brain areas.

The two kinds of learning demonstrated here closely match the properties of the two different forms of memory described by William James. Response learning correlates with James’s description of a habit as a practiced, ultimately rigid overt movement associated with a particular stimulus. Place learning is much like James’s concept of memory as network of associations that can be flexibly applied to solve new problems; this kind of memory also resembles explicit or declarative memory (discussed in the following pages) because it involves remembering events that occurred at a particular place.

Theme 3: The Concept of Multiple Memory Systems Unifies the Study of Learning and Memory

A chief observation in the experiment that probed rats' methods of learning and remembering mazes was that learning and memory exist in multiple forms, each of which operates with unique principles and depends on a distinct brain system. These findings offer compelling evidence that elements of both the behaviorist and the cognitive views are right. There are distinct forms of memory—one involving memory of a place and the other involving acquisition of a turning response—and they are distinguished by both performance characteristics and the brain pathways that support them.

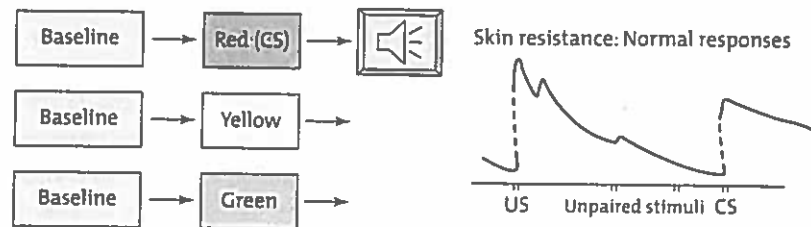
Perhaps the most convincing proof of the existence of multiple forms of learning and memory comes from observations of people with amnesia. The cases described earlier revealed selective loss of some aspects of memory while other learning abilities were still supported by those individuals' intact brain systems. Further amnesia studies have identified which brain areas support particular forms of learning and memory.

One particular study of amnesia has shown a remarkable double dissociation between the systems that support cognitive memory and emotional associations (Bechera et al., 1995). This work examined three people with selective damage to either the hippocampus or the amygdala (two temporal lobe structures). One subject suffered from Urbach-Wiethe disease, a rare disorder that destroys amygdala tissue while sparing the adjacent hippocampus. Another subject experienced multiple cardiac arrests; the associated oxygen loss shrank the hippocampus but spared the amygdala. The third subject suffered herpes simplex encephalitis, which damaged both the amygdala and the hippocampus.

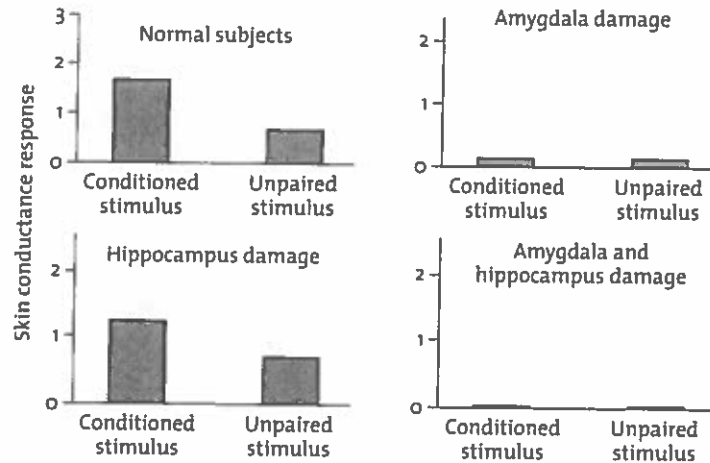
This study focused on a classically conditioned association between a neutral visual stimulus and a loud sound (Figure 1.8A). Subjects were initially shown different colors on a computer screen to habituate them to the visual stimuli. The first trials conditioned the participants to associate a particular visual stimulus with the startling loud sound. Each of three different colors appeared on the screen in random order for two seconds. After a particular color (red) was presented, the participants would hear a brief, loud boat horn sound. When the loud horn was unexpected, it produced involuntary emotional responses, including sweating, which could easily be measured with electrical recordings of skin conductance.

Normal control subjects showed skin conductance changes at the sound of the boat horn, along with robust conditioning to associate the sound with the color red. The subject with selective amygdala damage showed normal skin conductance responses to the boat horn but failed to learn the association between the color red and the sound of the horn (Figure 1.8B). In contrast, the subject with selective hippocampus damage showed normal skin conductance changes at the

(A) Conditioning task



(B) Results of conditioning



(C) Declarative memory for the task

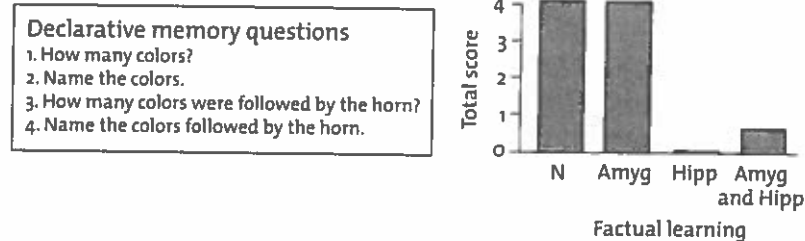


FIGURE 1.8 Emotional learning.

A. A loud boat horn followed the red stimulus but not the yellow or the green stimuli. Skin resistance changed after presentations of the boat horn (the US) and, after training, the red stimulus (the CS)—but not the yellow or the green stimuli, which were not paired with the boat horn. B. Normal subjects showed strong conditioning, whereas those with amygdala damage did not. After training, subjects were asked questions about their memories of the training experience. C. Normal subjects recalled the training events, whereas those with hippocampus damage did not.

sound of the boat horn and normal conditioning to the color stimulus. The subject with combined amygdala and hippocampus damage failed to condition, even though he showed the skin conductance response to the boat horn.

After the testing sessions, the subjects were asked several questions about the relationships between the stimuli (Figure 1.8C). Normal subjects and the subject with selective amygdala damage answered most of these questions correctly. But both subjects with hippocampus damage had trouble recollecting the task events. These findings simultaneously show that (1) a conditioned emotional response to a particular color depends on the amygdala and (2) explicit memory of the details of a conditioning experience depends on the hippocampus. This evidence that diverse forms of memory for a single learning event are affected differently when particular brain areas are damaged strongly supports the notion of multiple memory systems mediated by various brain structures.

Theme 4: The Underlying Bases of Learning and Memory Are the Same in Humans and Animals

Combining the views and experiments from the early philosophers and modern psychological and neuroscience experiments has allowed a tentative classification of memory systems (Table 1.1). The primary distinction is between **cognitive memory** (also called declarative or explicit memory), in which memories can be consciously recalled, and **behavioral memory** (also called nondeclarative or implicit memory), in which memories are expressed through changes in behavior, typically the speed with which we execute a behavior or change our preferences and aversions without conscious recollection.

Behavioral memory includes simple forms of memory that involve the habituation and sensitization of behavioral responses to repetitive stimuli. This form of memory also encompasses simple forms of associative learning, including classical conditioning and instrumental learning—basic paradigms that emerged early in thinking about learning mechanisms. Another simple form of memory involves

TABLE 1.1 A Taxonomy of Memory Systems.

Behavioral Memory	Cognitive Memory
Simple forms	Working memory
Habituation	
Sensitization	
Perceptual learning	Episodic memory
Procedural learning	Semantic memory
Emotional memory	

perceptual learning and memory: the improvement in perception of categories of stimuli that we are required to discriminate. Also, consistent with Maine de Biran's ideas, there are distinct systems for procedural learning (the acquisition of reflexive behaviors and habits) and emotional memory (the acquisition of attractions and aversions to otherwise neutral stimuli).

Cognitive memory also features distinct subtypes. Some are relatively short-lived—including short-term memory, which involves information that passively lasts a few seconds, and working memory, which involves information we keep in mind by active rehearsal or manipulation. The two principal subtypes of long-term cognitive memory are episodic memory, which provides a permanent record of personal experiences, and semantic memory, which we use to permanently organize factual information. This text will explain these types of memory in detail, in terms of both their psychological characteristics and the brain systems that support them.

The advances from the study of human memory, animal learning, and neuroscience are converging to comprehensively explain memory with considerable consistency between humans and animals and across species of animals. Both the psychological and neurobiological approaches have distinguished successive stages of memory processing, including separate properties of information processing associated with the acquisition, manipulation, storage, and retrieval of memories; these distinctions are found in both humans and animals. Also, each of these approaches has distinguished multiple forms of learning and memory in humans and animals. Some kinds of memory involve complex conscious thought, whereas others involve simple mechanisms that can be expressed unconsciously during task performance. The realization that there are distinct stages and different forms of learning has generated convergence among the different approaches. This book will explore this synthesis of knowledge about learning and memory.

Interim Summary

Early studies of human memory and animal learning ran separate but parallel courses. Both research areas were beset by controversy between behaviorists, who thought learning and memory could be reduced to associations between stimuli, behavioral responses, and reinforcers; and cognitivists, who believed that complex mental processing and memory organization play a major role in the determination and expression of learned behavior. Recently the behaviorist and cognitivist perspectives have merged in studies showing that both humans and animals have multiple forms of memory that are mediated by distinct systems in the brain. Modern research has generated a taxonomy of memory systems that distinguishes a cognitive memory system from several behavioral memory systems. Behavioral memory

includes simple forms of memory, like habituation and sensitization, as well as perceptual, procedural, and emotional memory. Cognitive memory includes working memory, episodic memory, and semantic memory. Outlining the psychological and neurobiological distinctions between these systems is a goal of this book.

Chapter Summary

1. Learning and memory contribute to our individuality. Whereas genes confer the range of capabilities to which we can aspire, our individuality is accumulated as a lifetime of memories. Learning and memory pervade every aspect of our daily lives, contributing to all our perceptual, emotional, behavioral, and cognitive activities. And they encompass many levels of behavioral expression—from how we perceive the world around us, to coordinated movements, to our attitudes and dispositions, to conscious recollection of facts and events.
2. The absence of memory is devastating. People who suffer amnesia usually recall some knowledge acquired early in life, including who they are, basic knowledge about language and things in the world, and personal childhood memories. However, amnesias are often stuck in the present; they may lose their sense of the continuous flow of time and of the future.
3. Early philosophers recognized distinctions between conscious recollection and simpler forms of memory, and between the acquisition and unconscious expression of habits and emotional dispositions. The first experimental psychologists sought to reduce memory to elemental rules of association but could not explain complex forms of memory expression with these rules. Observations from neurobiological studies have also boosted our understanding of learning and memory.
4. Although the different perspectives reflected by philosophy, psychology, and neurobiology began with dissimilar approaches and questions, a major theme of this book is that the observations from many approaches have converged on a comprehensive account of how learning and memory form a continuum from initial processing of incoming information to the organization, retrieval, and eventual expression of a stored memory.
5. A second theme of this book is that the observations from neurobiological studies have contributed strongly to our understanding of learning and memory, allowing us to test psychological theories and validating the distinctions in various kinds of memory—such as differences among conscious memory, stimulus–

response habits, and emotional conditioning. And the convergence of findings from neurobiological studies is evident in the parallels between the characteristics of different types of memory originally described by the ancient philosophers and pioneering psychologists and the distinctions in capacities associated with particular brain areas (demonstrated in studies of human amnesia and studies of selective brain area inactivation in animals).

6. A third theme is that multiple forms of memory are mediated by distinct brain memory systems. The two major categories are cognitive memory and behavioral memory, and these both have subtypes. Within cognitive memory, working memory maintains and manipulates information in consciousness; episodic memory allows us to remember specific experiences; and semantic memory lets us create and update a warehouse of knowledge about the world. Within behavioral memory, perceptual learning involves alterations in behavior associated with sensory stimuli; procedural memory gives us conditioned reflexes and habits; and emotional memory is the acquisition and expression of attractions and aversions.

7. The fourth theme of this book is that this memory taxonomy applies to both animals and humans. Of course there are differences in the intellectual capacities of humans and animals. But as you will read in the chapters that follow, the basic wiring diagram of the brain—including the systems that support different types of learning and memory—is essentially the same across mammalian species. And there are corresponding similarities between humans and animals in the kinds of information processed by these systems. These similarities give us insight into the evolution of the brain's cognitive functions and an appreciation of the primitive thought functions shared by animals and humans.

KEY TERMS

learning (p. 7)
memory (p. 7)
amnesia (p. 8)
anterograde amnesia (p. 9)
retrograde amnesia (p. 9)
familiarity (p. 13)
recollection (p. 13)
classical conditioning (p. 17)
instrumental conditioning (p. 18)
stimulus-response (S-R) association
(p. 18)

behaviorism (p. 18)
operational definition (p. 20)
independent variable (p. 21)
dependent variable (p. 21)
control group (p. 21)
experimental group (p. 21)
confounding variable (p. 22)
double dissociation (p. 23)
cognitivism (p. 24)
cognitive memory (p. 33)
behavioral memory (p. 33)

REVIEWING THE CONCEPTS

- How do learning and memory define us as individuals?
- Is memory an isolated function or a pervasive instrument in our daily lives?
- How can the study of amnesia (the loss of learning and memory capacity) tell us about normal learning and memory?
- How do scientists study learning and memory?
- What were the contributions of philosophy and psychology to our early understanding of learning and memory?
- How has modern research led to a convergence of views about learning and memory?
- What are the major forms of learning and memory in humans and animals?